it is possible greatly to alter the degree of sexual isolation of *D. pseudoobscura* from its close relative *D. persimilis* by artificial selection in less than 20 generations[12]. In the same way, selection of different parts of an originally freely interbreeding *Drosophila* or house fly population for bristle number, climbing ability or the ability to tolerate insecticides can lead to the incidental evolution of considerable reproductive isolation within a few tens of generations[13-15]. Even *Drosophila* populations kept at different temperatures for five years in the laboratory evolve considerable reproductive isolation among themselves[16]. These are periods trivial in relation to those interpreted by Williamson and others as 'punctuations' in the fossil record which can only be explained by new evolutionary mechanisms.

The efficacy of gradual evolutionary change in producing genetic subdivision and the reduction of gene flow in natural populations subject to the forces of gradual selection is particularly well seen in plants. Some annual grasses have evolved an ability to grow on mines polluted by concentrations of copper high enough to kill populations not exposed to this selective agent. The grasses on the mine flower about a week earlier than do the surrounding non-tolerant populations and have an increased ability for self-fertilization. These genetic differences — which have evolved in the one hundred years since the mines were opened — are enough to lead to considerable reproductive isolation between mine populations and their ancestors in the nearby pastures[17].

Once evolutionary change in the fossil record — even in a record as well characterized as that unearthed by Williamson — is placed in the context of the known ability of living organisms to respond to the forces of classical darwinian natural selection, it becomes clear that it is not necessary to invoke evolutionary forces 'qualitatively different' from those emphasized by Darwin. Depending on the time scale to which the investigator is accustomed, one man's punctuated equilibrium may be another's evolutionary gradualism. Williamson describes an extraordinarily complete page in the history of evolution but its contents do not force us to change our views on the genetic mechanisms of the origin of species. □

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Diversity changes of marine organisms through the Phanerozoic

from A. Hallam

ONE of the most important palaeontological debates of the past decade appears to have been resolved in an article published in this week's *Nature* (see page 435). The issue at stake is whether the diversity of life has increased substantially in the five hundred million years since the Cambrian period or whether it is only imperfections in the fossil record that give an appearance of increasing diversity while the true pattern is of equilibrium or even decrease in diversity.

The two chief protagonists in the debate, David Raup and James Valentine, are now in agreement and have joined forces with two other American palaeontologists, John Sepkoski and Richard Bambach, who have made notable contributions to the subject. Together they demonstrate that there is indeed, in their choice of phrase, a genuine "evolutionary signal" discernable in the fossil record of marine organisms despite possible preservational and taxonomic noise. The agreement is a firm vote of confidence in the reliability of the fossil record even though the conclusion drawn from it is a sort of compromise — diversity has increased since the Cambrian but the pattern is not one of a simple rise.

It is the existence of such massive data compilations as the American *Treatise on Invertebrate Paleontology* and the Geological Society of London's *The Fossil Record* that have allowed palaeontologists to analyse the pattern of diversity change of preservable organisms from the Cambrian to the present. To obtain reliable estimates of the extent of change through time it is clearly desirable to be able to eliminate possible complications due to preservational bias and the problems inherent in making taxonomic distinctions among fossils.

Originally, Valentine made the claim that marine invertebrate generic and family diversity increased substantially from the early Palaeozoic to the Cenozoic. This was challenged by Raup soon afterwards (*Science* **1977**; 1065, 1972). He argued that the large Mesozoic–Cenozoic increase may be an artefact. The Cenozoic record includes extant taxa, which biases it towards an overestimate, and preservational factors may have produced a major bias in the reverse direction further back in time. He generated a computer simulation model based on an increased probability of destruction of fossils with time, and showed that Valentine's data could be accounted for by postulating diversity rise from the Cambrian to a mid-Palaeozoic peak followed by a drop to an appreciably more modest level which remained stable through the Mesozoic and Cenozoic.

In a later paper (*Paleobiology* **2**; 289, 1976), Raup estimated the number of species described for each of the geological periods by tabulating new species reported in the *Zoological Record*, and established a strong correlation between apparent species numbers and the present areal distribution of rocks per system. This suggested that perhaps geological systems with more available rock have more species and hence more species are described.

In the analysis published this week, five independent measures of diversity, for different groups of organisms and different taxonomic levels, are shown to be highly inter-correlated, even when the ubiquitous correlation with time is removed. A simple underlying pattern is revealed of a rise from a low value in the Cambrian through the Palaeozoic, followed by a low Triassic value, after which there is a more or less accelerating increase through the Mesozoic and Cenozoic, the last era containing the highest diversity. The sharp drop at the end of the Palaeozoic is clearly the result of the Permian mass extinction. In sharp contrast the end Cretaceous mass extinction has no effect on the general trend. Above the family level the pattern of diversity change is different, due probably to the tendency for morphologically distinct groups to appear rapidly during the early phases of major radiations.

Palaeontologists will no doubt continue to argue about the meaning of diversity-change data, but at least they are now apparently assured that the data reflect the real world. □

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