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 ~3 to 4 MΩ through 3 M KCl single-pull pipettes. The oocyte bath solution for measurements contained 140 mM NaCl, 2 mM KCl, 2 mM CaCl₂, and 10 mM Hepes (pH 7.2).

12. A narrow crack connecting the capillary channel to a grounded electrolyte reservoir was made ~10 cm upstream from the capillary outlet with the technique described in M. C. Linhares and P. T. Kissinger [Anal. Chem. 63, 2076 (1991)].


14. Divalent cations in the separation buffer interacted with the capillary surface, causing a slow decrease in the electroosmotic flow rate until equilibrium was reached [see K. Yamamoto, S. Suzuki, M. Ueda, K. Kakih, J. Chromatogr. 588, 327 (1991)]. This decrease reduced the velocity of a slow species by a greater relative amount than the velocity of a fast species (assuming migration velocities remain positive).

15. A 50-ml culture flask of PC-12 cells, differentiated for 4 days in medium containing 6-MG (25 ng/ml) was pelleted, and cells were lysed in ~70 µl of 70% methanol containing ~0.1 M ascorbic acid to inhibit choline oxidation.

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 ~500 pl. This volume corresponds to ~10⁻⁶ of the entire lysate volume. Cells were differentiated at ~10% confluence (that is, ~5 x 10⁶ cells were incorporated into the lysate), so that the sample volume contained the equivalent of ~50 cells.


19. The Ca²⁺ response to BK was observed to decrease substantially when multiple CE runs were performed in a short period.


21. This result may be caused by simple dilution in the capillary-SCB transfer region.


23. At gap distances less than 20 µm, damage was sometimes apparent. Electrical and mechanical distress both may contribute to cell damage when very small gap distances are used.

24. “Grounding” through a crack in the capillary creates a voltage splitter, in which the relative current through the crack and to the end of the capillary is determined by the relative resistances of the two paths. Through most of the current passes through the crack, some residual current flows through the capillary outlet and interferes with the voltage-clamp measurement.


30. We thank L. Stryer and R. Dado for stimulating discussions, and T.-J. Xu, S.-C. Hsu, C. Sims, and R. Schneevis for technical assistance. We gratefully acknowledge the laboratories of E. Shooter and D. Julius for the donation of PC-12 cells and BHTic complementary DNA, respectively. J.B.S. is a Howard Hughes Predoctoral Fellow, and H.A.F. is a W. R. Grace Fellow. Supported by grants from the National Institute of Mental Health (MH4523-03 and MH45524-03) and Beckman Instruments.

2 September 1994; accepted 1 November 1994

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**Permian-Triassic Life Crisis on Land**

**G. J. Retallack**

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 provinciality of flora in southeastern Australia and extinction of the Glossopteris flora. Early Triassic vegetation was low in diversity and dominated by lycopsids and volvulacean 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 biostatigraphic schemes give grounds 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 palynoform 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 cheemostratigraphic studies of boreholes in the Canning Basin of Western Australia have demonstrated that δ¹³C/δ¹²C 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 claststone and parts 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 Volziaepis (15) or the lycopod Cylomeia (16). These volvulacean conifers and small Isoetes-like lycopsids are most closely allied to Eurasian Early Triassic genera such as Annapolis, Tomistrobias, and Volzia (17). Both Volziopis and Cylomeia persist into diverse later floras dominated by the Gondwanan endemic seed fern, Dicroidium zaberii. 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 rufolinar and vovnyovskyan cor-diates 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-
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 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. Acanthomorphic 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-lycoped 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 (15). 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.](image)
permest coal is onlapped from the north by six fluvial parasequences, which can be taken as evidence of about 6 \times 10^8 years of earliest Triassic nondeposition in the southeastern 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 relic bedding expressed to a degree compatible when a hiatus of no more than 10^8 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 fossiliferous 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 extinction 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 turnover 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 kannemeyeriid dicynodont from the Bowen Basin of Queensland provide evidence that Early Triassic terrestrial faunas of Australia were similar to Lystro-

$saurus$ 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 florals by Middle Triassic time. This culminated in the $Dicrodium$ 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 lycopsids 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.

**REFERENCES AND NOTES**

11. Surviving genera have been taken to include Glossopteris as a Lazarus taxon [W. B. K. Holmes, Geophyology 22, 19 (1992)], although there is merit also in referring distinctive Middle Triassic leaves of this kind to Gontriglossa. Other surviving form genera are Cladophlebis, Sphenopteris, and Phytochoa. The single surviving species is $Schizoneura$ australis.
12. The seed fern "Trinifidi" $callipteroides$ has been referred to $D. callipteroides$ by M. E. White (Australia's Prehistoric Plants (Reed, Balgowlah, New South Wales, 1984)).
Flow Mechanism of Glaciers on Soft Beds

Neal R. Iverson,* Brian Hanson, Roger LeB. Hooke, Peter Jansson

Subhourly measurements of bed deformation, bed shear stress, 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 such decoupling rather than from pervasive bed deformation, as has been commonly thought.

Many glaciers are underlain, at least in part, by un lithified sediment that may deform readily if basal water pressures are near the ice overburden pressure. Such deformation has been invoked to explain the rapid surface lowering of glaciers, in which the ice overburden pressure. Such deformation has been invoked to explain the rapid surface lowering of glaciers, in which the ice is thrust onto the bed (10). It is a natural conjecture is that the negative shear stress of the till with a roughened surface that would account for the observed surface lowering (12). The velocity peaks occurred during or slightly after till strain-rate minima, which were usually negative. The total downflow rotation of the tillmeter was measured 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 tillmeter recording the deformation was rotating up-glacier, the opposite of that expected. During acceleration of the glacier toward these peaks, the sediment shear stress tended to decrease rapidly, leading to a rapid increase in strain-rate 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 downflow rotation of the tillmeter was measured 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).

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