Evolution

Darwinism stays unpunctured

John Maynard Smith

OVER the years, palaeontologists have tended to distrust the account of the mechanisms of evolution given by population geneticists. The most recent challenge was the theory of punctuated equilibria¹. This asserted that the fossil record reveals that evolutionary changes are not gradual and continuous, but that long periods in which little or no change occurs (stasis) are interrupted by rather sudden changes (punctuation). It is further claimed that the sudden changes occur at times of lineage splitting (speciation), and it was at first argued that they occurred in isolated peripheral populations. Finally, in some more extreme statements of the theory^{2,3}, it is argued that the changes are not brought about by natural selection within populations, and that they are random relative to the overall trends of long-term evolution. But the latest contribution to the debate, from P.R. Sheldon on page 561 of this issue⁴, suggests that punctuation is not a universal pattern.

If punctuational changes are random, then the main features of evolution are not the summed consequences of changes caused by selection within populations, of the kind that can be studied today: macroevolution is decoupled from microevolution. How, then, is the adaptation of existing organisms to their ways of life to be explained? One response⁵ has been to deny that adaptation is as pervasive as it seemed to Darwin, and has seemed to most naturalists since. But adaptation cannot be wholly denied. It has therefore been suggested that it arose by 'species selection'. This is a process exactly analogous to selection within populations, in which individuals are replaced by species, birth by speciation, death by extinction, and mutation by the non-adaptive punctuational changes that occur when new species arise.

Geneticists, needless to say, have been unimpressed by the latter part of this argument. They have pointed out that species selection is quantitatively inadequate to account for the degree of adaptation observed, and that the claimed absence of intermediates between species is disproved by the facts of geographical distribution: every degree of difference can be observed between isolated populations from almost no difference up to differences as great as that separating good sympatric species. They have also noted that, in the two studies most often quoted in support of punctuational theory (Eldredge⁶ on trilobites, and Williamson⁷ on the molluscs of Lake Turkana),

populations intermediate between the earlier and later 'species' were found. These populations could not have been small, and it is therefore hard to see how the changes that took place in them could have been caused by anything except within-population selection (unless, as has been suggested for Williamson's molluscs, the changes were not genetic at all).

It would be quite possible, however, to accept the claim that the typical pattern of change is one of long periods of stasis interrupted by brief periods of rapid change, without also accepting the ideas of non-adaptive change, species selection,

Gnemidopyge, Ordovician trilobite from central Wales. (Courtesy of P.R. Sheldon.)

and the uncoupling of macro- and microevolution. This is a question for palaeontologists to settle.

Sheldon in this issue⁴ reports his study of eight genera of Ordovician trilobites, over about 3 million years, from central Wales. The classification of the group into species is largely based on the number of pygidial ribs — features of the exoskeleton (see figure). Sheldon examined about 15,000 specimens, from seven sections and 400 sampling sites, and was able to count the ribs of about 3,500 of them. In all eight genera, the number of ribs increased during the period, although there were changes of rate and several temporary reversals of direction.

The overall difference between the earliest and latest populations studied by Sheldon is such that they had, in all cases, been placed in different species, and in one case in different genera. But in no case is it possible to recognize a punctuational event marking the transition from an earlier to a later form. Most populations are intermediate between the

previously described species, and some are sufficiently variable to include specimens that, according to the previous criteria for classification, would have been placed in different species. However, these variable populations are probably not to be interpreted as mixtures of two species, because most are unimodal in rib count, and the few that are not can best be interpreted as reflecting a relatively rapid shift in mode. In fact, Sheldon thinks that no genus was represented by more than one species at any one place and time, and there is no sign of lineage splitting in any of the genera.

These results have implications for the application of linnaean nomenclature to fossils. Communication requires that we give names to fossils, and convenience suggests that they had better be linnaean names. Before Sheldon's study, these trilobites could successfully be assigned to linnaean species, and, as he remarks, this could have been interpreted as evidence for punctuation and stasis. His new, more detailed study shows that this interpretation is unjustified. The conclusion is that, no matter how we decide to name fossils, we should make statements about rates and patterns of evolution only on the basis of a statistical analysis of populations, and not on the presence or absence of named species or genera. I do not think that the attempt to explain morphological evolution by species selection can survive in the face of results of this kind. But there never was much sense in the idea anyway.

Stasis, however, is a different matter. As David Wake pointed out during an earlier debate on this topic, the existence of sibling species demonstrates the occurrence (but not, of course, the universality) of stasis. For example, the fruitflies *Drosophila melanogaster* and *D. simulans* are hard to distinguish morphologically: the only plausible explanation is that neither has changed appreciably in morphology since their divergence from a common ancestor several million years ago. Geneticists have tended to explain such stasis by normalizing selection for an unchanging optimum, and palaeontologists by developmental constraints: no doubt we shall continue to argue about their relative importance. But my own view, which will not be universally shared, is that we can forget about new paradigms and the death of neodarwinism. □

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3. Stanley, S.M. *Macroevolution* (Freeman, San Francisco, 1979).
4. Sheldon, P.R. *Nature* 330, 561–563 (1987).
5. Gould, S.J. & Lewontin, R.C. *Proc. R. Soc. B* 205, 581–598 (1979).
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7. Williamson, P.G. *Nature* 293, 437–443 (1981).

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