ablation of diploid ovular cells, the central cell, the egg cell, or both the central and egg cell simultaneously did not affect the ability of the embryo sac to attract pollen tubes. However, ablation of both synergid cells did abolish the competence of the embryo sac to attract pollen tubes; elimination of a single synergid cell weakened the attraction. When twice the normal number of pollen tubes were cultivated, almost 100% of embryo sacs with one of the two synergid cells left intact were still capable of attracting the pollen tubes. These observations establish that a single synergid cell is necessary and sufficient for pollen tube attraction. This work also resolves the debate, at least for *Torenia*, about the equivalence of the paired synergid cells in attracting the pollen tubes. The investigators went on to demonstrate that a fertilized embryo sac no longer attracts pollen tubes despite the presence of a remaining intact synergid cell. This is consistent with the idea that fertilization prevents additional pollen tubes from entering the embryo sac, thus avoiding the problem of polyspermy [see also (*7*)].

Recent observations of *Arabidopsis* pollen tubes labeled with green fluorescent protein show that the pollen tube also penetrates an *Arabidopsis* embryo sac through one of the synergid cells (*8*). Attraction of pollen tubes by synergid cells is likely to be very common if not universal among flowering plants. However, specificity must exist among guidance cues because pollen tubes from one species do not usually target ovules of a related species (*7*). The guidance cues released by synergid cells provide plants with a final checkpoint to prevent interspecies fertilization. But what are these cues? Observations from different plants suggest that pollen tube guidance is likely to rely on attractant and repellent molecules. Such long- and short-range signals may be similar to the chemotropic factors and their receptors that govern neural cell migration during embryonic development in mammals (*2–4*).

Architectural and biochemical diversity among pistils and pollen from different plant species and interspecies incompatibility strongly argue that a universal guidance system is unlikely to account for pollen tube growth in all flowering plants. Differences in the physical and chemical properties of the pistil tissues of a single species and distinct pollen tube behaviors at different phases of growth within the pistil of some plant species suggest that multiple factors contribute to guiding the pollen tube on its long journey (*2–4*, *9*). For example, the interface between lipid and water molecules on the surface of the wet stigma may provide the initial directional cue to the pollen tube tip emerging from the pollen grain, guiding it toward the stigma surface (*10*). The organized rows of cells within the "solid style" of some plant species appear well suited for the job of directing elongating pollen tubes along the correct track. Moreover, sugar concentration gradients created by glycoproteins secreted by the style, such as tobacco plant TTS proteins (*2*, *11*, *12*), may also contribute to directing pollen tube migration toward the ovary. The "hollow style" of other plant species, however, provides little structural confinement for the pollen tube. In this case, pollen tubes may bind to surface adhesive molecules expressed by cells lining the stylar canal, which may provide them with both support and guidance (*4*).

Carbohydrate-rich molecules secreted by the ovule (*9*), a high calcium ion concentration in synergid cells (*5*), and adhesion between ovular tissues and pollen tubes have all been suggested as possible chemotropic or contact guidance cues for pollen tubes as they approach the ovules. Biochemical characterization of a heat-labile guidance factor (*6*) from *Torenia* synergid cells may soon reveal the nature of the short-range diffusible molecule that attracts the pollen tube to the ovule. Together with a molecular and biochemical characterization of *Arabidopsis* mutants in which pollen tube targeting to the ovule is defective (*3*), these approaches should help to unveil the mystery of pollen tube guidance. The findings of Higashiyama *et al.* should invigorate efforts to understand the diverse guidance strategies that plants have evolved to ensure reproductive success.

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PERSPECTIVES: EARTHQUAKES

Himalayan Seismic Hazard

Roger Bilham, Vinod K. Gaur, Peter Molnar

Five major earthquakes have visited India in the past decade (*1*), culminating in the devastating Bhuj earthquake of 26 January 2001. That earthquake in particular called attention to the hazards posed by buildings not designed to withstand major but obviously probable earthquakes. It also focused the eyes of the public away from a part of India where even worse damage and loss of life should be expected—the Himalayan arc (see the figure). Several lines of evidence show that one or more great earthquakes may be overdue in a large fraction of the Himalaya, threatening millions of people in that region.

A wealth of geophysical evidence demonstrates that south of the Himalaya, the top surface of India's basement rock flexes and slides beneath the Himalaya—not steadily but in lurches during great earthquakes (see the inset in the figure) (*2*, *3*). This pattern resembles that found where lithospheric plates beneath oceanic regions converge rapidly: At deep-sea trenches, where the ocean floor flexes down seaward of the trench, the entire oceanic lithosphere plunges deep into Earth's mantle, and great earthquakes occur most commonly. Extreme examples are the great earthquakes in Chile in 1960 and in Alaska in 1964. Only during such earthquakes does the entire plate boundary rupture.

Second, Global Positioning System (GPS) measurements show that India and southern Tibet converge at 20 ± 3 mm/year (*4*). A 50-km-wide region centered on the southern edge of the Tibetan Plateau strains to absorb about 80% of this convergence. This region also shows localized vertical movement (*5*), and small earthquakes are most common here (*6*). The surrounding Himalaya accommodates the remaining 20%. Two meters of potential slip in earthquakes thus accumulate each century. In contrast, control points in southern India and southernmost Nepal approach each other no faster than a few millimeters per year (*7*). As the Bhuj earthquake shows, this deformation, although slow, is far from negligible.

R. Bilham and P. Molnar are in the Department of Geological Sciences and the Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, CO 80309, USA. E-mail: bilham@colorado.edu V. K. Gaur is in the Indian Institute for Astrophysics, Bangalore 560 034, India.

Third, in the Himalaya, the potential slip accumulates almost entirely as elastic rather than inelastic strain, which would permanently deform the rock. Analyses of deformed river terraces in the foothills of the Himalaya demonstrate an advance of 21 ± 3 mm/year in southern Nepal (*8*) during the past 10,000 years. The minor difference between this rate, measured at the southern edge of the Himalaya and applicable to durations spanning many great earthquakes, and the 20 ± 3 mm/year measured with GPS implies that at most a small fraction (<10%) of the strain could be inelastic. Earthquakes must therefore release most, if not all, of India's 2 m per century convergence with southern Tibet.

Little is known about Himalayan earthquakes in the 18th century and before. Great earthquakes in the Himalayan region occurred in 1803, 1833, 1897, 1905, 1934, and 1950 (see the figure). The 1803 earthquake caused damage between Delhi and Lucknow. Recent reevaluations of the 1833 Nepal (*9*) and 1905 Kangra earthquakes (*10*, *11*) indicate that rupture lengths were less than 120 km, smaller than previously believed (*2*, *12*). An analysis of geodetic deformation during the 1897 earthquake (*13*) confirms that it occurred 100 km south of the Himalaya and therefore did not relieve strain in that belt. Thorough studies of the destruction and thus the intensity of shaking for the 1934 Bihar-Nepal earthquake were carried out in Nepal (*14*) and India (*15*). Together with geodetic constraints (*16*), they imply that a 200- to 300-km-long segment of eastern Nepal ruptured (*17*). Similarly, locations of aftershocks of the 1950 Assam earthquake imply a rupture zone ~200 km long, with complexities at its eastern end (*3*, *18*).

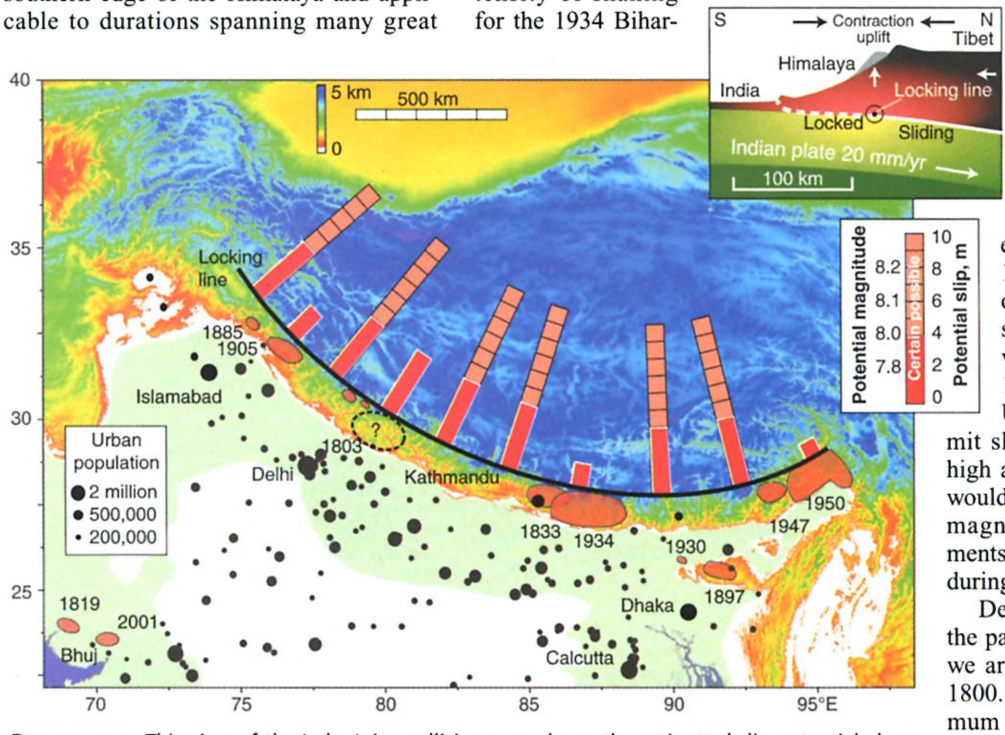
Although the major earthquakes that have occurred along the Himalaya since 1800 differed in dimensions, there is no doubt that they destroyed vast regions along the front of the Himalaya. More important today, however, is that less than half of the Himalaya (see the figure) has ruptured in that period.

Surface ruptures have not been found for any of these events. There are thus no geological constraints of recent ruptures, and geologists are concerned that paleoseismic investigations across Himalayan surface faults may yield misleadingly long recurrence intervals. Moreover, repeat surveys of trigonometrical points installed before the 1905, 1934, and 1950 earthquakes have yet to be made with modern techniques. The amplitudes of long-period seismic waves have provided quantitative measures of the seismic moments (a measure of earthquake size) of the 1934 and 1950 earthquakes (*18*). Knowledge of the lengths of the ruptures and sensible estimates of the width from various sources yield ~4 m of slip in 1934 and ~8 m of slip in 1950 (*19*). Uncertainties in these estimates permit slip as small as 2 m in 1934 and as high as 16 m for 1950, but such amounts would be unusual for earthquakes of their magnitude. These less direct measurements thus imply an average slip of ~4 m during great earthquakes.

Despite the diverse quality of data in the past two centuries, we can be sure that we are not missing any great event since 1800. This permits us to estimate the minimum slip potential that has accumulated along the Himalaya since the last great earthquake (see the figure). We divide the central Himalaya into 10 regions, with lengths roughly corresponding to those of great Himalayan ruptures (~220 km). With a convergence rate of 20 mm/year along the arc, six of these regions currently have a slip potential of at least 4 m—equivalent to the slip inferred for the 1934 earthquake. This implies that each of these regions now stores the strain necessary for such an earthquake. Moreover, the historic record (*20*–*22*) has no great earthquake throughout most of the Himalaya since 1700, suggesting that the slip potential may exceed 6 m in some places.

Given that geological investigations of the 1905 and 1934 ruptures did not reveal surface ruptures but that river terraces have been warped and the foothills have grown during prehistoric great earthquakes, we cannot rule out the possibility that parts of the Himalaya have not ruptured in major earthquakes for 500 to 700 years and will be associated with slip exceeding 10 m. The mid-Himalayan 20th century earthquakes would then have been atypically small.

The weakest link in the arguments



Danger zone. This view of the Indo-Asian collision zone shows the estimated slip potential along the Himalaya and urban populations south of the Himalaya (United Nations sources). Shaded areas with dates next to them surround epicenters and zones of rupture of major earthquakes in the Himalaya and the Kachchh region, where the 2001 Bhuj earthquake occurred. Red segments along the bars show the slip potential on a scale of 1 to 10 meters, that is, the potential slip that has accumulated since the last recorded great earthquake, or since 1800. The pink portions show possible additional slip permitted by ignorance of the preceding historic record. Great earthquakes may have occurred in the Kashmir region in the mid-16th century (*21*) and in Nepal in the 13th century (*8*). The bars are not intended to indicate the locus of specific future great earthquakes but are simply spaced at equal 220-km intervals, the approximate rupture length of the 1934 and 1950 earthquakes. Black circles show population centers in the region; in the Ganges Plain, the region extending ~300 km south and southeast of the Himalaya, the urban population alone exceeds 40 million. **(Inset)** This simplified cross section through the Himalaya indicates the transition between the locked, shallow portions of the fault that rupture in great earthquakes and the deeper zone where India slides beneath southern Tibet without earthquakes. Between them, vertical movement, horizontal contraction, and microearthquake seismicity are currently concentrated (*4*–*6*).

above is the uncertainty in the amount of slip during great earthquakes. Yet, because the longer the time since the previous earthquake, the larger the potential slip will be to drive the next one, the more severe those less frequent great earthquakes will be. Even if only one segment has stored potential slip comparable to that of the 1950 Assam earthquake, the largest intracontinental earthquake in recorded history (*19*), a replication of that earthquake along the more populous segments of the Himalaya would be devastating.

The population of India has doubled since the last great Himalayan earthquake in 1950. The urban population in the Ganges Plain has increased by a factor of 10 since the 1905 earthquake, when collapsing buildings killed 19,500 people (*10*). Today, about 50 million people are at risk from great Himalayan earthquakes, many of them in towns and villages in the Ganges plain. The capital cities of Bangladesh, Bhutan, India, Nepal, and Pakistan and several other cities with more than a million inhabitants are vulnerable to damage from some of these future earthquakes.

The enforcement of building codes in India and Pakistan mitigates the hazards to this large population, but a comparison between fatalities in the 1819 Kachchh and 2001 Bhuj earthquakes is not encouraging. The population of Kachchh has increased by a factor of 10. Two thousand fatalities occurred in 1819 (*23*), compared with the 19,000 confirmed fatalities this year. The implemented seismic code apparently did not lessen the percentage of the population killed. Like the Himalayan earthquakes, the Bhuj event occurred in an identified zone of heightened seismic hazard. Projecting these figures to just one of the possibly several overdue Himalayan earthquakes (for example, a repeat of the Kangra 1905 event) yields 200,000 predictable fatalities. Similar conclusions have been reached by Arya (*24*). Such an estimate may be too low by an order of magnitude should a great earthquake occur near one of the megacities in the Ganges Plain.

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PERSPECTIVES: BIOREMEDIATION

Anaerobes to the Rescue

Derek R. Lovley

Polluted groundwater systems are one of the most difficult environments to clean up. The most ancient of all life processes—microbial metabolism in the absence of oxygen (*1*)—is beginning to show significant potential for solving this very modern problem.

Removal of the contaminated water is often not viable because of the sheer volume of contaminated water that needs to be pumped and treated. Furthermore, contaminants continue to leach out from sediments and pollute more groundwater after the contaminated water has been extracted.

To treat contaminated groundwater in situ, reactive barriers may be placed in the subsurface to remove contaminants from groundwater. But this is only feasible and cost-effective for treating shallow, restricted areas of contamination. Microorganisms that naturally live in the subsurface may also degrade, detoxify, or immobilize contaminants (*2*), a process called in situ bioremediation.

Until recently, practical applications of in situ bioremediation have focused mostly on aerobic microorganisms (*3*), which gain energy by oxidizing organic compounds to carbon dioxide with oxygen serving as the electron acceptor. When oxygen is available in the subsurface, aerobes can clean up contaminated groundwater by oxidizing organic contaminants to carbon dioxide.

However, this approach has had limited success, not least because oxygen—an absolute requirement for aerobes—is scarce in many contaminated subsurface environments. The amount of oxygen dissolved in groundwater is low, and the rate of oxygen supply through diffusion from overlying unsaturated soils is slow. In subsurface environments polluted with organic contaminants, such as petroleum or leached materials from landfills, aerobes dutifully oxidize the contaminants to carbon dioxide, consuming the available dissolved oxygen in the process. Usually, the most heavily contaminated portions of the aquifer quickly become oxygen depleted; oxygen is only found at the fringes of the contaminant plume (see the figure).

The scarcity of oxygen in many contaminated subsurface environments has raised interest in the in situ bioremediation potential of anaerobes, which grow in the absence of oxygen. Anaerobes also oxidize organic compounds to carbon dioxide but use electron acceptors such as nitrate, sulfate, or Fe^{3+} oxides instead of oxygen.

The diverse metabolic capabilities of anaerobes represent a potentially potent force in the fight against groundwater contamination. The degree of natural degradation of hydrocarbon contaminants in the anoxic subsurface is much higher than previously thought. For example, benzene is often the contaminant of greatest concern in subsurface petroleum contamination because it is water soluble, toxic, and carcinogenic. Recent studies have shown that anaerobes recovered from the subsurface can degrade benzene. In some contaminated aquifers, substantial natural removal of benzene and other aromatic hydrocarbons in the anoxic zone was observed (*4*).

In some cases, natural degradation by anaerobes and aerobes may limit the spread of contamination; if no important water resources are threatened, no further remediation action may be necessary. If the natural rates of contaminant degrada-

The author is in the Department of Microbiology, University of Massachusetts, Amherst, MA 01337, USA. E-mail: dlovley@microbio.umass.edu