

environmental stress<sup>7</sup>. The Suregei and Guomde Level speciation events occur at times of lacustrine regression. The various molluscan lineages have similar vagilities, and occupy similar environments. All would therefore experience both isolation and stress during a major regressive phase. A broadly synchronous evolutionary response in all lineages is therefore reasonable.

Charlesworth and Lande are incorrect in assuming that evidence for substantial heritable variability in morphological characters implies that morphological stasis cannot be attributed primarily to developmental constraint. The question is not so much whether variation exists for selection to work on, but rather what, if anything, selection can actually *make* of this variation in nature. Developmental constraint may well block long-term directional morphological trends in large populations, even though the genetic potential for such evolutionary transformation exists. This is at least one tenable explanation for the fact that, in the fossil record, such long-term morphological trends are rare, or absent, in continuous phyletic sequences.

Morphological stasis is not, therefore, a reflection of selective neutrality of phenotypes or simple stabilizing selection. The idea that most phenotypes are selectively neutral is not widely held, nor supported by Charlesworth and Lande's own references<sup>8</sup>. Neither is simple stabilizing selection an adequate explanation for long term morphological stasis. Many species — perhaps most — exhibit stasis for millions of years. The idea that such species experience an unchanged selection regime for these immense spans of geological time seems inherently unlikely. Conventional neo-Darwinists have similarly recognised that simple stabilizing selection is an inadequate explanation for the analogous situation of range-wide phenotypic coherence in modern species; they therefore invoke developmental constraints of one form or another to explain this coherence<sup>9</sup>. In asserting such constraints to be the principal element in long-term *temporal* stasis, punctuationalists are following the lead of conventional neo-Darwinian students of *geographic* variation.

Certain neo-Darwinists have recognised the primacy of developmental constraint in maintaining evolutionary stasis. For example Rendel<sup>10</sup> states that "when a canalised character is to be changed . . . the unfitnes introduced when the fine adjustment between developmental processes is destroyed will always be counteracting directional selection . . . directional selection must always introduce unfitnes. This antagonism between fitness and directional selection will have to be taken into account in interpreting . . . long [term] stability. . ."

Charlesworth and Lande suggest that the greatly enhanced phenotypic variability I

document during periods of morphological transformation in the Turkana sequence simply represents a direct developmental response to increased heterogeneity of the environment. No evidence of any similar response is known from any modern population of the lineages concerned, even in the extremely wide range of environments many of them currently occupy; it hardly seems necessary to invoke them in this case. They then suggest that this variability might be due to 'mixing' of more- or -less evolved and stratigraphically adjacent populations. But as I point out<sup>5</sup>, the faunal units concerned seem to be undisturbed life assemblages with no evidence of reworking, and much of the variability derives from the presence of phenodeviants bearing as little relationship to the derived species as they do to the ancestral form. This does not suggest that the increased variability I document is due to the mixing of the products of a conventional neo-Darwinist evolutionary 'march of means'. It suggests pronounced developmental instability in the transitional forms. Charlesworth and Lande finally concede that this increased variability may represent developmental instability resulting from strong directional selection away from a zone of canalization — which is, after all, the explanation I offered in my original paper.

Ginzburg and Rost are correct in considering the gradualist and punctuational models to be, in part at least, alternate hypothesis about the *distribution* of rates of evolutionary change. But the critical issue in this context is the extent to which observed rates of change in a given interval can be extrapolated up into rates of change occurring in any longer time interval.

If Ginzburg and Rost's bacteria were evolving according to the gradualist model, the amount of change observed over any given sample interval could be extrapolated up to account for the net change occurring over any larger sample interval. If the bacteria were evolving according to the punctuational model, the amount of change observed over any given sample interval could not be extrapolated up into the net amount of change observed over a much larger interval. In the latter case, if a given sample interval happened to include a 'speciation event', estimated rates of net change over a larger sample interval would be much too high (long periods of stasis would occupy most of a longer time period). If, more likely, one happened to sample a period of stasis, extrapolated rates of change for a larger sample interval would be much too low, that is effectively zero.

The sampling time scale is therefore irrelevant to the punctuationalist-gradualist controversy. In any case, much more than simple differences in rate of evolutionary

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## 100 YEARS AGO

On Tuesday evening, April 11, the public thoroughfare stretching between Hatton Garden and the Old Bailey was lighted for the first time by the electric light. The novelty of the installation was the fact that the incandescent system had been adopted in preference to the arc system. The Holborn street lamps each contain two of Edison's bulbs suspended from a cross bar running through the top of the lantern. The light is of a golden tinge like gas, but much purer, brighter, and steadier. The lamps were switched on and off with the greatest ease, and altogether the experiment was a complete success.

Mount Etna has again been in an active condition. An eruption and a rain of ashes (rampilli) has quite recently alarmed the neighbouring inhabitants.

from *Nature* 25, 564-5; April 13, 1882.

change are involved in the differences between the punctuated and gradualist models: for example, the size of the populations in which significant evolutionary changes is thought to occur is also a critical distinction between these two models<sup>11</sup>.

Lindsay suggests that selection pressure is a *sine qua non* of evolutionary change. He ignores such staples of conventional neo-Darwinism as founder effect, genetic drift, mutation pressure and the appearance of 'super fecund' mutants, all of which phenomena are thought to effect evolutionary change irrespective of — or even in opposition to — selection pressure. But Lindsay ignores these, and suggests that the 'variation in rates' I observe in the Turkana section are the simple consequence of variations in the Suregei and Guomde Level although speciation events occupy only  $5 \times 10^3$ – $5 \times 10^4$  yrs represented by the Turkana sequence. In other words, according to Lindsay, for only 1 per cent or 0.1 per cent of the time represented by the Turkana Basin sequence were selection pressures adequate to elicit any evolutionary response in any lineage. For the remaining 99 per cent or 99.9 per cent of the time, selection pressures were 'so low or minimal' — for 5 Myr — that no significant change occurred whatsoever in any lineage. Lindsay describes this as unsurprising. I find it incredible! In fact, even the most conventional of neo-Darwinists would agree that rates of evolutionary change are controlled by many more factors than simple fluctuation in selection pressures.

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