mented by CRY1. CRY2 is not required to promote early flowering under continuous blue light, perhaps because cryptochrome 1 (CRY1) promotes flowering under these conditions. In agreement with this, mutations called *elongated hypocotyl 4* (*hy4*), which affect the CRY1 protein (*12*), delay flowering in response to blue light or under short photoperiods (*13*). However, *hy4* mutations seem to have little effect on flowering time under long photoperiods of white light. Perhaps therefore CRY2 promotes flowering under constant white light and long photoperiods, but under constant blue light CRY1 is required for early flowering. A division in function between CRY1 and CRY2 has been shown in development of the seedling, in which CRY1 mediates high-intensity blue-light responses and CRY2 mediates low-light responses (*10*).

The promotion of flowering in response to long days requires a timekeeping mechanism that enables plants to measure day length. An endogenous circadian clock is thought to provide the timekeeper in the photoperiodic control of flowering time (*2*). In *Arabidopsis* the circadian clock shows a shorter period under light than darkness, and phytochrome as well as a blue-light receptor were demonstrated to mediate this effect (*14*). Conceivably CRY2 may act as a blue-light receptor that signals to the clock, enabling long and short days to be distinguished. A link between blue light, the circadian clock, and the photoperiodic control of flowering was previously suggested by the *early flowering 3* (*elf3*) mutation (*15*). This caused photoperiod-insensitive early flowering, disrupted clock function under continuous light, and led to hypocotyl elongation under blue light. The effect of *cry2* on clock function and of *elf3* on the *cry2* phenotype can now be tested.

Isolation of the genes affected by the other flowering-time mutations in the same class as CRY2 should provide biochemical functions for other members of the pathway. Perhaps these will also help with the challenges of determining how the activity of the pathway is regulated by day length and in which tissues of the plant the different components of the pathway act.

References and Notes

1. W. W. Garner and H. A. Allard, *J. Agric. Res.* **18**, 553 (1920).
2. B. Thomas and D. Vince-Prue, *Photoperiodism in Plants* (Academic Press, San Diego, 1997).
3. J. L. Weller, I. C. Murfet, J. B. Reid, *Plant Physiol.* **114**, 1225 (1997).
4. E. Johnson, M. Bradley, N. P. Harberd, G. C. Whitelam, *ibid.* **105**, 141 (1994).
5. H. Guo, H. Yang, T. Mockler, C. Lin, *Science* **279**, 1360 (1998).
6. M. Koornneef, H. Blankestijn-de Vries, C. J. Hanhart, A. J. M. Peeters, *Genetics* **148**, 1 (1998).
7. J. Putterill, F. Robson, K. Lee, R. Simon, G. Coupland, *Cell* **80**, 847 (1995).
8. R. Simon, M. I. Igeño, G. Coupland, *Nature* **384**, 59 (1996).
9. K. Eskins, *Physiol. Plant.* **86**, 439 (1992).
10. C. Lin *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **95**, 2686 (1998).
11. D. E. Somers, R. A. Sharrock, J. M. Tepperman, P. H. Quail, *Plant Cell* **3**, 1263 (1991).
12. M. Ahmad and A. R. Cashmore, *Nature* **366**, 162 (1993).
13. D. J. Bagnall, R. W. King, R. P. Hangarter, *Planta* **200**, 278 (1996).
14. A. J. Millar, M. Straume, J. Chory, N.-H. Chua, S. A. Kay, *Science* **267**, 1163 (1995).
15. K. A. Hicks *et al.*, *ibid.* **274**, 790 (1996); M. T. Zagotta *et al.*, *Plant J.* **10**, 691 (1996).
16. We thank P. Puente for her comments.

EVOLUTION

After the End: Recovery from Extinction

Douglas H. Erwin

Shiva, the destroyer in the Hindu pantheon of gods, could be the patron of paleontologists as they scrutinize the intricacies of past biodiversity crises. Yet Shiva's dance of destruction clears the way for rebirth and renewal; it is this creative side of Shiva to which paleontologists recently have appealed as they investigate the recovery processes that follow mass extinctions. One particularly abrupt mass extinction, at the end of the Cretaceous period, provides a clean starting point for examining recovery patterns. An influential study of this period from the Texas Gulf Coast (*1*) revealed a pattern that has become the paradigm of recovery (*2*): A zone barren of fossils immediately above the extinction horizon is overlain in the more recent strata by a species-poor assemblage of surviving taxa, usually able to survive broad environmental conditions, and opportunistic blooms of some species, presumably taking advantage of empty ecological niches. This survival interval is succeeded by the diversification of new species and eventual rebuilding of communities.

But the generality of this model is called into question with the report on page 1327 of this issue of the first comparison of recovery patterns in several different biogeographic provinces (*3*). Jablonski has extended his previous studies of Late Cretaceous bivalves and gastropods through the mass extinction and into the first 10 million years of the Paleocene. In this detailed comparison of the recovery process in the U.S. Gulf Coast, northern Europe, northern Africa, and Pakistan–northern India, there is no evidence of opportunistic blooms outside of the U.S. Gulf Coast. The paradigm may not be so paradigmatic: It seems that the biogeographic complexities of the recovery process can overwhelm efforts to develop a general model.

Paleontologists have usually examined changing patterns of biotic diversity in one of two ways—as synoptic global compendia or as local investigations of a single section. Detailed comparisons of different regional diversity patterns have been uncommon in rocks older than 2 million years. This missing biogeographic component to recovery studies is particularly troubling, for the comparative analysis of recoveries is quite likely to yield ecologically and evolutionarily meaningful results. Distinct biogeographic regions are commonly semi-autonomous actors in the evolutionary play, and thus the "reality" of insights from global compendia has long been in doubt. Global compendia provide greater taxonomic scope than local studies, but they sacrifice ecological acuity and may average very different signals: Cretaceous oysters in Pakistan simply don't interact with carditid bivalves in Alabama. At the same time, the peculiarities of data from any individual location—with its particular preservational problems, changing substrates and environments, and restricted sampling—often limit the generality of conclusions drawn from such information. Although regional analyses are the most demanding sort of data to assemble, they provide the best trade-off among these competing problems.

The faunas of the four regions compared in the new report are each well documented; all of the regions show similar magnitudes of extinction and patterns of taxo-

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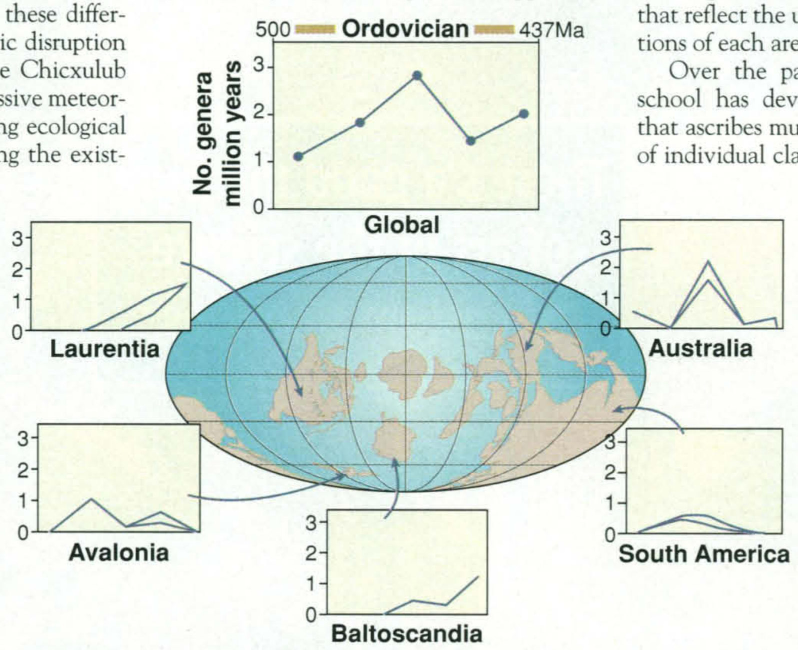
nomic selectivity during the extinction at the end of the Cretaceous. Yet the patterns of recovery are quite different. Earlier studies of the Gulf Coast revealed evolutionary bursts among four molluscan families immediately after the extinction (*1*, *4*) that produced a proliferation of new taxa. But in the new analysis, the other three regions show no such bloom taxa, either among these four families or among other groups. Furthermore, the Gulf Coast shows a higher proportion of invading species (relative to local survivors and newly evolved species) than the other regions. A simple explanation of these differences might be a greater ecologic disruption from the gulf's proximity to the Chicxulub impact site, the area where a massive meteorite slammed into Earth, changing ecological conditions worldwide and ending the existence of the dinosaurs. But if this were the case, why did the Gulf Coast experience the same percent of extinctions as in Pakistan or Northern Europe? More work is required to understand the unique events in the Gulf Coast at the end of the Cretaceous. Detailed phylogenetic studies will ferret out the source of the invading species, and comparative paleoecological studies will identify the conditions that encouraged the Gulf Coast opportunistic blooms.

Compiling regional information necessitates summing data from some time interval to ensure a sufficient sample size and accurate biostratigraphic correlations. But summed data can also obscure significant recovery processes occurring in the shorter term. With the possible exception of the unusually long Early Triassic recovery, many of the interesting complexities of recovery occur within 1 to 2 million years of the event (*5*). In the Texas Gulf Coast, the burst of bloom taxa decayed and was replaced by a stable, relatively diverse fauna within the first 2 million years of the extinction (*4*), the extent of Jablonski's first of five Paleocene units. Although Jablonski's data capture the Gulf Coast bloom taxa, the lack of evidence of blooms in other regions could in part be related to the length of the sampling interval. Studies from Northern Europe with finer time resolution do not show additional complexity, suggesting that Jablonski's interval duration was sufficient. But without detailed investigations of local sections, these regional compilations will be difficult to interpret. A complete view of the recovery process will require both methods of analysis.



The sum obscures the parts. The global data for new genera of bivalves during the Ordovician is an aggregate of varying patterns on different paleocontinents. Variations in sample size have been corrected.

SOURCE: DATA (*10*); MAP (*11*)

A recent paper in *Geobios* raises similar issues in a study of the Ordovician evolutionary radiation, the event that established the suite of marine communities that dominate the Paleozoic. This compilation of 6500 occurrences of Ordovician marine genera covers six different continental regions in sufficient detail to reveal regional differences in the evolutionary history of trilobites, articulate brachiopods, and mollusks (*6*). In all six paleocontinents, the Ordovician radiation reaches a peak in the Late Ordovician, as in the global compilation, but an Early Ordovician peak also appears in data from South China. A possible Middle Ordovician mass extinction appears in three of the regions but not in the other three, and the Late Ordovician decline in diversity is virtually absent in two areas. What accounts for these differences? Do any of these patterns accurately reflect the pattern of diversity? Were the various regions so isolated that the radiation took different paths in different areas?

Differences in the number of genera sampled in each stage of the Ordovician have been previously shown to distort the global diversity picture (*7*). Correcting both the global and regional diversity data for sampling differences reveals that the main pulse of the radiation occurred during the Early to Middle Ordovician, and then stabilized; the late Ordovician peak was an artifact of large sample sizes (*6*, *7*). Within the new regional data set, the correction for sample size reveals that the Early Ordovician peak in South China is likewise an artifact. Most important for the Ordovician as a whole, however, South China exhibits relatively low diversity and ancient North America and Bohemia the highest diversity. A clue to the regional environmental conditions that could cause these variations in diversity is the correlation between these diversity trends and the extent of siliciclastic sedimentation (an index of mountain-building activity) (*8*). Such a correlation has been suggested before (*9*), but without such convincing data. Although diversity trends in different regions are not fully independent, Miller's results suggest that regions follow independent trajectories that reflect the unique environmental conditions of each area.

Over the past 20 years, an influential school has developed within paleobiology that ascribes much of the differential success of individual clades to intrinsic properties of the clades themselves—for example, competitive ability or origination rates. Environmental events alter trajectories, but clade diversity can be considered independently from geological setting. Other paleontologists reject this view, arguing that biogeographic, environmental, and paleoecologic context is critical to any understanding of diversity change. The new studies suggest that the second view may be correct: Biogeographic context may well be critical in shaping the course of evolution. We can expect the number of regional comparative studies to grow (although not quickly, given the amount of time required to collect good data). These new data will clarify our view of how past biodiversity patterns were regulated—locally, regionally, and globally—within the context of a changing physical environment.

References

1. T. A. Hansen, *Paleobiology* **14**, 37 (1988).
2. P. J. Harries, E. G. Kauffman, T. Hansen, in (*5*), pp. 41–60; D. H. Erwin, in *Evolutionary Paleobiology*, D. Jablonski, D. H. Erwin, J. Lipps, Eds. (Univ. of Chicago Press, Chicago, 1997), pp. 398–418.
3. D. Jablonski, *Science* **279**, 1327 (1998).
4. T. A. Hansen *et al.*, *Paleobiology* **19**, 251 (1993).
5. See papers in M. B. Hart, Ed., *Geol. Soc. London Spec. Pub. 102* (1996).
6. A. I. Miller, *Geobios* **20**, 397 (1997).
7. ——— and M. Foote, *Paleobiology* **22**, 304 (1996).
8. A. I. Miller and S. Mao, *Geology* **23**, 305 (1995).
9. J. H. F. Umbgrove, *The Pulse of the Earth* (Nijhoff, The Hague, Netherlands, 1947); L. G. Henbest, *J. Paleontol.* **26**, 299 (1952).
10. A. Miller, personal communication.
11. C. R. Scotese and W. S. McKerrow, in *Palaeozoic Palaeogeography and Biogeography*, W. S. McKerrow and C. R. Scotese, Eds. (*Geol. Soc., London Mem. 12*, 1990), pp. 1–21.