moved from the oocyte by digestion with collagenase (2 mg/ml, type IA, Sigma). Two-electrode voltage-clamp measurements were performed with a TEV-200 amplifier (Dagan) in the virtual-current mode. Intracellular Ag-AgCl electrodes were constructed with an initial input impedance of $\sim$3 to 4 megohms through 3 M KCl single-pull pipettes. The oocyte bath solution for measurements contained 140 mM NaCl, 2 mM KCl, 2 mM $CaCl_2$, and 10 mM Hepes (pH 7.2).

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16. With the use of the Hagen-Poiseuille equation and estimations of diffusion and spontaneous fluid displacement [see H. A. Fishman *et al.*, *Anal. Chem.* **66**, 2318 (1994)], the injection volume was calculated to be $\sim$500 pl. This volume corresponds to $\sim 10^{-5}$ of the entire lysate volume. Cells were differentiated at $\sim$10% confluence (that is, $\sim 5 \times 10^6$ cells were incorporated into the lysate), so that the sample volume contained the equivalent of $\sim$50 cells.
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Permian-Triassic Life Crisis on Land

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Recent advances in radiometric dating and isotopic stratigraphy have resulted in a different placement of the Permian-Triassic boundary within the sedimentary sequence of the Sydney Basin of southeastern Australia. This boundary at 251 million years ago was a time of abrupt decline in both diversity and provincialism of floras in southeastern Australia and extinction of the *Glossopteris* flora. Early Triassic vegetation was low in diversity and dominated by lycopods and voltzialean conifers. The seed fern *Dicroidium* appeared in the wake of Permian-Triassic boundary floral reorganization, but floras dominated by *Dicroidium* did not attain Permian levels of diversity and provinciality until the Middle Triassic (244 million years ago).

The Permian-Triassic boundary has long been known as a major discontinuity in the history of life in the sea (*1*), but comparably severe extinctions have not been apparent from recent assessments of the fossil record of land plants (*2*) or animals (*3*). Geochemical approaches to the vexing problem of correlation between marine and nonmarine biostratigraphic schemes give grounds for reassessing Permian-Triassic boundary events on land. High-precision $^{206}Pb/^{238}U$ radiometric dating of zircons from a tuff at the Permian-Triassic boundary in marine sequences of China at 251 ± 3.4 (2σ) million years ago (Ma) (*4*), supported by dating of tuffs in coal measures of the Gunnedah and Sydney basins of New South Wales (*5*), now indicates that the Permian-Triassic boundary is near the contact between coal measures with *Glossopteris* and overlying fluvial deposits with *Dicroidium* throughout the Bowen-Gunnedah-Sydney basins of eastern Australia. Ironically, this was the traditionally recognized Permian-Triassic boundary in Australia until 1970 (*6*). At that time, correlation of palynomorph assemblages from Australia with those of Pakistan encouraged the view that the boundary was significantly higher in the sequence: at the top of the palynozone characterized by *Protohaploxypinus microcorpus* (*7*). Recent chemostratigraphic studies of boreholes in the Canning Basin of Western Australia have demonstrated that $^{13}C/^{12}C$ ratios in kerogen of marine shale became abruptly lower at the Permian-Triassic boundary (*8*). This dramatic isotopic excursion is characteristic of numerous marine sections through the Permian-Triassic boundary (*9*) and has been recognized also within nonmarine sequences of the Cooper, Bowen, and Sydney basins at the base of the *P. microcorpus* palynozone (*10*).

The transition from *Glossopteris* to *Dicroidium* floras is abrupt and profound. Only four genera and one species of megafossil plants are known to have survived the boundary in the Sydney Basin (*11*), an extinction of 97% of Late Permian fossil leaf species. Leaves of *Glossopteris* have been found in claystone partings of the uppermost (or Bulli) coal only 19 cm below shales bearing *Dicroidium callipteroides* (*12*). I restricted my analysis to fossil leaves (Fig. 1) to avoid duplication of names for fructifications (*13*), but the Permian-Triassic crisis also curtailed the Late Permian evolutionary adaptive radiation of glossopterid fructifications in Gondwana (*14*).

Fossil plants replacing the *Glossopteris* flora were low in diversity (Fig. 1). Although the zonal indicator is the distinctive seed fern *D. callipteroides*, many assemblages are dominated by the conifer *Voltziopsis* (*15*) or the lycopod *Cylomeia* (*16*). These voltzialean conifers and small *Isoetes*-like lycopods are most closely allied to Eurasiatic Early Triassic genera such as *Annalepis*, *Tomiostrobus*, and *Voltzia* (*17*). Both *Voltziopsis* and *Cylomeia* persist into diverse later floras dominated by the Gondwanan endemic seed fern, *Dicroidium zuberi*. Diversification of Gondwanan seed ferns continued with the appearance in the Middle Triassic of *Dicroidium odontopteroides*, a biostratigraphic event that has been dated in New Zealand at about 244 Ma (*18*). The seed fern *D. odontopteroides* is a prominent element of diverse fossil floras that show regional differentiation throughout southern Pangaea (*19*). In Eurasia similarly, extinction of ruflorian and voynovskyan cordaites was followed by an interregnum of conifers and lycopods, which were supplanted by diverse Middle Triassic floras dominated by the seed fern *Scytophyllum* (*17*).

The megafossil plant record of Permian-

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Triassic plant extinctions in the Sydney Basin is supported by basinwide palynological data for each palynozone (*20*, *21*). A pattern of declining then recovering diversity is once again apparent, with a clustering of first and last appearances near the Permian-Triassic boundary (Fig. 1). In addition, Early Triassic palynozones are found throughout Australia, but by Middle Triassic time there was provincial differentiation of eastern and western Australian palynofloras (*22*). There are indications of greater continuity of species through the Late Permian to Middle Triassic interval from palynological data than from megafossil data. This may be due in part to recycling of palynomorphs, which lessens the severity of extinctions to only 19% of Permian palynomorph species not found also in earliest Triassic rocks.

The floral crisis is also blurred by coarse temporal resolution of the palynozones. Short-term changes in vegetation across the Permian-Triassic boundary are best seen from counts of palynomorph abundance in samples of a single drill core from Lake Munmorah, New South Wales (Fig. 2). The core includes the uppermost Permian (Vales Point) coal and is overlain by the oldest preserved Triassic rocks in the basin, as determined by sequence-stratigraphic correlation of onlap relations (*23*). Palynological counts show dramatic floral overturn and a sharp peak of last appearances between the uppermost coal and the first few meters of overlying sandstone and shale. The loss of about 30% of pollen and spore species reflects extinction of the peat-forming flora at the Permian-Triassic boundary. Striate bisaccate pollen known to belong to a variety of Permian glossopterids and Permian-Triassic conifers (*24*) are displaced by an increased abundance of nonstriate bisaccate pollen. Of these, the most common is *Falcisporites*, which was produced by *Dicroidium*, among other plants (*24*). This dramatic reorganization of the dominant pollen producers matches the megafossil record.

A striking feature of these high-resolution palynological data (Fig. 2) is the abundance of acritarchs in samples immediately above the Permian-Triassic boundary. These presumed algal cysts represent a brief episode of marine influence in a predominantly nonmarine sequence. Acanthomorph acritarch swarms and abrupt marine transgression are found also in other Permian-Triassic boundary sequences worldwide (*24*, *25*).

In addition, fungal, fern, and lycopod spores show transient high abundance immediately above the Permian-Triassic boundary in the Lake Munmorah core (*26*). Abundant fungal spores may represent a period of plant destruction and decay, with lycopod and fern spores indicating regeneration of herbaceous plants after catastrophe, as inferred for the Permian-Triassic boundary in other parts of the world (*25*, *27*). Similar interpretations have been made of the better known "fern spike" at the Cretaceous-Tertiary boundary (*28*).

It could be argued that the abrupt decline then protracted recovery in diversity of fossil floras above the coal measures is an artifact of an erosional disconformity between Permian coal measures and Triassic deposits. However, the transient high abundances of fern and lycopod spores and of acritarchs is characteristic of the Permian-Triassic boundary in high-resolution marine sequences (*24*–*27*, *29*). The uppermost coal seam in the Sydney Basin is little eroded away from local tectonic structures such as the Lochinvar Dome (*23*) and can be correlated over distances of 200 km. The up-

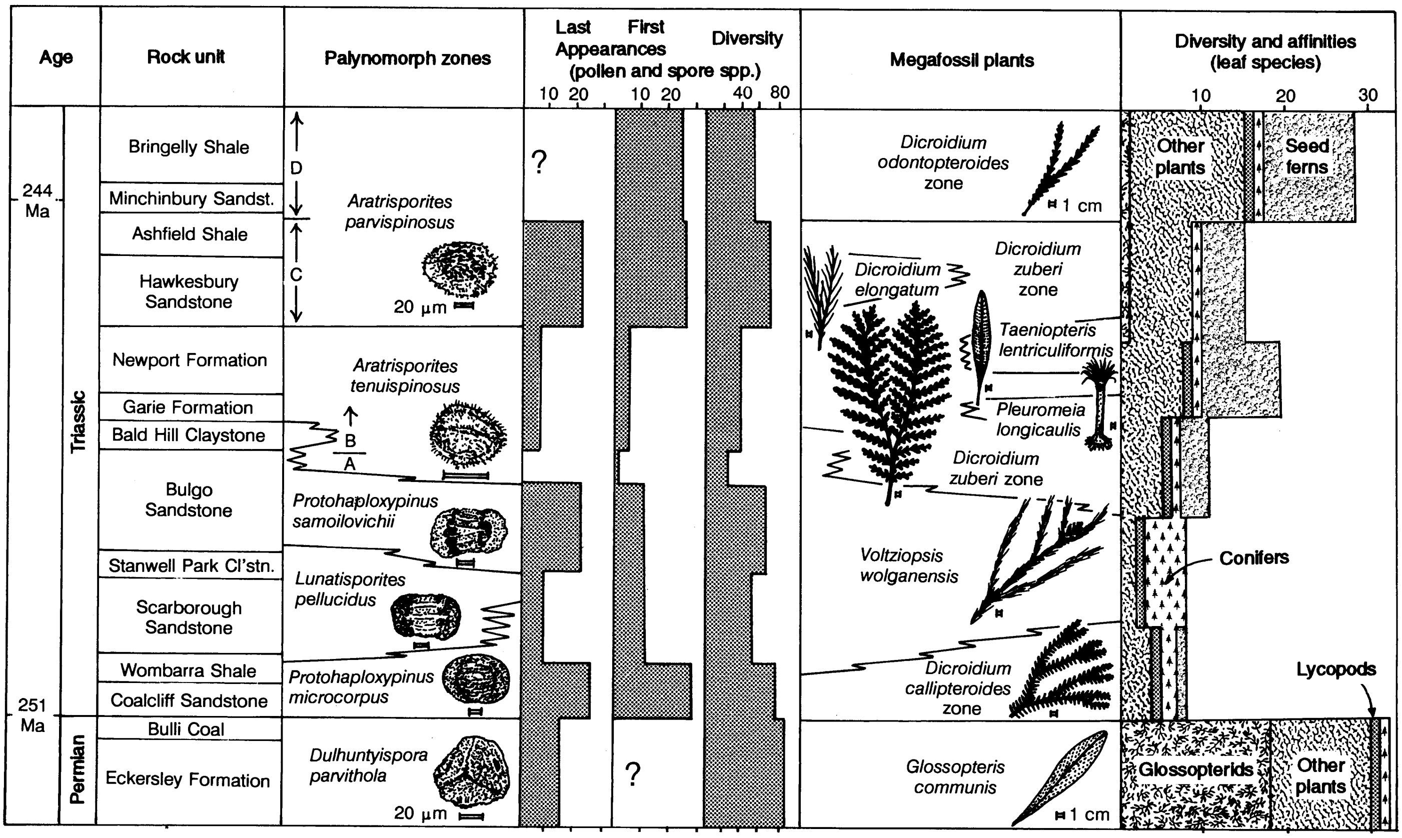

Fig. 1. Changes in fossil floras across the Permian-Triassic boundary within the Sydney Basin, Australia, showing abrupt extinction of the peat-forming *Glossopteris* flora and replacement by a low-diversity conifer-lycopod flora that was later supplanted by adaptive radiation of the *Dicroidium* flora. Palynological data (*20*, *21*) have been used to calculate standing diversity and first and last appearances, whereas only standing diversity and taxonomic composition have been computed from megafossil data (*13*). Events recently redated radiometrically include the Permian-Triassic boundary (*4*) and first appearance of *Dicroidium odontopteroides* (*18*). Bar scales for pollen and spores are 20 µm and for plant fossils are 1 cm.

permost coal is onlapped from the north by six fluvial parasequences, which can be taken as evidence of about 6 × 10^5 years of earliest Triassic nondeposition in the southern coalfield that is represented by rock in the northern coalfield (*23*). Around Lake Munmorah in the north, unusually thick fluvial conglomerates of Permian and Triassic age are evidence of rapid sedimentation (*23*) and thus a high probability of stratigraphic completeness (*30*). A paleosol developed on the uppermost coal at Wybung Head on the coast near Lake Munmorah includes relict bedding expressed to a degree compatible with a hiatus of no more than 10^4 years by comparison with surface soils of known exposure age (*31*). Resolution of the Permian-Triassic boundary in this northeastern part of the Sydney Basin is probably of the order of 10^5 years.

It could also be argued that the apparent catastrophic extinction of the *Glossopteris* flora in the Sydney Basin is compromised by poor preservation of plant fossils in Triassic red beds, recycling of Permian palynomorphs into Triassic deposits, and preferential paleobotanical attention to fossil floras of large coastal exposures of Permian coal measures near Newcastle and Triassic Newport Formation of the northern Sydney coastal cliffs. These arguments lose force given the consistency of the palynological and megafossil record of floral change, despite the different constraints on preservation of leaves versus pollen (*30*). There are carbonaceous shales with abundant fossil plants at many levels within earliest Triassic rocks exposed in coastal exposures that are the equal of those of both the coal measures and Newport Formation.

In contrast, the fossil record of nonmarine animals in the Sydney Basin is not so robust but compromised by taphonomic biases. Lacustrine shales with insects are uncommon in this dominantly fluvial sequence, but include the Late Permian Belmont fauna with 145 species (*32*), a single insect wing from earliest Triassic shales of the Birthday Shaft near Sydney (*33*), the Middle Triassic (Anisian) Brookvale fauna with 15 species (*34*), and the later Middle Triassic (Ladinian) Glenlee fauna with 12 species (*35*). The composition of these local faunas is compatible with recent global compilations (*36*) indicating that the Permian-Triassic boundary was a time of marked extinctions and modernization of insect faunas. Conchostracans are represented by 25 species in the Belmont insect beds, but only four in Early and Middle Triassic rocks (*37*). This low diversity is not due to scarcity, because conchostracans are locally abundant in Early Triassic rocks. These fossil arthropod localities are not spaced sufficiently close stratigraphically to reveal the abruptness of faunal overturn from Permian to Triassic.

Fossil land vertebrates are most abundantly preserved in calcareous red paleosols of the kind forming in dry climates (*30*), but paleosols of the Sydney Basin are noncalcareous and deeply weathered, indicative of a humid climate (*38*) in which bones are dissolved by soil acids. This may account for the poverty of vertebrate remains other than fish and aquatic labyrinthodonts in the Sydney Basin. There are fossil footprints of a variety of terrestrial reptiles (*39*), but identifiable skeletal remains have yet to be reported. Fragmentary remains of a procolophonid and a kannemeyerid dicynodont from the Bowen Basin of Queensland provide evidence that Early Triassic terrestrial faunas of Australia were similar to *Lystrosaurus* and *Cynognathus* faunas of South Africa and Antarctica (*40*).

In summary, terrestrial ecosystems suffered marked losses in diversity at the Permian-Triassic boundary, after which a cosmopolitan flora of lycopods and conifers prevailed as new groups of endemic seed ferns underwent an evolutionary adaptive radiation to dominance of regionally differentiated floras by Middle Triassic time. This culminated in the *Dicroidium* flora of southern Pangea (*13*) and the *Scytophyllum* flora of northern Pangea (*17*). The floras of the Early Triassic interregnum in the Sydney Basin included needle-leaved conifers and herbaceous aquatic lycopods in oligotrophic forest and marsh assemblages very different from the deciduous seed fern swamps of the Late Permian and wet forests of the Middle Triassic (*13*). Early Triassic oligotrophic lycopod-conifer vegetation can be recognized also in Europe, Russia, and China (*17*). The *Lystrosaurus* fauna is similarly widespread and low in diversity compared with Permian therapsid faunas and Middle to Late Triassic rhynchosaur faunas (*40*). The Permian-Triassic life crisis thus ushered in an Early Triassic terrestrial ecosystem that was lower in diversity and globally more homogeneous than ecosystems of the Late Permian and Middle Triassic.

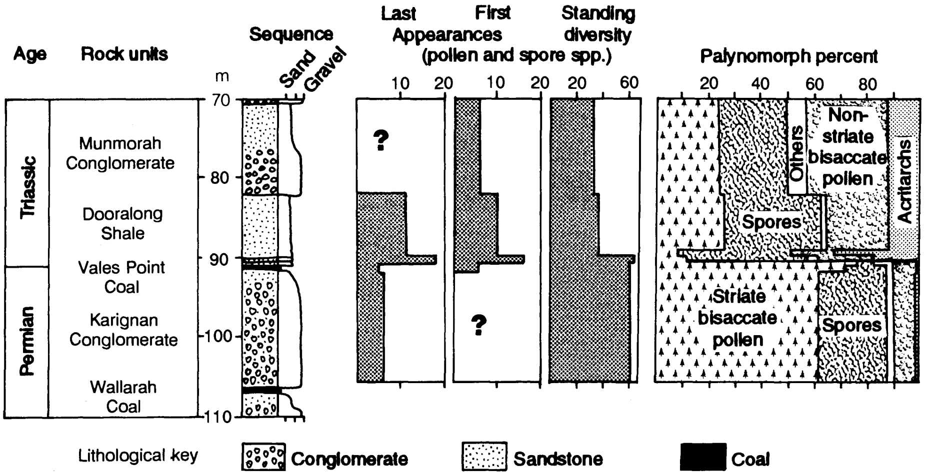

Fig. 2. Changing taxonomic composition of palynofloras across the Permian-Triassic boundary measured by counting palynomorphs in preparations from Newvale diamond drill hole number 28, Lake Munmorah, New South Wales (*21*). All palynomorphs are shown in percent composition (to the right), but presumed marine algal acritarchs were not included in diversity and appearances of pollen and spores (to the left).

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Flow Mechanism of Glaciers on Soft Beds

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Subhourly measurements of bed deformation, bed shear strength, subglacial water pressure, and surface speed at Storglaciären, a glacier in northern Sweden, showed that the shear-strain rates of the bed decrease during periods of high water pressure and surface speed. High water pressures appear to be accompanied by a reduction in the coupling of ice with the bed that is sufficient to reduce or eliminate shearing. The instability of large ice masses may result from similar decoupling rather than from pervasive bed deformation, as has been commonly thought.

Many glaciers are underlain, at least in part, by unlithified sediment that may deform readily if basal water pressures are near the ice overburden pressure. Such deformation has been invoked to explain the rapid motion and instability of modern and former ice masses (*1–4*). To further study this process, we obtained simultaneous continuous measurements of bed deformation and glacier surface velocity on Storglaciären in northern Sweden. Basal water pressures vary over a wide range of values at Storglaciären; thus, this glacier can be used to study the critical relation between water pressure and bed deformation rate.

Storglaciären is a well-studied, wet-based valley glacier (*5*). Resistivity measurements (*6*), penetration testing, and sampling in boreholes drilled to the bed indicate that much of the ablation area is underlain by a layer of till that is decimeters thick. We studied the deformation of this till in the lower part of the ablation area on the upstream side of a gentle transverse ridge in the bed. The average glacier thickness in this area is $\sim$95 m. We measured bed deformation in boreholes using small dual-axis, leaf-spring tiltmeters (*7*). We also measured the shear strength of the till with a roughened horizontal cylinder with conical ends that was dragged through the till. The force on the cylinder was measured, and geotechnical theory associated with cone-penetration testing was adapted to estimate the shear strength from this force (*8*). We determined surface speed by measuring the down-glacier displacement of a stake at the site every 10 min with an automated distance meter (*9*). Water pressure was measured continuously in boreholes.

During the period of record in 1992 (Fig. 1), a tiltmeter inserted in sediment near the ice-bed interface rotated down-glacier a total of 52°, corresponding to a mean shear-strain rate of $25\ \text{year}^{-1}$. The till thickness at the site, estimated from penetration tests, was 0.33 m. If the full thickness were shearing uniformly, the displacement of the surface of the glacier would have been at least twice what was observed. The observed displacement thus indicates that shearing was not uniform and was instead focused near the glacier sole, as has been both measured (*2*) and predicted from theory (*2, 10, 11*). During two peaks in velocity resulting from rain storms on 15 and 22 July, negative shear-strain rates were recorded (Fig. 1). Such negative values, which have also been observed elsewhere (*7*), imply that the tiltmeter recording the deformation was rotating up-glacier, the opposite of that expected. During acceleration of the glacier toward these peaks, the sediment shear strength tended to decrease; it then increased rapidly during deceleration of the glacier (Fig. 1).

The glacier and till exhibited similar behavior in 1993 (Fig. 2). Diurnal peaks in surface velocity were coeval with maxima in water pressure, which never exceeded the ice overburden pressure (*12*). The velocity peaks occurred during or slightly after till strain-rate minima, which were usually negative. The total down flow rotation of the tiltmeter was 9°, which would account for only 5% of the glacier displacement, even if the full 0.35 m of till were deforming uniformly. The tiltmeter was inserted 0.10 m lower in the till layer in 1993 than in 1992, which may account for the lower mean strain rate.

It appears from these data that the coupling between the ice and the till is reduced during periods of high water pressure and most rapid flow. This decoupling is presumably caused by uplift of the basal ice and reduction of the applied shear stress. A natural conjecture is that the negative strain rates arise because of squeezing of the till into the zone of uplift. This would thicken the till and cause the tiltmeters, which were inclined in the down flow direction, to rotate up-glacier. The up-glacier rotation

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