genuine article[2]. For the future, however, there is an urgent need to improve our understanding of the influence of soil conditions on the course of succession, the mechanisms of colonization by typical calcicolous grassland species and the interaction with management treatments. If the simple study of Gibson, Watt and Brown[11] can stimulate more detailed work on these outstanding problems then we may be on the way to providing an effective response to the implications of 'agricultural retirement' for conservation throughout Britain.

References

1 Milne, R. (1987) *New Sci.* 116, 10–11

2 Sutherland, W. and Gibson, C. (1988) *New Sci.* 117, 70

3 Smith, C.J. (1980) *Ecology of the English Chalk*. Academic Press

4 Bush, M.B. and Flenley, J.R. (1987) *Nature* 329, 434–436

5 Wells, T.C.E., Sheail, J., Ball, D.F. and Ward, L.K. (1976) *J. Ecol.* 64, 589–626

6 Ratcliffe, D.A. (1984) *New Phytol.* 98, 73–100

7 Lloyd, P.S. and Pigott, C.D. (1967) *J. Ecol.* 55, 137–146

8 Cornish, M.W. (1954) *J. Ecol.* 42, 359–374

9 Hope-Simpson, J.F. (1940) *J. Ecol.* 28, 386–402

10 Keever, C. (1950) *Ecol. Monogr.* 20, 230–250

11 Gibson, C.W.D., Watt, T.A. and Brown, V.K. (1987) *Biol. Conserv.* 42, 165–183

12 Wells, T.C.E. (1983) In *Conservation in Perspective* (Warren, A. and Goldsmith, F.B., eds), pp. 215–232, John Wiley

13 Graham, D.J. and Hutchings, M.J. *J. Appl. Ecol.* 25, 253–263

14 Marrs, R.H. (1985) *Biol. Conserv.* 34, 307–332

15 Graham, D.J. and Hutchings, M.J. *J. Appl. Ecol.* 25, 241–252

The Nature of an Adaptive Radiation

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THE NOTION OF AN ADAPTIVE RADIATION is a familiar concept, whether it be on the small scale (e.g. colonization of an island) or a large scale (e.g. the radiation of the mammals after the extinction of the dinosaurs). However, relatively little is known about the nature of major radiations and how they occur. How long do they last, do they involve abnormally high rates of evolution, are they triggered by the origin of new adaptations, or are they opportunistic responses to the emptying of ecospace by a mass extinction?

The key phases of an adaptive radiation, such as that of the placental mammals 65 million years (Myr) ago seem to be the following[1,2]:

(1) An initial phase of rapid diversification from a single ancestor. The placental mammals arose and radiated modestly in the late Cretaceous, side by side with the dinosaurs, but then radiated rapidly into many new lineages in the Palaeocene and early Eocene (65–55 Myr ago).

(2) The establishment of a diversity of new body plans in this early phase. All of the existing mammal orders, from bats to whales, from carnivores to rodents, were established in this key 10 Myr period.

(3) Early extinctions amongst the initial elements of the radiation. As available ecospace fills up, it is assumed that levels of competition will increase, and a phase of 'weeding out' occurs. Amongst mammals, a number of early lineages flourished for a while, and then disappeared.

(4) A final phase of stabilization of the lineages. After the initial 10 Myr radiation phase, no new mammalian orders have arisen. The last 55 Myr have seen small modifications of the 20 or so basic placental body plans, but no serious innovations.

A new study by Erwin, Valentine and Sepkoski[3] looks at two much larger radiation events, each lasting for about 180 Myr: the early Palaeozoic explosion of marine invertebrates, and the second major phase of radiation in the sea, during the Mesozoic. They explore the nature of these two diversifications on a global scale, and study how they correspond and differ in terms of the rates of appearance of new body plans and the breadth of adaptation.

The first phase, from Vendian to late Ordovician times (620–438 Myr ago) raised the diversity of skeletonized marine animals (i.e. those with hard parts that fossilize readily) from one family to 470 families (Fig. 1). The second phase, from the Triassic to the Cretaceous (245–66 Myr ago) raised the level from about 200 to over 600 families. Thus, the overall number of families added in each phase is roughly the same, and it would be easy to assume that both radiations show similar patterns and rates of evolution.

However, at higher taxonomic levels, the two events turn out to be very different. The first radiation was dominated by the appearance of new orders, classes and phyla, while such novel higher taxa were much rarer in the second radiation.

The Vendian–Ordovician radiation occurred in two steps, one from Vendian to Cambrian times, and one in the Ordovician. As many as 10–11 new skeletonized phyla appeared in the Vendian–Cambrian interval (115 Myr) – such as Arthropoda, Brachiopoda, Mollusca, Echinodermata, and Chordata. Certain orders and phyla that arose in the Vendian and Cambrian did not last long. After the Cambrian, the only new skeletonized phylum was the Bryozoa (early Ordovician, but with (?) Cambrian ancestors). Soft-bodied phyla, such as the Sipuncula, Nematoda and Nemertea, apparently arose after the Ordovician, but their fossil records are too patchy for this to be certain[4].

In terms of classes, more than half of the 62 fossil and living invertebrate and vertebrate examples arose in the Vendian and Cambrian, and 54 of these 62 were in place by the end of the Ordovician. Appearances of new orders match this pattern, with more than twice as many

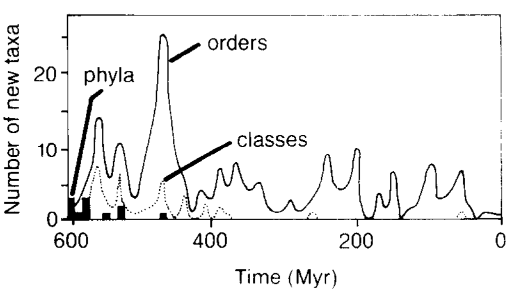

Fig. 1. The pattern of diversification of families of skeletonized marine animals. The graph shows the numbers of new phyla, classes and orders that appeared in each time interval. *Modified from Ref. 3.*

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(152) appearing in the Vendian–Ordovician interval, as in the Triassic–Cretaceous interval (73).

This second major radiation in the Mesozoic saw the appearance of no new skeletonized phyla or classes at all. The new post-Ordovician classes are nearly all vertebrates (four of 'fishes' in the Silurian and Devonian, Reptilia in the Permian, and Mammalia in the Eocene). The latter two are of course introductions of terrestrial groups into the sea. Half as many new orders arose in the Mesozoic diversification phase as in the early Palaeozoic, as just noted, and these include major groups of bivalves, gastropods, malacostracans, echinoids, fishes and reptiles (Fig. 1).

Whereas both phases are similar in terms of the rate of appearance of new families, the second phase shows only half as many new orders, and no new skeletonized classes or phyla at all. Erwin *et al.*[3] relate these profound differences to the scope of adaptive novelty. In the Vendian to Ordovician interval, there were great opportunities for the exploitation of new adaptive space in the sea. Novel morphologies arose and became established in essentially empty habitats. Through time, the potential number of habitats was increased, and individual habitats were progressively subdivided. For example, organisms became able to burrow deeper into the sea-bed sediments, or they grew longer stalks to allow filter-feeding higher in the water, or wholly new opportunities arose in reefs – habitats that had not existed before. In addition, each class of organisms diversified, on average, into more major adaptive zones through time.

The second phase of diversification was triggered by a massive extinction event at the end of the Permian. Again, ecospace was made available for radiation. However, all of the Palaeozoic phyla survived this event. Apparently, there was less scope for entirely new body plans to become established (i.e. new classes or phyla).

These studies suggest that some caution is required before calling such phases of diversification, 'adaptive' radiations. Indeed, Cracraft[5] has argued that this term prejudges the nature of a diversification pattern; instead it should simply be called a radiation. It is not clear whether the Vendian–Cambrian radiation followed a major mass extinction event or whether it was triggered solely by the appearance of major new adaptations. The Mesozoic radiation, however, like the classic radiation of the mammals, seems to have been enabled by a preceding extinction event that largely emptied the available ecospace. In a sense then, these two radiations were opportunistic, and it is a moot point how much the competitive ability, or 'progressive adaptations' of the radiating groups influenced the beginning of the radiation[6]. Can we say that we live now in an age of mammals because of their superior characters, or because the mammals were able to begin to radiate before the birds or the lizards, or the turtles did so in the Palaeocene? Can these radiations be related causally to single characters – 'key adaptations' – as is often assumed, or are they more complex affairs?

References

1 Stanley, S.M. (1979) *Macroevolution, Pattern and Process*, Freeman
2 Kemp, T.S. (1982) *New Sci.* 93, 4 Mar 1982, 581–584
3 Erwin, D.H., Valentine, J.W. and Sepkoski, J.J., Jr (1987) *Evolution* 41, 1177–1186
4 Conway Morris, S. (1985) in *The Origin and Relationships of Lower Invertebrates* (Conway Morris, S., George, J.D., Gibson, R. and Platt, H.M., eds), pp. 343–359, Oxford University Press
5 Cracraft, J. (1985) *Ann. Missouri Bot. Gard.* 72, 794–822
6 Benton, M.J. (1987) *Biol. Rev.* 62, 305–338