

## PALEONTOLOGY

# Flourishing After the End-Permian Mass Extinction

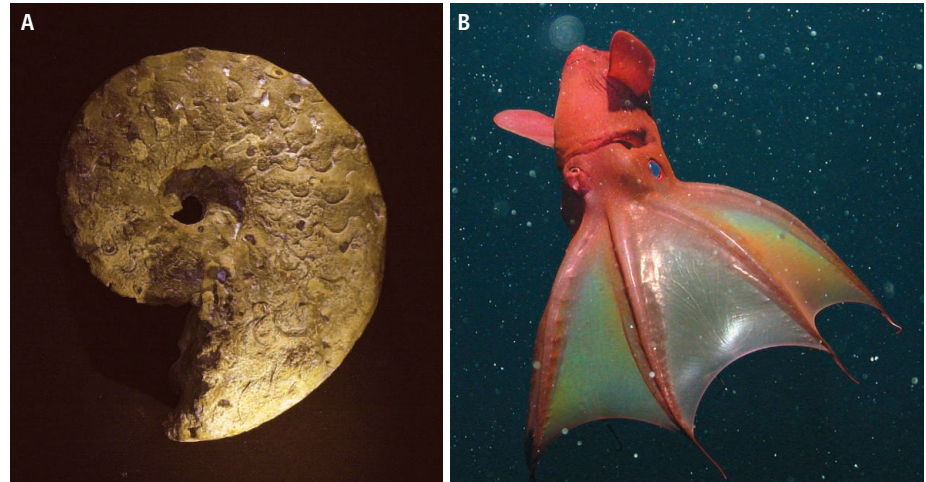
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Two hundred and fifty-two million years ago, the Paleozoic Era came to a cataclysmic close with the end-Permian mass extinction, when as much as 85% of readily fossilizable marine species became extinct. It took 5 million years for the biosphere to begin to recover from the event. At least this has been the conventional view. However, on page 1118 of this issue, Brayard *et al.* (1) show that ceratitid ammonoids (see the figure, panel A) recovered much faster than did most other marine groups, attaining considerable diversity just 1 million years after the mass extinction. Moreover, these mollusks reached a peak in their diversity at the end of the Early Triassic, when the diversity and body size of most other groups (particularly bivalves and gastropods) was still depressed (2). What do these data tell us about the post-apocalyptic world of the Early Triassic, and about the cause of the end-Permian extinction event itself?

The cause of the end-Permian mass extinction has long been controversial (3). There is increasing agreement that toxic waters decimated bottom communities in shallow waters, but it remains unclear whether the kill mechanism was hypercapnia (high CO<sub>2</sub> levels) (4), euxinia (anoxic water infused with H<sub>2</sub>S) (5), or something else. There is even less agreement on what might have caused the toxicity.

One possibility is that the Siberian traps were responsible—a vast outpouring of basalts that released huge volumes of CO<sub>2</sub> as they passed through thick coal sequences. Between 1 and 3 million km<sup>3</sup> may have been disgorged (enough to bury Texas under 1.4 to 4.3 km of lava). Under this scenario, the increased CO<sub>2</sub>—with atmospheric concentrations possibly 10 times as high as at present—led to massive global warming. This warming decreased the oxygen content of the oceans, permitting the biologically mediated generation of H<sub>2</sub>S in the deep oceans, which, upon upwelling, caused the extinctions (6).

Whatever the ultimate cause(s) of the



**Tips for flourishing after a mass extinction.** *Ceratites nodosus* (MCZ-7232) (A), from the Triassic of Germany, was similar to the ceratitid ammonoid species that thrived in the water column in the Early Triassic (1), while bottom-dwelling species languished. Key to the ceratitids' rapid success after the end-Permian mass extinction were their ecological tolerances, which may be inferred by reference to their closest living relatives, the coleoids (squids, octopuses, and cuttlefish), including the low-oxygen specialist *Vampyroteuthis infernalis* (B).

extinction, the proximal cause appears to have been the inability of many species to handle the physiological demands of a changed ocean chemistry. Evidence that conditions remained difficult for 5 million years after the extinctions comes mainly from the observation that the diversity and size of fossil bivalves and gastropods remained low, indicating stressed conditions (2). Furthermore, the carbon cycle was unusually volatile (2), although the exact meaning of this volatility is not understood (7). Another indication of difficult times is the delay in the recovery of reef communities: The two major clades of Paleozoic coral (the Rugosa and Tabulata) became extinct at the end of the Permian, but modern corals (the Scleractinia) did not emerge until the Middle Triassic (8).

The ammonoid data reported by Brayard *et al.* suggest a much more rapid recovery, at least for part of the biosphere. Unlike the bottom-dwelling gastropods and bivalves, ammonoids live in the water column. Thus, Brayard *et al.*'s study suggests that conditions in the water column were better than those on the bottom. Or does it?

If the ceratitid ammonoids were active predators requiring high oxygen, this would indeed suggest a healthy water column, but if they preferred low oxygen conditions, then

Cephalopods, which live in the water column, recovered much faster from the end-Permian mass extinction than did bottom-dwelling fauna.

their rapid rise in diversity suggests that the water column may also have been stressed, like the shallow bottom waters in the Early Triassic. The latter scenario is consistent with a major extinction of ceratitids at the start of the Middle Triassic (1), when the bottom dwellers began their full recovery. In fact, the ammonoids are a characteristic component of the lost biotope (9)—faunas dominated by taxa that thrived in the water column in the Paleozoic and Mesozoic while the benthic fauna was low in diversity. Furthermore, ammonoids are known to have diversified quickly after a wide range of environmental crises, not just after the end-Permian mass extinction.

To better understand the meaning of Brayard *et al.*'s data, we need to know more about the biology and physiological tolerances of ammonoids in general, and of ceratitids in particular. Although the group is extinct, we can turn to their nearest living relatives, the coleoids (squids, octopods, and cuttlefishes)—and also *Nautilus*, which looks superficially similar to the ammonoids (10). Although many modern coleoids are active predators in oxygenated waters, others like *Vampyroteuthis infernalis* (“vampire squid from hell”) (see the figure, panel B) and *Nautilus* require little oxygen. These species lie deep in the evolutionary trees of living coleoids and liv-

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ing cephalopods, respectively, suggesting that a tolerance for low oxygen was ancestral for living cephalopods. These observations support an affinity for low-oxygen conditions for many ammonoids, consistent with the dysoxic paleoenvironmental setting in which they are frequently found.

Identification of physiological and ecological commonalities among both the victims and the survivors (4) is a powerful route to elucidate the causes of major biotic turnovers, including the cataclysmic end-Permian mass extinction

(3). The task of establishing the environmental requirements of extinct fossil groups can be aided by studying their living relatives. These data will allow increasingly refined interpretation of past environments, including those associated with mass extinctions.

#### References and Notes

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## PHYSICS

# Chasing Arcs in Cuprate Superconductors

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Important clues to the origin of high-temperature superconductivity in cuprate compounds lie within the normal phase of these compounds, which forms above the transition temperature  $T_c$ . One unusual feature of the normal phase is the presence of a pseudogap; depending on the momentum of the charge carrier, its excitation energy is either zero or finite (1). Two reports in *Science*, by Pushp *et al.* (2) in June and by Lee *et al.* (3) on page 1099 of this issue, have used scanning tunneling microscopy to provide dramatic new insights into the pseudogap phase and to elucidate how the electronic excitations, both above and below  $T_c$ , differ for different values of the carrier momentum.

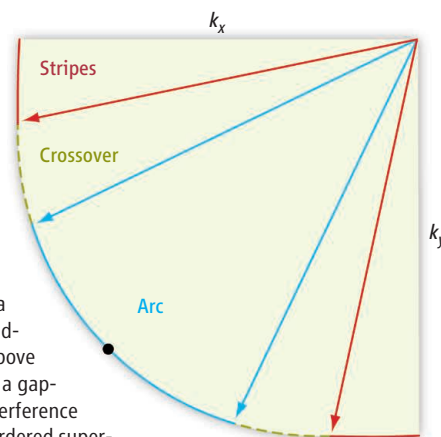
The cuprate superconductors are formed by chemically doping compounds that simple energy-band models predict to be conductors, but that actually are insulators because of strong electronic correlations. Chemical doping creates charge carriers and, at some optimal level, maximizes  $T_c$ . For lower doping levels, the “underdoped” normal state is characterized by a pseudogap—that is, a partial depletion of the charge carriers (1). Angle-resolved photoemission studies, which probe electronic states in momentum space, were the first to show that some parts of the Fermi surface that separates occupied and unoccupied states are gapless as in a conventional metal, but other parts have an energy gap. That is, the Fermi surface of the underdoped normal phase is truncated (4, 5) when portrayed in momentum space, forming arcs instead of full curves that bound a region (see the figure).

**The three-part electronic structure of underdoped cuprates.** The curve represents the Fermi surface in one quadrant of momentum space, defined by momenta in the  $x$  and  $y$  directions of the copper oxide planes,  $k_x$  and  $k_y$ . In the superconducting state at temperatures below  $T_c$ , the lower-energy blue region has a simple d-wave gap; the node, where the energy gap vanishes, is marked by a black dot. In the antinodal regions marked in red, the energy gaps are largest, and there are incoherent states with a stripe-like pattern. The dashed green region marks a crossover between these two regimes, as seen in the studies of Pushp *et al.* and Lee *et al.* In the normal state above  $T_c$ , the energy gap in the blue region collapses to form a gapless arc. In the dashed green region, quasiparticle interference patterns remain that imply the presence of phase-disordered superconductivity. The incoherent red regions are largely unaffected by  $T_c$ .

These arcs have provoked controversy ever since they were first observed, because Fermi surfaces should form closed contours (which in special circumstances can reduce to gapless points). The idea of a Fermi surface holds rigorously only at absolute zero temperature; thus, the arcs may be generated by thermally broadening the nodes (the gapless points) of the d-wave superconducting state into segments. It is also possible that they are only part of the boundary of a closed region, or pocket, but that the rest of the boundary is too weak to be observed.

Interest in Fermi arcs has been renewed by a number of recent studies that tie them into the debate over the mechanism of superconductivity. The arc length appears to scale linearly with temperature (6), which supports the idea that they originate from thermally broadened d-wave nodes. However, recent quantum oscillation studies (7, 8) have found evidence for closed pockets in the under-

Scanning tunneling microscopy studies of cuprate superconductors clarify the origin of their unusual electronic structure.



doped regime; these pockets are likely to be a result of some ordering of the charge carriers. Some recent photoemission studies also show evidence for pockets (9–11).

Scanning tunneling microscopy also provides information on the local density of electronic states as a function of energy, and although the data are obtained in position space, they can be mathematically inverted to provide a momentum-space picture. This technique is complementary to photoemission in that it can reveal local variations in the material. Use of this technique has revealed that the electronic excitations of the superconducting phase are inhomogeneous in real space (12). For underdoped samples, this inhomogeneity is so drastic that a localized stripe phase forms that dominates the electronic structure on an energy scale comparable to the pseudogap (13).

However, lower-energy excitations appear to be quite homogeneous. Pushp *et*

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