Protean evolution

Jerry A. Coyne

Macroevolutionary Dynamics: Species, Niches, & Adaptive Peaks. By Niles Eldredge. *McGraw-Hill: 1989. Pp.226. Hbk $28.95; pbk $14.95.*

EVOLUTIONARY biologists have found it hard to wrestle with the theory of punctuated equilibrium, for, like Proteus, it changes form when firmly grasped. Having gradually abandoned many of the key concepts, its proponents still insist that it is a revolutionary explanation of macroevolution, the large-scale changes in the types and numbers of organisms during the history of life.

Punctuated equilibrium's newest incarnation, described in *Macroevolutionary Dynamics*, is missing further parts. Gone are the ideas that evolutionary stasis is caused by ontogenetic resistance to change, that key evolutionary innovations begin as maladaptive features fixed by genetic drift, that macromutations play a large role in evolution, and that evolutionary trends result from species selection. Although the new, truncated theory is barely recognizable as punctuated equilibrium, Eldredge implies that it has not changed much since the controversial original version of 1972. But those who have followed this controversy will be astonished at Eldredge's revisionism, including the assertion that he and Stephen Gould always "remained neo-Darwinian gradualists in the sense that the brief periods of relatively rapid change involved intergradational, rather than saltational, phenotypic transformation, presumably under the control of natural selection" (p.66).

This short volume, apparently written for those with a professional interest in evolution, describes the two remaining tenets of punctuated equilibrium. The first is the familiar idea that species change very little over most of their evolutionary history. This stasis is no longer attributed to developmental homoeostasis, but to a combination of behavioural habitat selection (organisms seek out familiar niches when the environment changes, therefore experiencing no new selection) and disruptive natural selection (different populations adapt to different local environments, and the 'average' environment among populations of a species does not change).

These ideas may correctly explain unchanging species, but they certainly do not predict them. Not many plants, for example, can avoid unpleasant environments. Even in animals, habitat selection causes stasis only when a familiar habitat can be found in a changing world, but this must often be impossible (why else is there extinction?). Disruptive selection is even less plausible, for the argument assumes that there is never any change in the 'average' habitat among populations, and that directional selection cannot apply over a species' entire range. The former idea seems unreasonable, and the latter clearly wrong. It is easy to think of geographically widespread forms of natural selection, including the introduction of new parasites or diseases, selection for crypsis, sexual selection and mutations that increase fecundity.

The second tenet — and the only non-darwinian one — is that large changes of morphology are allowed only by speciation. There are, of course, good darwinian reasons for expecting an *association* between morphological change and reproductive isolation. Natural and sexual selection can cause reproductive isolation as a by-product, the classical explanation of adaptive radiations. Also, as Douglas Futuyma has noted, when a population becomes reproductively isolated it may keep adaptations that would normally be diluted away by gene flow from the rest of the species. This would likewise cause an association between speciation and morphological change. But Eldredge proposes something more radical: that reproductive isolation actually *triggers* adaptive change in geographically isolated populations.

Reproductive isolation is, however, a property of pairs of species that is seen only when they become sympatric, and it is difficult to see how its evolution in allopatry could somehow cause a species to acquire new adaptations. Indeed, Eldredge himself is hard pressed to come up with an explanation, suggesting only that new species could evolve rapidly by competing with their relatives. But such character displacement will affect only adaptations that reduce competition, and fails to account for many other features, especially those distinguishing related but geographically isolated species (for example, flightlessness in island birds). Because Eldredge has largely abandoned the only other non-darwinian part of punctuated equilibrium (species selection), the weakness of this argument brings down the last barrier separating his theory from neo-darwinism.

Unless *Macroevolutionary Dynamics* was intended as yet another revision of punctuated equilibrium, the reasons for the book's existence are unclear. Most of the material has been widely discussed elsewhere, the only novel element being a long and rather abstract discussion of the role of communities and ecosystems in evolution. The extensive philosophizing, as well as the dearth of biological examples supporting Eldredge's arguments, suggest that punctuated equilibrium is gradually losing its connection with the real world of organisms. □

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Mischance for Mr Darwin

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The Correspondence of Charles Darwin, Volume 4 1847–1850. Edited by Frederick Burkhardt and Sydney Smith. *Cambridge University Press: 1989. Pp. 711. £32.50, $32.50.*

THE fourth volume of Charles Darwin's correspondence covers a period of four years in which, although he was intensely active, comparatively little went on of obvious excitement for the reader. Very little of this volume will give material for sensationalist literary writers (although I can recommend Darwin's use of chloroform in childbirth and his heroic remedies for toothache — did they simply kill the tooth?). This was one of those periods of heavy slogging work, with slow progress, and doubts developing about earlier ideas, that make up so much of any working scientist's life, and are usually characterized afterwards (sometimes rightly) as periods of consolidation. He had already sketched out his ideas on evolution, and published his *Journal* and his geological volumes. In the present period he published his contribution to the *Admiralty Manual of Scientific Enquiry* (1849).

All the usual mischances of life were bothering him in the usual way. Parcels of priceless specimens on loan to him went astray, guests had to be instructed on how to get to Down, references were required for friends for various jobs (he refused flatly to write one for someone he didn't know), there were difficulties over shares and farm rents and Emma Darwin's trust fund, his artist was (he thought) inexcusably dilatory, the printers of the *Admiralty Manual* made a hash of his contribution. But in addition his health was often very poor, and much time was spent on treatments which made only temporary improvements. His wife's pregnancies were sometimes difficult, scarlet fever attacked the family, one child had a convulsive fit, and his deeply respected father died. No wonder that he reported to Hooker on one occasion that "all things [have] gone on badly".

All this time he was keeping up his vast correspondence — with nurserymen and amateur breeders about variation, hybridity and inheritance, with other naturalists on effects of acclimation, taxonomic variation, geographical distribution, coral reefs, transported boulders (erratic blocks), the maximum inclination at which a lava stream could solidify, craters of volcanoes, raised sea beaches, salt from salinas, rock cleavage and foliation, ripple-marks on the sea bed at various depths, and especially the so-