populations such as the well-characterized strain WI-38. Yet it took 10 years for the production of polio vaccine in WI-38 to be accepted by the Division of Biologics Standards (now the Center for Biologics Evaluation and Research of the U.S. Food and Drug Administration), even as the risk of SV40 exposure continued.

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On Punctuated Equilibria

In their technical comment of 6 December (p. 1748) on a report of punctuated patterns of evolutionary change in a laboratory culture of *Escherichia coli*, Jerry A. Coyne and Brian Charlesworth perpetuate several incorrect perceptions of the original notion, and subsequent discussions, of punctuated equilibria (*1*).

They are correct that punctuated equilibria apply to sexually reproducing organisms and that morphological evolutionary change is regarded as largely (if not exclusively) correlated with speciation events. However, they err in suggesting that we attribute stasis strictly to "developmental constraints," which represent only one of a set of possible mechanisms that we have suggested for the causes of stasis. Others include habitat tracking and the internal structure of species themselves [for example, (*2*)].

Habitat tracking [as when the distributions of Pleistocene species oscillate on a north-south gradient in concert with global temperature fluctuations (*3*)] demonstrates the stability of species morphologies in the face of environmental change as long as suitable habitat can be found and occupied. Although habitat tracking does not rule out developmental homeostasis, it suggests that stabilizing selection, rather than directional selection, will be the rule as long as species can continue to "recognize" and occupy suitable habitat elsewhere under a regime of environmental change.

Moreover, the very structure of species, broken up into semi-isolated populations each integrated into different ecosystems, should for the most part preclude the possibility of any widespread species evolving *as an entirety* in any one particular direction (*4*). Genetic theory should have explicitly predicted stasis in numerically rich species. B. S. Lieberman *et al.* (*5*) present empirical data suggesting that stasis in two species lineages of Devonian brachiopods was governed more by such constraints of species organizational structure than by habitat tracking.

Coyne and Charlesworth further state that "the punctuated changes in the fossil record are said to occur via 'species selection,' in which descendant species rapidly supplant their ancestors"—a statement they attribute to Santiago F. Elena *et al.* (Reports, 21 June 1996, p. 1802). Species selection is one of a set of models proposed to explain evolutionary trends in the fossil record—given the absence of strong evidence that long-term trends are merely the accumulated outcome of within-species gradual directional evolution (*1*, *2*, *6*). Replacements of ancestral species by presumed descendants (which usually appear "punctuational" in the fossil record) are generally interpreted as ecological or biogeographic

replacement events [for example, (*2*, *7*)] and not as the result of differential species births, direct competition, or any other phenomenon that might be considered "species selection."

Coyne and Charlesworth conclude with a critique of punctuated equilibria—asserting that when one excises the "novel and non-Darwinian" mechanisms of punctuated equilibria, "the theory reduces to the noncontroversial statement that morphological evolution sometimes occurs episodically." The documentation that (i) morphological stasis is the overwhelming rule in the fossil record of metazoan species and that (ii) morphological change does indeed seem to be correlated to a strong and unexpected degree with true speciation constitutes a two-pronged empirical pattern that requires careful analysis. To so mischaracterize punctuated equilibria not only impugns the significance of our model, it misstates the dominant empirical evolutionary pattern of the history of life itself.

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Response: In the past 25 years, Eldredge and Gould have proposed so many different versions of their theory that it is difficult to describe it with any accuracy. Initially, punctuated equilibrium theory described an ubiquitous pattern of morphological stasis in fossil lineages, interrupted by rare but rapid bursts of change that accompanied the splitting of lineages (speciation). These rapid changes were also said to be random with respect to long-term evolutionary trends, which were caused by the differential persistence of species having different traits (*1*).

Our concern as evolutionary geneticists (*2*) has been with Eldredge and Gould's repeated revisions of the *mechanisms* proposed for stasis and rapid evolution. Punctuated equilibrium originally attracted great attention because it invoked distinctly non-Darwinian mechanisms for stasis and change (*3*). These mechanisms were said to decouple macroevolution from microevolution, leading to Gould's pronouncement that "if Mayr's characterization of the synthetic theory [of evolution] is accurate, then that theory, as a general proposition, is effectively dead, despite its persistence as textbook orthodoxy" (*4*, p. 120). Yet many evolutionists saw no obvious contradiction between punctuated pattern and Darwinian process: Stasis can result from stabilizing selection (for example, long periods of environmental stability); rapid evolution can result from selection-driven responses to sudden environmental change or invasion of new habitats; and the association

of morphological change with speciation can result from the fact that both are promoted by adaptation to new environments (*5*).

Eldredge and Gould originally ascribed stasis to developmental constraints: Organisms could not respond to selection because their developmental programs were inherently resistant to change (*1*, *3*, *4*, *6*). This non-Darwinian explanation, which was severely criticized (*5*), was supplanted by the notion (*7*) that species show morphological stasis because their constituent populations adapt to diverse local habitats, resulting in no net change in the "average" phenotype of the species. This idea is inconsistent with their view that developmental constraints often prevent adaptive change.

Gould and Eldredge now suggest that stasis may be caused by species tracking their habitats as the environment changes [an idea proposed earlier by Maynard Smith (*8*)], which is a form of stabilizing selection. They also appeal to Sewall Wright's shifting balance theory of evolution, suggesting that a species composed of partially isolated populations cannot evolve as a unit. This suggestion appears to be a misinterpretation of Wright's theory, which he consistently presented as a mechanism for adaptive transformation of an entire species (*9*). Partial isolation of populations resulting from spatial separation does *not* preclude favorable or neutral mutations from spreading through an entire species (*10*). The suggestion by Eldredge and Gould that "[g]enetic theory should have explicitly predicted stasis in numerically rich species" contradicts theoretical arguments showing that natural selection is most effective in large populations (*11*) and does not account for abundant evidence from artificial selection experiments confirming this prediction (*12*).

Eldredge and Gould have proposed an equally diverse array of explanations for rapid "punctuated" evolution. It was initially ascribed to the breakdown of developmental constraints in small, speciating populations (a non-Darwinian process) (*1*) and later to the occurrence of single mutations with large effects (including homeotic mutations) or to chromosome rearrangements affecting gene expression (*3*, *4*, *6*). Gould, for example, asserted (*4*, p. 127)

> I envisage a potential saltational origin for the essential features of key adaptations. Why may we not imagine that gill arch bones of an ancestral agnathan moved forward in one step to surround the mouth and form proto-jaws?

But Gould and Eldredge later said (*13*, p. 226; see also *10*, p. 66) that "Opponents now accept that punctuated equilibrium was never meant as a saltational theory. . . ." Yet even this statement was later qualified. Commenting on the experiments of Elena *et al.* in *E. coli* (*14*), which showed punctuated change in cell size resulting from sporadic mutations of large effect, Gould noted that these results are "deeply similar to [punctuated equilibrium]. There is an underlying commonality in the style of change" (*14*). Eldredge and Gould now appear to see no connection between punctuated equilibrium and the results of Elena *et al.*

Eldredge and Gould's disclaimer about the role of species selection in punctuated equilibrium theory (our attribution of this idea to Elena *et al.* was a typographical error) is not consistent with their numerous published statements that species selection is a major engine of macroevolution (*4*, p. 119; see also *3*, *6*).

If a scientific theory is to be of any value as a tool for exploring the real world, it must have some stability as a set of propositions open to empirical test. Punctuated equilibrium has undergone so many transformations that it is hard to distinguish its core of truth from the "statement

that morphological evolution sometimes occurs episodically."

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Molecular Chirality Control and Amplification by CPL: Correction

In our report "Dynamic control and amplification of molecular chirality by circular polarized light [CPL]" (20 Sept., p. 1686) (*1*), a sentence in column 2 on page 1687 could lead to misinterpretation. The sentence reads, "A large pitch (p = 580 μm based on helical twisting power 0.1) is seen in the cholesteric phase as a result of low resolution of 1 by CPL irradiation." This might be read as if a pitch of 580 micrometers had actually been determined.

Such a large pitch cannot be measured directly, so the following procedure was used. The cholesteric phase with a large pitch was based on the observed texture and control experiments where an increase in pitch of the cholesteric texture with decreasing enantiomeric excess of the dopant was seen. We then calculated what the pitch of the cholesteric phase must be after irradiation by CPL on the basis of the helical twisting power and the enantiomeric excess determined by circular dichroism. We are grateful to G. B. Schuster of the Georgia Institute of Technology for bringing this matter to our attention.

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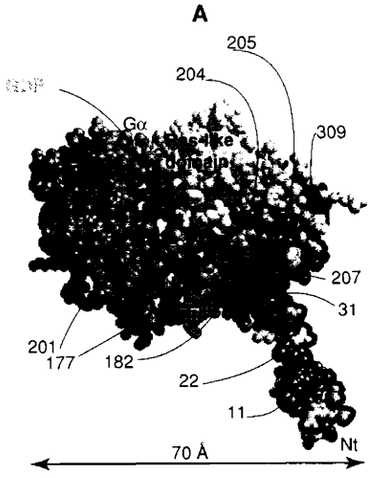
Corrections and Clarifications

In the 14 March News & Comment article "Court invalidates expert panel report" by Jocelyn Kaiser (p. 1560), the judge's name should have been Paul L. Friedman and the date of the preliminary injunction 5 March.

In figure 3, A and D, on page 383 of the report "Receptor and βγ binding sites in the α subunit of the retinal G protein transducin" by R. Onrust *et al.* (17 Jan., p. 381), the left edge was inadvertently cropped. The correct figure 3A appears below. In figure 3D, the label "GDP" should have appeared at the top left end of the line leading to guanosine diphosphate, which is highlighted in pale yellow.



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