and one diffuse horizon, within a variety of unrelated molluscs. This certainly is a strange coincidence from an evolutionary point of view, although entirely plausible from the ecophenotypic point of view if a major change in lake water chemistry and concentration affecting an arm of a large lake was involved. The long stratigraphic range of those stocks still represented today makes it clear that they were present in the region throughout the entire time interval, whereas all of the morphologies derived from them during the brief intervals of morphologic change lasted a very short time — this situation is entirely consistent with either local speciation under unknown physical conditions, or under locally isolated conditions involving different enough conditions to produce distinctive ecophenotypes. ☐

Morphological stasis and developmental constraint: no problem for Neo-Darwinism

from Brian Charlesworth and Russell Lande

THE critical issue stemming from Williamson's papers is the explanation of stasis and increased variability associated with the episodes of change. The view he holds, that stasis is due to developmental constraints[2], is equivalent to saying that the characters concerned lack genetic variability, so that selection is ineffective. But there is evidence for substantial levels of heritable variability in most morphological characters that have been studied[1,4], including snail shell traits[5,6].

Stasis cannot, therefore, be explained by developmental constraints; either the characters are selectively neutral and population sizes are too large for genetic drift to be effective, or natural selection acts towards an intermediate optimum phenotype. Direct evidence for such stabilising selection on shell characters in snails was provided by the early biometricians[7,8], and similar data is available from many other traits[9]. Williamson is also incorrect in implying that stabilising selection has only recently been invoked by neo-Darwinists as an explanation of stasis; for example, Simpson (ref. 10, pp148–150 and 327–355) discusses this question at length.

The observation of increased variability at times of rapid change could have several explanations not discussed by Williamson. He neglects the possibility that it could be caused by a direct developmental response to increased heterogeneity of the habitat, or by the effects of temporal fluctuations during individual lifetimes, at periods when the environment is changing. Furthermore, since fossils classed as belonging to one geological horizon almost certainly span many generations, rapid evolutionary change over the period of sampling could generate increased variation. For these reasons, we are not convinced that the increased variation is a genuine evolutionary phenomenon. But even if this is granted, there would be no difficulty for neo-Darwinism. Selection experiments have demonstrated that stabilising selection can enhance developmental stability, or zones of 'canalisation', around an optimum phenotype by altering the patterns of genetic and non-genetic variation[11–13]. Relaxation of stabilising selection[14], and/or directional selection away from a zone of canalisation[15–17], would then be predicted to produce an increase in phenotypic variability, until the population is recanalised by stabilising selection around a new optimum phenotype[18] (Kirkpatrick, *Am.Nat.*, in press). However, many characters under weak stabilising natural selection are not appreciably canalised in their development, and can be artificially selected to change a great deal without substantially increasing their variability[4]. The exact temporal patterns of variability expected thus depend on factors whose relative weights are difficult to assess for fossil material. ☐

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Are 'punctuations' artefacts of time-scales?

from Lev R. Ginzburg and Jay D. Rost

WE would like to give a brief explanation of why the 'punctuated' pattern of evolutionary change seen in Williamson's and other, less well documented, findings may well be an artefact of the sampling time scales. A more detailed argument is presented elsewhere[1].

Consider the following imaginary example: A population of *E. coli* is cultivated in a chemostat under a fixed environment for a number of years. Assume that we sample cells from the culture with different time intervals to discover whether the culture has evolved or not with respect to a quantitative trait. If we do this, bi-weekly, for instance, we will find most of the time that nothing has happened. Occasionally will we find changes that appear as punctuational, since the replacement time in a chemostat is typically much shorter than two weeks. Now, if we make our observations hourly, the details of the replacement process will be obvious and the evolutionary change will appear gradual. If we make only yearly observations, the process may look gradual for a different reason; we would average a number of changes during the year into one yearly change.

If we repeat the experiment with a number of isolated chemostats, and carry out bi-weekly sampling for a period of a few months, we expect most of the populations to show no change, but some of them will evolve away from the majority. This may look like a punctuative "speciation event." Too fine or too coarse a time scale will always lead to a more "gradual" picture, whereas at some intermediate scale, the process will appear as "punctuational." In the work of Williamson the mean time scale resolution is between 30,000 and 35,000 years. (The value is the sum of the time spans of segments 2, 3, 4 and 5, about 2.5 Myr,

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0028-0836/82/150610-02$01.00