

PROGRESS AND COMPETITION IN MACROEVOLUTION

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(Received 13 August 1985, accepted 23 February 1987)

CONTENTS

I. Introduction	305
II. Improvements in competitive ability through time	306
(1) Evolutionary progress	306
(2) Increase in morphological complexity	307
(3) The expansion of life.	307
(4) Evolutionary trends	308
(5) Increased effectiveness of adaptation	309
III. Competition in microevolution	310
(1) Competition and natural selection	310
(2) The evolutionary effects of interspecific competition	311
(3) The effects of interspecific competition on community structure	311
IV. Competition in macroevolution	313
(1) Extinction and competition	313
(2) The Red Queen.	314
(3) The community paradigm.	315
(4) Evolutionary rates and competitive ability.	316
V. Competition and major ecological replacements	317
(1) Key adaptations and replacements.	317
(2) Patterns of ecological replacement.	318
(3) The evidence for double-wedge patterns (differential survival) in the fossil record	320
(4) The evidence that differential survival was caused by competition	326
(5) Alternatives to competition	327
VI. The problems of invoking large-scale competition	328
VII. Summary.	330
VIII. Acknowledgements	331
IX. References	331

I. INTRODUCTION

The history of life is often viewed by biologists and palaeontologists as illustrating the progressive nature of evolution, and this is an important element in explanations of major adaptive radiations and faunal replacements of the past. In many cases, it is stated that a key adaptation arose within a particular group which enabled that group to compete and replace a previously dominant group. The new group is then regarded as competitively superior to the one that it replaced and thus 'improved' in some way. For example, Schaeffer (1965, p. 318) wrote: 'The transition from one higher level of organization to another always involves some form of biological improvement for the same or a new way of life.' Stanley (1979, p. 184) states 'paleontologists have almost universally accepted the idea that certain body plans have been rendered obsolete during modernization of the world ecosystem. From evidence of adaptive morphology alone,

the progressive nature of evolution has long been recognized... ' Van Valen (1980, p. 291) views competition as a uniform process that occurs within species, between species and between supraspecific taxa, over time spans ranging from hours to hundreds of millions of years. Tappan (1971) has equated global displacements amongst phytoplankton, lasting for millions of years, with ecological succession in the present day.

The view that the history of life has proceeded to a large extent through competition and 'improvement' through time pervades many macroevolutionary theories. Particular examples include the idea that extinction is generally triggered by interspecific competition (Simpson, 1953; Mayr, 1963); the Red Queen hypothesis (evolution is driven by biotic factors; diffuse competition; Van Valen, 1973); the community paradigm (in which communities are moulded by interactions between species which have long-term stability: Olson, 1966; Valentine, 1968, 1973; Bretsky, 1969; Boucot, 1975, 1978); the idea that levels of competition within different groups of organisms control their overall rates of evolution (Stanley, 1974, 1977); and the view that most major ecological replacements in the past have been associated with large-scale competition (Simpson, 1944, 1953; Stebbins, 1974; Stanley, 1979; Maynard Smith, 1983).

The role of competition in macroevolution has been questioned recently (Gould & Calloway, 1980; Raup, 1982; Benton, 1983*a, b*, 1986). Macroevolution is understood here in a broad way, as the patterns and mechanisms relating to the origins of major taxonomic groups, rates of change, and the timing of major events in the history of life (Levinton, 1983). The aims of this paper are to argue that the history of life does not necessarily record an improvement in competitive abilities through time, that the idea of large-scale competitive replacements by the appearance of key adaptations is not supported by the evidence, and that the other macroevolutionary models that involve competition as a major factor are open to question. My intentions are to criticize the assumption that competition has a central role in macroevolution, and to question the use of microevolutionary concepts in describing major events in evolution.

II. IMPROVEMENTS IN COMPETITIVE ABILITY THROUGH TIME

(1) *Evolutionary progress*

Progress in evolution has been defined as 'systematic change in a feature belonging to all members of a sequence in such a way that posterior members of the sequence exhibit an improvement in that feature' (Dobzhansky *et al.*, 1977, chapter 16). Simpson (1949, 1953) and others have argued that it is not possible to identify examples of *uniform* progress; that is, steady advances in a single direction in a lineage. However, in his view, *net* progress is readily seen when a larger view is taken.

There have been many suggestions as to how progress in evolution could be assessed (Huxley, 1942, 1958; Simpson, 1949, 1974; Williams, 1966; Stebbins, 1969; Rensch, 1971; Ayala, 1974). Examples include measures of the relative information content of DNA, ecological dominance, invasions of new environments, expansion of life, replacements, improvements in adaptation or adaptability, the possibility of further progress, increased specialization, increased complexity, increase in general energy, and increase in the range and variety of adjustments to the environment. There are severe difficulties with a number of these measures (Schaeffer, 1965; Williams, 1966; Simpson,

1974; Dobzhansky *et al.*, 1977), and most of them are assumed to be maximised in humans. As Dobzhansky *et al.* (1977, p. 516) note, 'Organisms are more or less progressive depending on what criterion of progress is used. By certain criteria, flowering plants are more progressive than many animals.'

In modern Darwinian evolutionary theory, the idea of progress could be said to have very little meaning at all since, in any particular example, it is only a *post hoc* adaptive story, and it is in no way predictive of future trends. Before the modern synthesis, evolutionary progress was often viewed in various teleological ways: as a ladder that every lineage ascended of necessity (*scala naturae*; lamarckism), as a preordained path within a lineage (orthogenesis), or as a trend that is propelled and guided towards some goal (finalism; aristogenesis) (Gould, 1977; Bowler, 1984). None of these viewpoints is acceptable now in the neodarwinian paradigm (Dobzhansky, 1974; Simpson, 1974) and, with the removal of the law-like properties of progressionism, the concept becomes much weaker. Gould (1985) argues that progress is deeply engrained in Western thought, and that it 'continues to obsess evolutionists' despite the fact that there is little evidence for it. An identification of progressive improvement in the history of life suffers from the faults of the Whig interpretation of history: past events are viewed through present-day spectacles, and particular events, such as the appearance of humans, are made to seem inevitable. There is no evidence for that view (Schopf, 1979).

Many of the definitions of progress involve a belief that there has been an overall improvement in competitive ability through time; that different lineages improve their chances of survival during evolution, either relative to each other, or relative to their forebears. Four definitions of progress in evolution are particularly relevant here; increase in morphological complexity, the expansion of life, evolutionary trends, and the increased effectiveness of adaptation.

(2) *Increase in morphological complexity*

The idea that there has been evolutionary progress towards greater complexity through time is hard to quantify (Williams, 1966). There has clearly been an overall increase in complexity if we compare living organisms with the earliest prokaryote. However, specific comparisons are less clear. Is a present-day mammal more, or less, complex than an ancestral mammal-like reptile? The mammal brain may be more complex, but the skull of a mammal-like reptile contained more separate bones than does that of a mammal. It would be hard to define criteria by which to assess the relative complexity of such pairs of supposedly primitive and advanced organisms. Schopf *et al.* (1975) suggested that a tentative measure of complexity was the number of morphological terms used by biologists to describe an organism. In any case, as Stanley (1979, p. 184) notes, increase in morphological complexity is not a necessary correlate of improved competitive ability.

(3) *The expansion of life*

The expansion of life could be measured in terms of increases in the number of species, increases in the number of individuals, increases in total biomass, and increases in the total rate of energy flow (Simpson, 1949). It is clear that all of these measures have shown a net increase if we compare the present-day situation with the time at which life arose in the Precambrian, and it is possible that all of the measures have also

increased during the Phanerozoic (Ayala, 1974). Only the first measure, the number of species through time, has been assessed with any confidence.

There is now strong evidence that the total number of species has increased during the Phanerozoic, although not in a uniform way. This has been indicated for marine organisms (Valentine, 1969; Sepkoski *et al.*, 1981; Signor, 1982; Flessa & Jablonski, 1985), terrestrial plants (Niklas *et al.*, 1983) and terrestrial vertebrates (Benton, 1985 *a, c*).

The increases could be explained in terms of competition and niche division (resource partitioning and character displacement on the grand scale), particularly if the entire biosphere is equated with an ecosystem, and evolution is equated with ecological succession (e.g. Wilson, 1969; Tappan, 1970; Bretsky & Bretsky, 1975). According to this view, species turnover is associated with adaptive improvements, and turnover slows down when an equilibrium state of functional optimisation is approached. The alternative, and more probable, view is that species radiate rapidly when a breakthrough into new empty adaptive zones is achieved (Simpson, 1944, 1953; Newell, 1952; Mayr, 1963; Walker & Valentine, 1984). The expansion of life has probably been largely opportunistic, rather than simply the result of improved competitive ability and adaptive progress.

(4) *Evolutionary trends*

The idea that evolutionary progress is recorded in trends that are discerned in the history of life is widely held (discussed in Schopf, 1979). A trend is a 'persistent change in a given direction' (Raup & Stanley, 1978, p. 333). A trend is only identified *post hoc*, but the assumption is generally that it corresponds to a real evolutionary phenomenon; that the lineage from organism A to organism B demonstrates a progressive alteration in a morphological feature, or features, and that the alteration was induced by natural selection. For example, in the sequence from the early horse *Hyracotherium* to the living *Equus*, there are trends to larger size, more deeply rooted teeth, relatively longer legs, and less toes. Progress is observed, and adaptive explanations have been given, to the effect that *Hyracotherium* lived a secretive life in humid woodlands, feeding on leaves. Somewhat later, there were major climatic and habitat changes which led to the spread of open dry grasslands. Horses became bigger, fleet of foot (longer legs, less toes), and they changed to a diet of hard grasses (more deeply rooted teeth).

Many biologists and palaeontologists would argue that *Equus* is more advanced than *Hyracotherium* in most respects. Strong defences of the adaptively progressive nature of the record of life have been given (e.g. Rensch, 1959, chapter 7; Stanley, 1979, chapter 7). Stanley (1979, p. 184) finds it 'inconceivable that a typical Palaeocene family of adaptively primitive... mammals could flourish for long at high diversity if introduced into the modern world'. In other words, he regards the modern mammal as competitively superior to the extinct form. Van Valen (1985, p. 140) repeats this view: 'An average Cenozoic starfish would be expected to outcompete an average Paleozoic one.'

I disagree with this view of the progressive nature of evolution for four reasons. Firstly, this definition of progress as corresponding to an evolutionary lineage is *ad hoc* (Simpson, 1974). If the known phylogenetic sequence were reversed, and *Hyracotherium* were alive today, and if *Equus* had lived in the past, biologists might well identify a progressive trend and also find ready adaptive explanations for it. They might cite the

trends towards smaller size and a secretive life style in the forests, coupled with changes in diet and consequent modifications of the teeth. Directional change need not imply progress (Ayala, 1974). Secondly, the modern world is different from the Eocene world. A reincarnated *Hyracotherium* might fare just as badly today as would an *Equus* that was transported back in time. In their own worlds, *Hyracotherium* and *Equus* were well adapted. Who is to say that one is better than the other in general terms? Thirdly, adaptive improvements over the immediate ancestors should be demonstrated in their successors by means of functional arguments, and that has rarely been done (Walker & Valentine, 1984). It is merely a tautology to identify the later animal (the 'winner') as a 'superior competitor' in the absence of any other evidence (Schopf, 1979). Fourthly, it has been suggested that long-term trends might be epiphenomena of the differential survival of lineages, and not simply the result of organism-level natural selection for a particular adaptation (e.g. Stanley, 1979; Gould, 1980; Vrba, 1980; Cracraft, 1982).

Huxley (1942, 1958) argued that the case of human evolution was qualitatively different from all other trends since it was an example of truly open-ended progressive evolution. The sequence of evolution from invertebrate to human demonstrates the gradual acquisition of more and more advanced characters (backbone, jaws, lungs, amniote egg, internal thermoregulation, large brain). Progress along this line is measured by the overall increase in control over, and independence from, the environment. On these criteria, invertebrates and fish achieve low scores, while 'higher' mammals, and humans in particular, score well. However, this kind of criterion of progress has been criticised as being overly anthropocentric (Haldane, 1932; Simpson, 1974). What would the *scala naturae* composed by a goldfish look like?

Grant (1977, chapter 33) redefined progressive evolution as adaptation to environments successively further removed from the ancestral environment of life. So the line from invertebrate to human shows shifts from the ocean to the water's edge, from the water's edge to warm, damp lowlands, from there to dry warm areas, and finally to all parts of the Earth's surface, including the polar zones. If this definition of progressive evolution applies to other major trends, then the question of competitive ability is largely excluded. The emphasis shifts to the exploitation of new habitats as the cause of major 'advances' in evolution (e.g. lungs, amniotic egg, endothermy) rather than increases in competitive ability. It could be argued that, for example, the first reptiles were poor competitors: they opted out of the struggle in the coal swamps and invaded previously empty ecospace. The amphibians that they left behind (traditionally regarded as being less progressive than the reptiles) were better adapted and better competitors in the context of the coal swamp.

(5) *Increased effectiveness of adaptation*

The idea that adaptation becomes more effective through time within a single lineage forms part of one interpretation of evolutionary trends, as has just been discussed. In general terms, improvements in adaptation have been defined in terms of those features that reduce the likelihood of the extinction of a population through time (Thoday, 1958). The palaeontological record has been used in two ways in an attempt to demonstrate this point: first of all by a study of average global extinction rates, and secondly by a study of major ecological replacements in the history of life.

Raup & Sepkoski (1982) found that the total extinction rates (i.e. extinctions per million years) of families of marine animals declined through geological time. The so-called 'background extinction rate' (that is, the total family extinction rate at normal times, excluding extinction rates during mass extinctions) declined from about 4.6 families dying out per million years in the early Cambrian to about 2.0 families dying out per million years in the late Tertiary. If the rates are modified to take account of the increase in standing diversity during that span of time (i.e. divided by the number of families present at a particular time, to give the per-taxon extinction rate), the decline in extinction rates is even more striking. The per-taxon rate (or probability of extinction for any family) declined from 0.591 in the early Cambrian to 0.0013 in the Pleistocene (Van Valen, 1984).

Raup & Sepkoski (1982) interpreted their results in terms of an overall optimisation of fitness through evolutionary time which reduced the likelihood of extinction. Van Valen (1984), on the other hand, viewed his results as evidence for a minimisation through time of ecological interference.

Walker & Valentine (1984), and Flessa & Jablonski (1985), have argued that the data do not necessarily support such views. The lower family extinction rates may simply reflect increases in the average numbers of species in each family through time. If the average rates of extinction of species remain constant, and the species/family ratio increases, the family extinction rate inevitably declines. Flessa & Jablonski (1985) argue that, if background probabilities of species extinction are stochastically constant, speciose families will increase in numbers relative to species-poor families (Valentine, 1969; Raup, 1975).

Studies of other data sets suggest that total extinction rates do not always decline through time. For non-marine tetrapods, for example (Benton, 1985*a, b*), total extinction rates *increase* from the Devonian to the present day, and per-taxon extinction rates decline only marginally.

Generalized extinction rate data, then, do not unequivocally demonstrate a genuine improvement in the ability of organisms to resist extinction. The second kind of palaeontological evidence for increased effectiveness of adaptation comes from the study of major ecological replacements in the past. Many examples have been cited, and these involve ideas of large-scale competition and key adaptations, topics that deserve more detailed consideration below. First of all, there is some discussion of the nature of competition, in microevolution and in macroevolution.

III. COMPETITION IN MICROEVOLUTION

(1) *Competition and natural selection*

Competition is often regarded as an important prerequisite for natural selection. Darwin's original formulation of the theory of natural selection was that more individuals are born than can survive, and resources (food, or other necessities of life) are in short supply. Competition for those limited resources will occur, and the better adapted individuals will survive. A typical definition of competition in ecology follows this line of thinking: 'Competition occurs when a number of animals (of the same or of different species) utilize common resources, the supply of which is short; or if the resources are not in short supply, competition occurs when the animals seeking that resource nevertheless harm one another in the process' (Birch, 1957, p. 6). This

definition should also apply to plants and micro-organisms. Competition may occur between the members of different species (interspecific competition) or between members of one species (intraspecific competition).

Competition and natural selection are not always correlated. Natural selection can act independently of competition, for example, when the selective forces are produced by the physical environment, or when the genetic variation in a population is concerned mainly with maximizing the numbers of offspring (*r*-selected or opportunistic species). In the latter case, population growth is initially rapid when food is abundant, competition is minimal and selection occurs in terms of reproductive rate and of response to the physical environment. When the population is large, food is in short supply, and competition occurs, the genetic variation in reproductive rate loses its expression, and selection ceases (Williams, 1966; Pianka, 1981).

(2) *The evolutionary effects of interspecific competition*

The main long-term consequence of interspecific competition is generally taken to be ecological diversification or niche separation (Pianka, 1981). Several kinds of evolutionary changes have been ascribed to interspecific competition (Arthur, 1980).

(1) Character displacement: selection for adaptations that result in sympatric species differing in their use of resources (for example, differences in beak size that are correlated with differences in the size of seeds consumed, or differences in body size that correspond to different microhabitats).

(2) Character convergence: selection for increasing similarity in the characters of two species in sympatry.

(3) Character release: an increase in the variance of a character, or characters, when a population moves into a relatively competitor-free environment.

(4) Evolution of competitive ability: selection for better competitive ability in terms of resource utilization or in terms of inhibiting other species.

(5) Genetic feedback: selection for increased interspecific competitive ability in the rarer species which thus becomes competitively superior. The process is then reversed, and oscillations result, leading eventually to the stable coexistence of the two species.

Arthur (1980) finds that there is experimental and observational evidence for character displacement (1) and for the evolution of increased competitive ability (4) in certain cases. There is also limited evidence for character release (3), but very little for character convergence (2), or for the genetic feedback model (5).

The link between character displacement and interspecific competition has been debated recently. Strong *et al.* (1979), Simberloff & Boecklen (1981), Strong (1983), Simberloff (1984), and others, have argued that there is no clear evidence of character displacement in any published case. On the other hand, Schoener (1982, 1984), Case & Sidell (1983), Schluter *et al.* (1985), and others, have presented evidence that character displacement has occurred and that interspecific competition is probably the cause.

(3) *The effects of interspecific competition on community structure*

Most of the other postulated effects of interspecific competition affect the distribution of organisms and other ecological parameters, but they do not cause evolutionary change by affecting allele frequencies. These sorts of effects are (Diamond, 1978; Roughgarden, 1983; Schoener, 1983):

(1) Competitive exclusion: species that are too similar ecologically have disjunct ranges. One species displaces another by competition.

(2) Resource partitioning: sympatric species may divide up the available resources and so avoid competition.

(3) Number of coexisting species: interspecific competition may reduce the number of species that can coexist in an area.

(4) Species-area relations: the number of species present on an 'island' depends on its area, and this relates largely to levels of competition between the species.

(5) Number of species per genus ('S/G ratio'): this ratio appears to be smaller in small geographic areas than in large ones.

These postulated results of interspecific competition are currently being debated by ecologists. Most seem to agree that species/genus ratios (5) are simply statistical artefacts (Harvey *et al.*, 1983; May, 1984). However, ecologists are divided over the role of competition in shaping the other aspects of community structure (1-4).

One critical approach has been to test real situations that were supposedly produced by competition against null hypotheses that such patterns were randomly produced. These studies have suggested that competition is not involved in competitive exclusion and resource partitioning (e.g. Connor & Simberloff, 1979, 1983), in species-area relationships (e.g. Connor & McCoy, 1979), or in determining numbers of coexisting species (e.g. Simberloff, 1981, 1984; James & Boecklen, 1984). However, there have been strong criticisms of the validity of the null models used in these studies, and arguments have been made for the role of interspecific competition in structuring communities (e.g. Diamond & Gilpin, 1982; Harvey *et al.*, 1983; Colwell & Winkler, 1984; Gilpin & Diamond, 1984; May, 1984).

A second approach to assessing the true role of competition in ecology has been to evaluate statistically the hundreds of empirical studies that have been published. Schoener (1983), Connell (1983) and Branch (1984) found that most field studies did detect competition, although Connell wondered if cases in which competition was not observed might be underrepresented in the literature because they could be viewed as 'non-results'. Pontin (1982) records extensive evidence of the coexistence of competing species, and he denies the ubiquity of competitive exclusion and resource partitioning. In another review of empirical examples, Strong (1983) has argued that competition is often a minor aspect of the community ecology of a wide range of organisms.

Several alternative models to the competition paradigm have been presented by ecologists (reviewed by Price, 1984). Some of these models (1-3) have been given as universally applicable alternatives, while others (4, 5) probably apply in only specified cases.

(1) Enemy impact paradigm: Connell (1975) argued that predation was much more important in shaping certain modern communities than was competition.

(2) Individualistic response paradigm: this is the view that species respond individually to selection pressures and resources, independently of the evolution of other species (Strong, 1983). Some species might be controlled mainly by the climate and weather, others mainly by predation, and others mainly by competition, for example.

(3) Resource heterogeneity paradigm: in simple terms, this paradigm states that the number of species in an area depends on the number of resources. An example is the resource heterogeneity viewpoint (Wiens, 1977, 1984) which stresses the influence of abiotic factors. It is assumed that populations normally live well below the carrying

capacity of the environment, and that competition occurs only infrequently and randomly during periods of particular hardship.

(4) Island or patch size paradigm: this is the view that the number of species present depends on the area that is available, and it is closely linked with competitive models (see above).

(5) Time paradigm: this is the view that the number of species present depends on the time that has been available for colonisation.

The balance of the evidence suggests that competition commonly occurs, and that it is an important evolutionary force in shaping certain communities, but predation, disturbance, or abiotic factors, prevent many communities from reaching a competitive equilibrium (Branch, 1984). Hairston *et al.* (1960) proposed that competition might regulate the population size of the large predators at the tops of terrestrial food chains, but that their prey, the intermediate herbivores, were more probably controlled by predation than competition. For example, many studies on herbivorous and decomposer insects, which together make up nearly half of all living macroscopic species, show that communities are controlled by resource patterns, predation and the weather, rather than by interspecific competition (Strong, 1983; Strong *et al.*, 1983; Lawton, 1984). The bottom level of the food pyramid – the green plants – would again be controlled by competition. Schoener (1982, 1983) found evidence in support of this view – that competition is more important at the top and bottom of food chains than in the middle – but Connell (1983) was not convinced by the data. On the other hand, Connell (1983) found consistently higher frequencies of competition among marine organisms than terrestrial organisms, and in large-sized organisms than in smaller ones.

IV. COMPETITION IN MACROEVOLUTION

Ideas of competition and of the progressive, or ‘improving’ nature of evolution have often been linked into general hypotheses about macroevolution. These hypotheses include the assumption that extinction is generally triggered by interspecific competition, the Red Queen hypothesis (evolution is driven by biotic factors – diffuse competition), the community paradigm (in which communities are real evolutionary units, structured by biotic interactions), hypotheses about evolutionary rates and competitive ability, and major ecological replacements (in which a superior group with a key adaptation ‘outcompetes’ an inferior one).

In most of these cases, the hypotheses involves an assumption that competition of some kind causes genomic change. This change may be produced by more or less continuous interspecific interactions (the Red Queen), or by the cumulative effects of competition on a much larger scale (extinction and/or major replacements). However, certain of these models describe patterns of change through time that need not involve any evolutionary change (i.e. change in gene frequencies). For example, a major extinction and replacement event might occur as a result of immigration and competition between the members of two clades, but there need be no phenotypic or genotypic change in either group.

(1) *Extinction and competition*

Darwin viewed the history of life as progressive, and he believed that all places in the economy of Nature were filled at any time (‘the principle of plenitude’), and if a new species were to arise, it could only be by driving another species to extinction. Thus,

natural selection inevitably leads to the formation of new species, but only by the extinction of other, less well-adapted, ones. Darwin's view of extinction by competition has been espoused to varying extents by many proponents of the modern synthesis (e.g. Simpson, 1953; Fischer, 1958; Mayr, 1963; Wright, 1967; Bock, 1972; Maynard Smith, 1984).

Two major aspects of this view have been criticized: the notion of a necessary progression in evolution, and the 'principle of plenitude'. It is usually only an assumption that evolutionary development is progressive, that a replacing species is adaptively superior to its ecological forerunners (see above). The 'principle of plenitude' is a further metaphysical assumption – there is no evidence that there is a fixed number of niches on the Earth, nor even that any particular area is saturated with species (Pianka, 1981; Rieppel, 1984; Walker & Valentine, 1984). The numbers of species that coexist depend on the species' own characteristics, and not on some notional sum of occupied and 'empty' niches. Organisms make their own niches to a large extent (Lewontin, 1983), and they may 'insinuate' into a fauna without causing wholesale extinction (Simberloff, 1981): an 'empty' niche can only be recognized after it has been filled.

In recent years, competition has been cited as a cause of diversity-dependent extinction in equilibrium models of species diversity (e.g. Rosenzweig, 1975; Sepkoski, 1978; Levinton, 1979). These models were based explicitly on the MacArthur & Wilson Theory of Island Biogeography (e.g. MacArthur, 1969; Rosenzweig, 1975; Sepkoski, 1978), and it has been questioned whether that theory can be justifiably extrapolated over evolutionary time (Hoffman, 1983, 1985; Kitchell, 1985). In particular, the evidence against the 'principle of plenitude' has suggested that the model of diversity-dependent extinction is 'unnecessary and unproductive' (Walker & Valentine, 1984).

Extinction might be better regarded as a stochastic phenomenon, rather than as a predictable and deterministic one (Raup, 1981). For example, the extinction of a species is the disappearance of all individuals of that species. While the death of each individual has a definite cause (e.g. predation, starvation, illness, accident), the sum of these causes would render the extinction of the whole species stochastic (Raup, 1977; Rieppel, 1984). In other cases, one cataclysm (e.g. a volcanic eruption, or a cometary impact) could wipe out all members of a species in a restricted area, or a wide area, respectively – this is a deterministic explanation. The other kind of deterministic explanation – competition – is not likely to be the sole cause of extinction in many particular cases.

(2) *The Red Queen*

The Red Queen hypothesis (Van Valen, 1973), that species evolve as a result of biotic interactions (coevolutionary effects of predator-prey relationships and competition) remains controversial. Stenseth & Maynard Smith (1984) have suggested that the Red Queen would produce a definite pattern in the fossil record which could be tested: there should be constant probabilities of speciation, extinction and phyletic evolution, even when ecosystems are at equilibrium diversity and in the absence of abiotic environmental change. They contrast this Red Queen pattern with a Stationary model of multispecies evolution, in which the rates fall to zero at equilibrium and in the absence of change in the physical environment. Bursts of evolution, extinction and speciation occur only in response to changes in the physical environment.

The palaeontological tests are difficult, however. The main problem is in finding a situation in which it can be shown that change in the physical environment has not occurred. In a periodically disturbed environment, both the Red Queen and the Stationary models can yield stepped patterns of speciation or extinction rate which are hard to distinguish (Hoffman & Kitchell, 1984). Further, a gradually changing environment could produce a gently sloping graph in both cases, and it would be very hard to disentangle biotic and abiotic factors in such a case. One palaeontological test so far (Hoffman & Kitchell, 1984) seems to lend support to the Red Queen, while another (Wei & Kennett, 1983) seems to point to the Stationary model.

Van Valen (1984) has used a larger-scale test in which he plotted family extinction and origination rates for all marine animals against time. These rates declined exponentially in two stages, having been 'reset' to a higher level by the major end-Permian extinction event. Van Valen (1984) argues that the decline corresponds to a decrease in 'negative interactions among taxa' rather than simply a 'general optimization of fitness through evolutionary time' (Raup & Sepkoski, 1982). The results upon which these conclusions have been based, however, may be artefacts of the techniques (Flessa & Jablonski, 1985; see above). The main problem with these kinds of tests is that the patterns that are detected in the fossil record can usually be interpreted in different ways, depending upon one's understanding of processes in modern ecosystems.

The Red Queen implies that an organism's relative state of adaptation is continually maintained, but not necessarily improved (Lewontin, 1978). Van Valen (1973) saw progress in evolution occurring by relative differences in lineage splitting, as well as by individual selection. However, an assumption of evolutionary progress, or improvement in the adaptation of species through time, together with Van Valen's Law of Constant Extinction, presents a paradox (McCune, 1982). The Law of Constant Extinction states that the probability of the extinction of a species is independent of its age, and thus of the period during which adaptations have been improving. Thus, evolutionary progress, in terms of improving resistance to extinction, cannot occur.

The Law of Constant Extinction could be explained by a static model for communities in which the Red Queen assumption, that adaptations are constantly tracking a deteriorating biotic environment, does not apply (Vrba, 1980). The implication of a static model would be to deny the necessity of improvements in competitive ability through time. Thus, competition could be excluded from interpretations of the Law of Constant Extinction, and of the Stationary model for multispecies evolution.

(3) *The community paradigm*

In the community paradigm, it is assumed that communities are real biological units that have a definite structure moulded by ecological integration and coevolution among the species (e.g. Olson, 1966; Valentine, 1968, 1973; Bretsky, 1969; Boucot, 1975, 1978; Kitchell, 1985). Niches are defined by competition and predator-prey interactions between species, and although the exact species occupying particular niches may change through time, the community itself has long-term permanence.

This view has been strongly challenged on several grounds (Hoffman, 1979, 1983, 1985). Firstly, studies on modern communities show only weak interactions between species, and these do not seem strong enough to cause structural changes: coevolution

among competitors is probably extremely rare (Connell, 1980). Secondly, the community paradigm assumes that ecological communities achieve an equilibrium state that reflects the optimum partitioning of habitat and resources among the component species, as a result of long-term interspecific competition and coevolution. However, it is unlikely that a community could for long remain in an equilibrium state because it would be disturbed by random environmental changes (Huston, 1979). Thirdly, Hoffman (1979, 1983) objects to the implication that the community paradigm involves group selection in that communities, rather than individual organisms or species, are regarded as subject to independent selection pressures.

(4) *Evolutionary rates and competitive ability*

Stanley (1974, 1977) argued that mammals have a higher rate of evolution than bivalves because of their higher degree of interspecific competition. Competition between lineages of mammals is said to have caused them to radiate widely and rapidly in the early Tertiary because they could not occupy similar adaptive zones. In general, competition has supposedly led to high rates of origination and extinction among mammalian taxa. This argument rests on three assumptions: that mammals have evolved faster than bivalves, that competition is much more common between species of mammals than between bivalves, and that rates of evolution are mainly controlled by interspecific competition.

These three assumptions have been criticised. Firstly, Schopf *et al.* (1975) have argued that perceived rates of morphological evolution may tell us more about the overall complexity of the organisms involved, rather than about true rates of genomic change. Further, Novacek & Norell (1982) have thrown doubt on the value of these taxonomic rate calculations because of poor estimates of stratigraphic ranges and inconsistent phylogenetic analysis. Gingerich (1983) and Levinton (1983) have argued that the apparent differences in the rates of evolution of mammals and bivalves depend on the time spans over which the rates are measured, and that there is probably in reality no difference.

The second criticism is that it has not been possible to generalise about levels of interspecific competition in different modern taxonomic groups on the basis of ecological studies (Connell, 1983; Schoener, 1983). If any generalisations can be made, they concern broad habitats, size, and trophic position (see above).

The third criticism concerns the notion that interspecific competition is the sole or main agent controlling rates of evolution, either in terms of speciation rates or rates of morphological change. As has been noted above, interspecific competition is probably not the predominant cause of species-wide genetic change either during phyletic evolution, or at speciation by the allopatric model (Walter *et al.*, 1984). In the nonallopatric models, speciation might occur by stochastic chromosome rearrangements (e.g. White, 1978; Bush, 1982; Dover, 1982; Rose & Doolittle, 1983), or by some process involving divergent selection pressures (Rosenzweig, 1978; Templeton, 1981; Bush, 1982). The latter form of 'competitive speciation' (Rosenzweig, 1978) or 'adaptive speciation' (Bush, 1982) involves diffuse interspecific competition, but its relative importance compared to the other models is not clear.

Rates of evolution may depend on generation time and body size (Simpson, 1953; Mayr, 1963; Maynard Smith, 1976; Fowler & MacMahon, 1982). Large animals with

long generation times tend to have high extinction rates because they cannot respond as rapidly to natural selection as small animals with short generation times. Rates of evolution for large mammals may also be high because of their small population sizes. Conversely, small animals with short generation times tend to have higher rates of speciation (Fowler & MacMahon, 1982). Branch (1984) has proposed a number of other explanations for the supposedly lower rates of evolution of bivalves compared to mammals: the sea is physically more constant than the land; bivalve larvae are widely dispersed; isolation of small populations is easier on land; isolation of mammals is easier because of their internal fertilization and complex mating behaviours.

V. COMPETITION AND MAJOR ECOLOGICAL REPLACEMENTS

(1) *Key adaptations and replacements*

Major ecological replacements, in which one taxon is replaced by another, within the same broad adaptive zone, have formed an important part of the history of life. The term ecological replacement is used in the sense typically intended by palaeontologists (e.g. ecologic replacement, Raup & Stanley 1978; evolutionary relay, Simpson, 1953, 1983) to refer to patterns in which one supraspecific taxon is replaced by another, either within a circumscribed geographic area, or more often globally. The replacement may be a drawn-out affair, supposedly involving long-term competition, or it may occur after a mass extinction event. The successful taxon is said to undergo an adaptive radiation, a rapid proliferation of lineages from a single ancestral group.

The term adaptive radiation implies a mechanism that underlies the proliferation of lineages. There is a clear indication that it was caused by the improved competitive ability bestowed on a particular group of organisms by the acquisition of a key adaptation (Simpson, 1944, 1953; Schaeffer, 1965; Stebbins, 1974; Stanley, 1979, chapter 4; Maynard Smith, 1983). A key adaptation is generally a single attribute, or a complex of interrelated characters, that may, or may not be, observed in the fossil record, such as the possession of endothermy or lactation in mammals, the erect gait of the dinosaurs, the improved jaw apparatus and lighter skeleton of the teleost fishes, the flower and efficient fertilization system of the angiosperms, and so on. The key adaptation is also generally a synapomorphy, or complex of synapomorphies, of the clade in question. Kemp (1985) has pointed out that in real cases it is most unlikely that an adaptive radiation will be based on the acquisition of a single key adaptation. Organisms are too complex for that. The idea that the acquisition of the 'key characters' endothermy and lactation triggered the adaptive radiation of the mammals is most unlikely and impossible to demonstrate in any case.

There are five ways in which we can interpret an ecological replacement in which the successful group appears to have a key adaptation.

(1) The key adaptation appears in clade B, which competes successfully with, and replaces, clade A. Clade B has demonstrated the competitive superiority conferred upon it by the key adaptation, by causing the extinction of clade A.

(2) There is a mass extinction event, and survivors of clade B (with its key adaptation) compete successfully in the disturbed post-extinction ecosystems with the survivors of clade A (which lacks the key adaptation) and clade B prevails. Again, clade B has demonstrated its competitive superiority.

(3) There is a mass extinction event, and clade B resists extinction. Clade A lacks the ability to resist extinction, and it dies out. Clade B has demonstrated its competitive superiority in terms of its ability to resist extinction. This ability might be bestowed by a key adaptation that is the same as, or different from, the adaptation which permits the group to radiate subsequently. There is no reason to assume that an adaptation for survival in the disturbed times of a mass extinction is the same as an adaptation for survival in normal (or background extinction) times (Gould & Calloway, 1980; Jablonski, 1986).

(4) There is a mass extinction event during which many A and B organisms die out and, by chance, only a few B organisms survive. These evolve into clade B, which has a key adaptation that ensures a successful adaptive radiation into many niches. Clade B has not demonstrated its competitive superiority over clade A.

(5) There is a mass extinction event during which all, or most, of clade A, and most of clade B die out by chance. The survivors of clade B radiate, but there is no particular key adaptation that ensures the success of that radiation. This is an entirely stochastic model for mass extinction and radiation (cf. Raup *et al.*, 1973; Gould *et al.*, 1977; Raup, 1977), and any 'key adaptations' that are postulated have no reality.

The important question now is to attempt to determine whether the key adaptation model is a correct general description of major adaptive radiations in the past. In order to do this, it is necessary to consider patterns in the fossil record to see whether they fit any of the key adaptation models (1)–(4) listed above. The stochastic model (5) is always an alternative explanation for any kind of major ecological replacement. However, there is no easy way to test its validity against adaptive explanations (models 1–4), other than by personal belief. The stochastic model, then, will not be considered in the particular examples given below, although it must be retained as a possibility.

(2) *Patterns of ecological replacement*

The five key adaptation models just listed correspond to two gross patterns in the fossil record: those in which competition from the replacing group caused the extinction of the other group (model 1), and those in which the extinction was triggered by a mass extinction produced by other causes (models 2–5). The first pattern has been termed ecologic displacement (Raup & Stanley, 1978), active replacement (Raup & Marshall, 1980; Marshall, 1981), or differential survival ('competitive') replacement (Benton, 1983*a, b*). The second pattern has been called passive replacement (Raup & Marshall, 1980; Marshall, 1981), or opportunistic ('mass extinction') replacement (Benton, 1983*a, b*).

These two broad patterns should be distinguishable in the fossil record by assessing the relative abundances of the two groups in question through time. In general terms, the 'competitive' pattern would be like a pair of matched wedge-shaped clades, one decreasing upwards and the other increasing upwards side-by-side – a negative correlation between the two groups. The 'mass-extinction' pattern would show one group coming to an end abruptly, and the other increasing thereafter. As Gould & Calloway (1980) noted, however, the 'double-wedge' pattern might or might not imply a correlation between the two groups in question.

The double-wedge pattern (Fig. 1*a*) is familiar from many spindle diagrams drawn by palaeontologists. These may represent the numbers of species, genera or families at

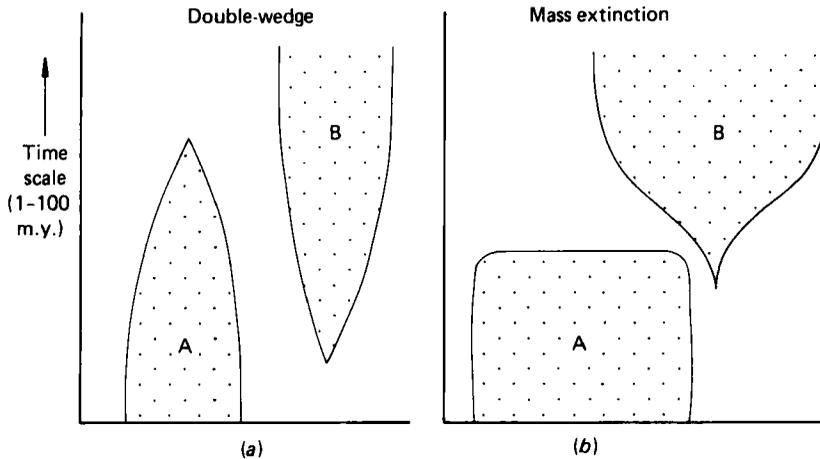


Fig. 1. A comparison of two patterns from the fossil record in which clade B replaces clade A. The vertical axis is a time scale, and the horizontal axis is some measure of the relative 'importance' (e.g. number of species, number of families, relative proportion in faunas) of each clade through time.

different times in the history of a clade, relative abundances of the taxa in particular dated faunas, or they may simply be subjective estimates of the 'importance' of the groups through time. The time scale during which one clade declines, and the other increases, is generally in the order of millions of years (say, 1–100 Ma in the examples of 'competitive' replacements cited below). The double-wedge pattern is contrasted with the mass-extinction pattern (Fig. 1b) which shows one clade disappearing geologically instantaneously (in less than 1 Ma?) and the other radiating afterwards. On a typical palaeontological time scale of 1–100 Ma, the patterns are quite distinct, but there is the usual problem of stratigraphic resolution over shorter time scales.

In more detail, a typical double-wedge pattern of the replacement of group A by group B (Fig. 1a) would have the following features.

(1) A decreases in abundance and B increases in abundance over time (A has an elevated extinction rate (or reduced origination rate) and B has an elevated origination rate (or reduced extinction rate)).

(2) The rate of replacement is gradual (i.e. over a time span of many years, and usually many millions of years in typical examples).

(3) A and B are found together, and either could be dominant in any particular formation.

(4) The replacement is not necessarily associated with climatic or other environmental change.

On the other hand, a typical mass-extinction pattern of the replacement of group A by group B (Fig. 1b) would have these features.

(1) B appears or radiates significantly only *after* the extinction of A. The gap may be geologically short, or as long as 30 Ma (replacement of ichthyosaurs by whales: Simpson, 1983).

(2) The rate of replacement is rapid in that group A may disappear geologically instantaneously, and group B may show an elevated rate of origination during its subsequent radiation.

- (3) A and B are not found together, or B is unobtrusively present when A is dominant.
 (4) The replacement is associated with an environmental change of some kind, which could be catastrophic, but need not be.

(3) *The evidence for double-wedge patterns (differential survival) in the fossil record*

Competition on a large scale (key adaptation model 1) has been used as an explicit or implicit explanation for many major ecological replacements. These include the cases of rhyniophytes vs. trimerophytes in the early Devonian (Knoll, 1984), trimerophytes vs. progymnosperms in the middle Devonian (Knoll, 1984), progymnosperms vs. pteridosperms in the late Devonian and early Carboniferous (Knoll, 1984), gymnosperms vs. angiosperms in the Cretaceous (Williams, 1966; Doyle, 1977; Raup & Stanley, 1978; Tiffney, 1981), Vendian and Cambrian marine invertebrates vs. later Palaeozoic marine invertebrates (Sepkoski, 1979, 1981), later Palaeozoic marine invertebrates vs. 'modern' marine invertebrates (Sepkoski, 1981), cyclostome vs. cheilostome bryozoans in the Cretaceous (Cheetham, 1971), brachiopods vs. bivalves in the Palaeozoic–Mesozoic (Stanley, 1968, 1977); Mesozoic nautiloids vs. ammonites (Newell, 1952), agnathans vs. gnathostomes (Schaeffer, 1965; Williams, 1966; McFarland *et al.*, 1979), hybodont sharks vs. 'modern' sharks in the Jurassic (Schaeffer, 1965), chondrosteans vs. holosteans in the Triassic–Jurassic (Schaeffer, 1965; Colbert, 1969), holosteans vs. teleosts in the Jurassic–Cretaceous (Schaeffer, 1965; Colbert, 1969), amphibians vs. reptiles in the Carboniferous–Permian (Carroll, 1977), mammal-like reptiles vs. archosaurs in the late Triassic (Charig, 1980, 1984; Bonaparte, 1982), pterosaurs vs. birds in the Cretaceous (Camp, 1952), dinosaurs vs. mammals in the late Cretaceous (Van Valen, 1985; Sloan *et al.*, 1986), marsupials vs. placentals in the late Cretaceous of North America (Simpson, 1965), multituberculates vs. rodents, and other placentals, in the early Tertiary (Jepsen, 1949; Simpson, 1953, 1980; McKenna, 1961; Wood, 1962; Maynard Smith, 1966, 1983; Van Valen & Sloan, 1966; Colbert, 1969; Clemens & Kielan-Jaworowska, 1979; Prins & Schoch, 1984), perissodactyls vs. artiodactyls in the mid-Tertiary (Simpson, 1944, 1953; Stanley, 1974), creodonts vs. carnivores in the mid-to late Tertiary (Simpson, 1953; Williams, 1966; Colbert, 1969; Maynard Smith, 1983), South American vs. North American mammals in the Great American Interchange (Simpson, 1950, 1965; Mayr, 1963; Maynard Smith, 1966; Stanley, 1974; Flessa, 1975; Webb, 1976; McFarland *et al.*, 1979).

A number of the better-studied of these examples are discussed below and, in these, the patterns and proposed mechanisms are considered together.

(a) *Brachiopods vs. bivalves*

The classic textbook example of 'competitive' replacement of one group by another has been brachiopods vs. bivalves. The brachiopods dominated the seas in the Palaeozoic, but they declined and they were largely replaced by the ever-radiating bivalves in the Mesozoic. This radiation has been explained by the acquisition of a key adaptation in bivalves: fusion of the mantle and the consequent production of siphons, and the formation of a tight seal for the mantle cavity, both useful features for burrowing to avoid predation (Stanley, 1968, 1977). Thayer (1985) has found that living mussels are eaten in preference to articulate brachiopods, by a variety of predators. He argues

that predation does not explain the decline of the brachiopods, but prefers a model 1 situation in which bivalves had a long-term advantage because of their mobility.

Gould & Calloway (1980) examined the evidence of numbers of genera of each group through time, and found that the replacement was not gradual, with brachiopods declining and bivalves increasing over a long period of time. The replacement was associated with the end-Permian extinction event which profoundly and permanently reduced the diversity of brachiopods, but only temporarily depressed the diversity of bivalves which subsequently recovered and reached an even higher level. The data suggest a mass-extinction and opportunistic replacement pattern, and there is little evidence for a double-wedge pattern.

It is most unlikely, then, that the bivalves *caused* the decline of the brachiopods. On the other hand, it could be that the mantle fusion of bivalves enabled them to radiate after the mass extinction event (key adaptation model 4). This adaptation had probably arisen in the Devonian, and the siphonate bivalves were already diversifying during the Carboniferous and Permian, and they continued to do so during the Mesozoic (Stanley, 1977). Another suggestion has been that only non-planktotrophic brachiopods survived the extinction event, while the bivalves were planktotrophic, and the latter developmental mode allowed them to radiate more rapidly (Valentine & Jablonski, 1983), an expression of key adaptation models 2 or 4. It has been argued (Stanley, 1977; Gould & Calloway 1980) that bivalves also resisted the effects of the end-Permian extinction better than did the brachiopods, although these authors differ in the emphasis that they place on a key adaptation as the controlling factor (? key adaptation model 3).

(b) *Hybodonts vs. 'modern' sharks*

The hybodont sharks apparently declined in abundance during the late Jurassic and the Cretaceous, and it has been argued that this was caused by competition with the newly evolved neoselachian ('modern') sharks (e.g. Schaeffer, 1965). In fact, the Neoselachii radiated in the Triassic, or earlier, and much of their radiation in the Jurassic and Cretaceous was into new adaptive zones that had never been exploited by the hybodonts (Thies & Reif, 1985). The fossil record of sharks is not good enough to determine whether the decline of the hybodonts was triggered by a mass extinction event at the end of the Triassic, or not. Thies & Reif (1985) indicate that the replacement of hybodonts by neoselachians was partly the result of direct competition (key adaptation model 1), but largely the result of a radiation into empty ecospace as a result of new adaptations in the locomotory and feeding apparatus (model 2 or 4).

(c) *Mammal-like reptile vs. archosaurs*

Another classic example in which 'competitive replacement' (model 1) has been given as an explanation is the radiation of the archosaurs, and in particular of the dinosaurs. According to the standard view, the mammal-like reptiles, which were dominant on land in the late Permian, declined gradually in importance in the Triassic, and they were replaced by the thecodontians, and finally by the dinosaurs during the middle and late Triassic. Many authors have argued explicitly that the advanced thecodontians and dinosaurs competed successfully, and over long periods of time, with the mammal-like reptiles, and that the extinction of the latter and the great success of the dinosaurs is to be explained in terms of competition alone (e.g. Charig, 1980, 1984;

Bonaparte, 1982). The competitive advantage of dinosaurs has been stated to be their 'improved' locomotor ability (erect gait), or their advanced thermoregulatory ability (whether endothermy or inertial homeothermy).

The evidence does not support these views. Firstly, an analysis of the major Permo-Triassic reptile faunas has shown that the thecodontians never succeeded in displacing the mammal-like reptiles, and the dinosaurs radiated to achieve dominance only *after* the extinction of the formerly dominant groups (mammal-like reptiles, rhynchosaurs, thecodontians) (Benton, 1983b). Dinosaurs were present in the late Carnian as very rare faunal elements (less than 1% of all specimens) and then radiated to dominance in the Norian, in particular after an end-Carnian extinction event (*c.* 225 Ma).

A second analysis (Benton, 1986; also Olsen & Sues, 1986) of all records of families and genera of late Triassic tetrapods confirms this view. The rhynchosaurs and most families of mammal-like reptiles died out at the end of the Carnian. The first dinosaurs (podokesaurids, prosauropods) radiated in the late Carnian and the Norian. The last thecodontians and various layrinthodonts and mammal-like reptiles died out at the end of the Triassic (*c.* 208 Ma), and the carnivorous and herbivorous saurischian dinosaurs, and various lines of ornithischians, radiated worldwide in the early Jurassic. In both cases, the dinosaur radiations occurred *after* the mass extinction events.

A third study of the relatively complete Triassic record of terrestrial vertebrates from SW Germany (Benton, 1984b, 1986) also confirms these findings. Dinosaurs radiated rapidly in the Norian, and within a time span of probably less than 4 Ma, rather than in a time of up to 30 Ma, as formerly postulated.

The initial radiation of dinosaurs appears to have followed a mass-extinction pattern rather than a double-wedge pattern. Benton (1983a, b, 1984a, b, 1986) argued that the key adaptation model (4) applied here. The radiation of the dinosaurs was seen as having occurred by chance after mass extinction events, but it was indicated that the biology of the dinosaurs might have allowed them to adapt to the apparently more arid conditions represented by the latest Triassic and early Jurassic reptile beds, and the new worldwide conifer-bennettitalean floras which replaced the *Dicroidium* flora of Gondwanaland at that time (Tucker & Benton, 1982; Benton, 1983b, c). Zawiskie (1986) has extended this viewpoint to argue that it was the locomotory and feeding adaptations of the dinosaurs that allowed them both to resist extinction and to radiate (key adaptation model 3).

The classic long-term competitive model of dinosaur success (model 1) relied upon the assumption that the dinosaurs had a superior key adaptation compared to the mammal-like reptiles and thecodontians (Charig, 1980, 1984; Bonaparte, 1982). This key adaptation was said to be the possession of endothermy (Bakker, 1971) or inertial homeothermy (Benton, 1979), but neither of these views can be proved, and it is just as likely that the advanced mammal-like reptiles (their supposed inferior competitors) had some equivalent kind of internal temperature control. The locomotory scenario, that thecodontians and dinosaurs evolved semi-erect and erect gaits which were competitively superior to the sprawling gait of mammal-like reptiles (Charig, 1972, 1980, 1984), is also flawed. Advanced mammal-like reptiles and rhynchosaurs also had semi-erect gaits (Kemp, 1980; Benton, 1983ad), and yet this did not ensure their survival. Further, several groups of archosaurs that died out before the dinosaurs radiated extensively also

had erect gait: the aetosaurs, the rauisuchian thecodontians (Rauisuchidae, Poposauridae), and the Saltoposuchidae (crocodilomorphs) (Benton, 1984*a*; Bonaparte, 1984; Parrish, 1984; Chatterjee, 1985). The Poposauridae, and possibly also the Saltoposuchidae, had also achieved bipedal gait, formerly considered to be a superior dinosaurian patent. The elucidation of the pattern of the fossil record of Triassic reptiles, and the model (1) competitive scenarios for dinosaur success have become so entwined that it has been hard to disentangle the two. The fact of competition has been assumed, and elaborate scenarios have been developed to the extent that the supposed patterns and the stories have lent each other mutual support.

(d) *Dinosaurs vs. mammals*

Earlier authors often explained the extinction of the dinosaurs 66 Ma ago as the result of competition with mammals or predation by mammals. Van Valen (1985) notes that the evolutionary explosion of mammals began before the extinction event in the late Cretaceous and that it 'may have been causally involved in it'. There is evidence for a gradual decline in dinosaur abundance in Montana over a time span of 7 Ma or so before their final disappearance, and this seems to be matched by a gradual rise in mammalian diversity. Sloan *et al.* (1986) interpret the replacement as a result of environmental changes, floral changes, and 'diffuse competition from new mammalian herbivores most likely introduced to this continent from Asia'. They are suggesting in part a type (1) model of direct competitive replacement, but the weaker models (2), (3) or (4) could apply. The gradualist interpretation of dinosaur extinction and mammal adaptive radiation, as outlined by Van Valen, Sloan, and others, is probably more properly explained by a differential environmental response model (see below), since only diffuse competition is supposed to be involved.

(e) *Multituberculates vs. placentals*

Van Valen and Sloan (1966; see also Van Valen, 1978; Clemens & Kielan-Jaworowska, 1979) argued that competition from condylarths, primates and rodents led to the extinction of the multituberculates. The pattern of declining numbers of genera of multituberculates was apparently matched by the increasing diversity of ecologically similar placentals during the period from the late Cretaceous to the Oligocene, a time span of 55 Ma. It is argued that first condylarths, then primates, and finally rodents, successively occupied multituberculate niches and eventually drove them to extinction by successful competition. Other authors (e.g. Jepsen, 1949; Simpson, 1953, 1983; McKenna, 1961; Wood, 1962; Maynard Smith, 1966, 1983; Colbert, 1969) have accepted this view, and they have stressed the role of the rodents which had the key adaptation of large continuously-growing incisors. Van Valen and Sloan (1966) list numerous characters of the skull and skeleton of multituberculates in which they are apparently 'primitive' with respect to the placental mammals, but they note that this does not demonstrate competitive inferiority.

Landry (1965) criticized the multituberculates vs. rodents hypotheses as being too simplistic, and he presented contrary evidence. Subsequently, Black (1967) and Fox (1968) have argued that the fossil record of multituberculates is biased and incomplete, and Krause (1980) has stated that the decline in diversity of multituberculates was not gradual and continuous, as Van Valen and Sloan (1966) assumed. For example, there

was a marked drop in diversity (from 9 to 2 species) between the Tiffanian and Clarkforkian Land-Mammal Ages (late Palaeocene), which could indicate a mass extinction event. The simple differential survival and key adaptation model (1), as indicated by Van Valen & Sloan (1966), has not been confirmed.

(f) *Perissodactyls vs. artiodactyls*

During the Tertiary, the artiodactyls (cattle, pigs, antelopes, camels, and so on) apparently largely replaced the perissodactyls (horses, rhinos, numerous extinct groups) as major terrestrial herbivores, and this has been explained in terms of the competitive advantage of various characters of their limbs and teeth, and the ability to ruminate (e.g. Simpson, 1953; Stanley, 1974). Cifelli (1981) analysed trends in the diversity of perissodactyl and artiodactyl genera and families during the Tertiary, and he found no evidence of a double-wedge pattern. In fact, the patterns of radiation and extinction of both orders run more in parallel with each other than in opposition – periods of increased diversity seem to coincide – and it is likely that each group was evolving essentially independently and responding similarly to a variety of environmental stimuli. The standard competitive model (key adaptation model 1) for artiodactyl success involves scenarios in which they are said to be competitively superior to perissodactyls, but such scenarios turn out to be seriously flawed (Janis, 1976), and they cannot be used to bolster up such an assumed pattern. The caecal digestion of perissodactyls is not inferior to the ruminating digestion of artiodactyls in all situations – it is better adapted to coping with highly fibrous fodder.

(g) *South American vs. North American mammals*

One of the most cited and most studied examples that supposedly indicates a double-wedge pattern and competitive replacement is the 'Great American Interchange' (e.g. Simpson, 1950, 1965; Mayr, 1963; Maynard Smith, 1966; Stanley, 1974; Flessa, 1975; Webb, 1976). Three million years ago, the Panamanian land bridge appeared and permitted the previously isolated faunas of North and South America to intermingle. The standard story is that the markedly superior North American mammals created havoc amongst the inferior South American forms, and drove them to extinction by intensive competition. However, the facts do not support such a simple view (Marshall, 1981; Marshall *et al.*, 1982; Hoffman, 1985). In the last 3 Ma, 15 families of North American mammals invaded South America, one of which has died out, and 15 families of South American mammals invaded North America, three of which have died out: at the family level, the interchange was balanced.

In terms of genera, the classic story at first seems to be confirmed: 50% of the present-day mammal genera in South America are derived from members of immigrant North American families, whereas only 21% of the present-day mammal genera in North America had their origins in South America. However, the total number of mammal genera in South America increased markedly after the land-bridge appeared – from 72 before, to 170 today – and the total number of mammal genera in North America increased only marginally – from 131 before, to 141 today. The great increase in the diversity of mammals in South America consisted of North American immigrants which 'insinuated' – that is, they found themselves niches without competing and causing extinctions among the genera already present. South America and North

America show similar levels of extinction of native genera immediately after the formation of the land bridge: 13 and 11% respectively. Thus, the interchange was balanced in terms of extinctions of genera.

The only major characteristic in which the North American mammals prevailed over their South American counterparts was in their ability to insinuate themselves into narrower niches. The extinction of various endemic groups in South America may be linked to environmental changes at that time which included a spread of dry forests, pampas and deserts, and also to the arrival of man 15,000 years ago. Competition may have occurred between certain North and South American mammal species when they first came into contact, but there is little evidence for the large-scale competitive displacement of South American forms that has often been assumed.

Some specific aspects of the Great American Interchange have been cited as examples of differential survival. For example, Webb (1976) suggested that the South American 'ungulates' were replaced as a result of competition with invading North American ungulates or predation by superior northern carnivores. Generic diversity of the South American forms fell from 13 to 0, while the North American invaders increased from 0 to 20, but later dropped to 11, over the 3 Ma after the land bridge formed. However, Marshall & Hecht (1978) and Marshall (1981) have disputed this conclusion. They note that the South American 'ungulates', the litopterns and notoungulates, were already declining before the invaders arrived. Further, several of the South American lines survived well into the Pleistocene, and these died out much later along with their supposed competitors, the invading mastodonts and horses. Thirdly, many of the South American megaherbivores, such as glyptodonts, ground sloths and toxodonts, were so different from the North American forms, that it is hard to see how they could have competed. Fourthly, when all of the genera of megaherbivores are added together, it is clear that no gradual replacement took place – the numbers of genera of South American forms went from 26 to 21 after the interchange, and then rose to 26 again. The North American invaders insinuated themselves into the faunas, and increased the overall diversity of megaherbivores. Then, in the late Pleistocene, 2.5 Ma after the land bridge appeared, there was a major extinction event and the diversity of native megaherbivores fell from 25 to 1 and of invaders from 28 to 10. The double-wedge pattern and competitive replacement hypothesis (model 1) is not supported for the Great American Interchange.

(h) *Fossil record of vascular plants*

Knoll (1984) and Niklas *et al.* (1985) have argued strongly for the role of competition in major adaptive radiations of vascular plants. In particular, they describe key adaptation models (type 1) for the replacement of rhyniophytes by trimerophytes in the early Devonian, the subsequent replacement of trimerophytes by progymnosperms in the middle Devonian, and the replacement of the latter by pteridosperms in the late Devonian and early Carboniferous. Their conclusion is based on the lack of any evidence for associated mass extinctions, the poor evidence for correlated climatic changes, and the evidence for adaptive advances in each successor group. Similar models are presented for later radiations of vascular plants.

Knoll (1984) contrasts the possible role of large-scale competition in plant evolution with the apparent rarity of this mode in animal evolution. He suggests that mass

extinction has played a smaller role than competition in vascular plant evolution because of the vulnerability of plant species to extinction as a result of competition from newly-appearing taxa, their vulnerability to extinction as a consequence of climatic change, and their resistance to environmental stresses, such as the agents of catastrophic mass extinction.

(4) *The evidence that differential survival was caused by competition*

The cases discussed above that have been thought of as typical examples of differential survival (competitive) replacement (key adaptation model 1) in the evolution of animals turn out to be quite different upon detailed study. Three of them represent mass extinctions and opportunistic replacement (brachiopods vs. bivalves; mammal-like reptiles vs. archosaurs; dinosaurs vs. mammals: models 3 or 4), one shows no evidence for replacement at all, but simply the independent evolution of two groups (perissodactyls vs. artiodactyls), and one shows the effects of insinuation and an increase in diversity without replacement (the Great American Interchange). Other less studied cases are equivocal (e.g. hybodonts vs. 'modern' sharks; multituberculates vs. placentals). Nevertheless, there is no reason to assume that the double-wedge patterns of differential survival cannot be found in the fossil record; but they must be demonstrated by careful documentation. There is, however, some evidence for the application of key adaptation model 1 to major replacement events in the evolution of vascular plants.

The demonstration of a double-wedge pattern does not prove that it was caused by long-term competition. If both groups are extinct, it is impossible to demonstrate that competition was involved. However, the likelihood of competition as the mechanism may be assessed when there are living representatives. Connell (1980) presented a set of three criteria that must be satisfied in order to demonstrate that competition has taken place: (1) divergence in adaptation or mode of life has occurred; (2) competition, rather than some other mechanism, is responsible (i.e. competition must be demonstrated between living members of the taxa involved, and its evolutionary effects must be shown); and (3) the divergence has a genetic basis. The assessment of divergence can be made from the fossil record (e.g. Eldredge, 1974; Kellogg, 1975; Schindel & Gould, 1977; Stanley & Newman, 1980; Newman & Stanley, 1981). Competition and the genetic basis of the divergence may be detected by experimentally manipulating living populations (Connell, 1980, 1983; Schoener, 1983). In fact, these experiments have rarely been fully done, and their interpretation remains controversial in certain aspects (Connell, 1983; Roughgarden, 1983). Nevertheless, there is one example in which it has been claimed that these criteria have been met.

Stanley & Newman (1980) and Newman & Stanley (1981) argued that the balanoid barnacles have been competitively replacing the chthamaloids over the past 40 Ma or so. The fossil record and present distributions of both groups appear to show that the balanoids are radiating and the chthamaloids are declining (double-wedge pattern), although this has been strongly questioned (Paine, 1981; Branch 1984). Further, the chthamaloids have a disjunct bathymetric distribution, being concentrated in the intertidal zone and in deep water. The balanoids occupy the intermediate intertidal and shallow water zones. Stanley and Newman argue that the chthamaloids once occupied all bathymetric levels but were progressively excluded from shallow waters and low intertidal zones by the balanoids. Secondly, Stanley and Newman argue that there is

strong evidence that chthamaloids and balanoids compete for space in the intertidal zone today, and that the balanoids generally win (Connell, 1961). However, Connell (1970, 1975) later argued that competition between the different kinds of barnacles was usually prevented by intense predation by gastropods and starfish. Dungan (1985) has shown that the relative competitive success of living acorn barnacles does not necessarily relate to their morphology (and taxonomic affinities) but rather to their relative settlement density. Ecological factors seem to be more important than morphology. Paine (1981), Palmer (1982) and Branch (1984) also argued that differential predation pressures and environmental factors were more important than competition in regulating barnacle distributions. The third criterion for 'competition past', the genetic basis of the divergence, has not been demonstrated. The case for competitive replacement of chthamaloid by balanoid barnacles is by no means fully convincing. This example shows how difficult it will be to demonstrate a large-scale competitive replacement.

(5) *Alternatives to competition*

Many cases in which large-scale competition has been assumed in the past (double-wedge pattern) have in fact turned out to correspond to the mass-extinction pattern. Competition could be involved as a mechanism in both patterns (key adaptation models 1 and 2–3 respectively), but it would be hard to demonstrate in most cases. A mass-extinction pattern might involve no competition (key adaptation model 4), or possibly no key adaptation at all, either before or after the event (model 5).

The double-wedge pattern could be produced by a number of mechanisms other than competition, such as predation, differential response to the environment, or chance. None of these would be easy to demonstrate, but they should be borne in mind as alternative possibilities.

(a) *Predation*

Predation has frequently been cited as a dominant factor in producing double-wedge patterns of replacement (Stanley, 1977, 1979, pp. 200–204; Kitchell, 1985). For example, the endobysate bivalves have dwindled in numbers from the late Palaeozoic onwards. These forms live partially or fully buried in the bottom sediment, attached by a byssus, but they are largely immobile and are subject to heavy predation. In the late Mesozoic, there was a great radiation of new kinds of marine predators – crabs, teleost fishes, and carnivorous snails (Stanley, 1977, 1979; Vermeij, 1977) – and these groups account for most predation on modern bivalves. Endobysate bivalves have been replaced largely by other kinds of bivalves which have reduced the chances of predation by living in rock crevices, by the growth of spiny or thick shells, or by living in the intertidal zone. Others (the scallops) have an advanced escape swimming response. The rise of marine predators in the late Mesozoic may also have reduced the diversity of crinoids, forced snails to evolve strong predator-resistant shells, and hastened the decline of the solenopore algae (Stanley, *et al.* 1983; Steneck, 1983).

(b) *Differential environmental response*

A third explanation for differential survival patterns in the fossil record stresses the importance of abiotic, as well as biotic, factors (in comparison with the competition and predation models which emphasise only biotic factors). The relative success of different

taxa could depend on their responses to certain long-term environmental changes, such as temperature changes, sea-level changes, or changes in habitat diversity. A long-term decline in taxon A, and an increase in taxon B, could be caused simply by the fact that the two taxa responded differently to an environmental change, and taxon B was able to adapt better to the new conditions than taxon A. Taxa A and B need never have interacted directly, and yet a double-wedge pattern would be detected in the fossil record. The gradualistic models of the extinction of the dinosaurs and the rise of the mammals (e.g. Sloan *et al.* 1986) are based on differential responses of the two groups to major changes in the physical environment and in the floras.

There are clearly parallels here with the individualistic response paradigm in community ecology (see above). It is assumed that the characteristics of each taxon determine its fate independently of other taxa, and that its fate is not regulated by large-scale competition or by predation.

(c) *Chance*

Chance may also play a role in many cases for which we seek deterministic explanations. A pattern of 'decreasing taxon A-increasing taxon B' could be a chance pairing of taxa that never had anything to do with each other (? competition) and never responded differentially to other biotic stresses (? predation) or abiotic stresses (? differential environmental response). Further, it has been argued that many kinds of clade shapes could arise stochastically and without any particular moulding influence (Gould *et al.*, 1977), and these include patterns that mimic the double-wedge pattern.

VI. THE PROBLEMS OF INVOKING LARGE-SCALE COMPETITION

The foregoing descriptions of particular cases from the fossil record have shown that there are many problems associated with models that postulate competition as the main cause of extinction and radiation (key adaptation model 1). Some of these problems are listed below.

(1) *Confusion of pattern and mechanism.* Many, if not all, of the classic examples of long-term 'competitive' replacements have involved a confusion of empirical patterns from the fossil record with assumed competitive scenarios that purport to explain the patterns. The patterns and mechanisms become inextricably tangled up together and can result in circular reasoning. A few quotations from recent works exemplify the confusion: 'most of the mammal-like reptiles... vanished because of the highly progressive nature of their descendants [the mammals]. They evolved themselves into oblivion' (Colbert, 1969, p. 167). '...the great increase in selection pressure caused some species to become extinct, while others survived either by evolving into bigger and better carnivores or by adapting themselves to some specialised alternative diet...the vegetarian one' (Charig, 1980, p. 209). 'It is quite probable that this extinction [of the 'archaic' gymnosperms] was not a chance event, but one resulting from the competitive pressure from the increasingly efficient angiosperms... However, it should be noted that the competitive ability of some gymnosperms remained undiminished, as evidenced in particular by the Pinaceae, which evolved to a considerable degree in the Cretaceous and Tertiary' (Tiffney, 1981, p. 220). 'The competition between archosaurs and therapsids began in the earliest Triassic... The time of termination of the process is doubtful' (Bonaparte, 1982, p. 369).

(2) *Over-simplification*. Competition scenarios usually boil down to explanations of major faunal replacements in terms of simple key adaptations that gave their possessors great advantages over all others. Such stories often turn out to be untenable (see also studies above), and they probably do not reflect the reality of the true complexity of living organisms. For example, the success of mammals is not just the result of endothermy, or of lactation, but of a whole complex of anatomical and physiological features that seem to have evolved piecemeal over a long span of time (Kemp, 1982, 1985).

(3) *Lack of proof*. Cases in which large-scale competition has been assumed have rarely been properly dissected and all possible explanations explored. This is a hard task. From the evidence presented here, and elsewhere (e.g. Gould & Calloway, 1980; Benton, 1983*a, b*), it seems that most major faunal replacements have been triggered by mass extinction events, rather than by long-term competitive interactions between pairs of supraspecific taxa.

(4) *Incorrect scaling of concepts*. There are several problems in scaling up the concepts of evolution within present-day communities on an ecological time scale to major features of the history of life on a palaeontological time scale.

The first problem is that the concepts of microevolution, including intra- and interspecific competition, may be wholly inappropriate to macroevolution. Competition may be important in determining the extinction and replacement of species in particular localised communities, but that does not mean that it has anything to do with the worldwide extinctions and replacements of higher taxa over millions of years. Palaeontologists tend to use the term 'competition' in different ways from ecologists. They often apply it to supraspecific taxa, and there is little evidence for such a process above the species level. Palaeontological data on 'competition' usually apply to the continental or the global scale, whereas the ecological literature refers to much smaller areas. In palaeontology, too, time scales are generally many orders of magnitude greater than in ecological studies (millions or tens of millions of years compared with time spans of generally less than 10 years). Finally, palaeontologists tend to use data on numbers of species, genera or families, and they point to extinction and speciation caused by competition. Ecologists, on the other hand, generally refer to individual organisms, and there is no known example in the ecological literature of global extinction caused by competition. Faunal replacement and mass extinction are not phenomena that can be predicted from the principles of community ecology and microevolution.

The second problem of scaling identified by Gould & Calloway (1980) concerns adaptive explanations for the success of whole groups: bivalves or dinosaurs are said to have particular superior adaptations to brachiopods or mammal-like reptiles respectively. Such adaptations might be to the advantage of the first species to possess them: the first bivalve that had mantle fusion and siphons, or the first dinosaur that had erect gait and inertial homeothermy. However, it is hard to see how adaptations of these kinds can have much relevance for higher taxa, whether viewed in a reductionist way (what are the selective advantages of the same adaptation in dozens or hundreds of different species?) or in a holistic way (what are the rules for particular 'adaptations' of orders, classes or phyla?). The first bird with efficient wings was at a competitive advantage over his non-flying dinosaur relatives since he could catch flying insects better. But is this true of every subsequent bird species? The possession of wings by

birds (a key adaptation) has more probably allowed them to adopt a variety of new lifestyles and to radiate into largely empty ecospace in an essentially non-competitive way. Some taxa simply have a greater capacity than others to adopt a wide range of morphologies (high versatility: Vermeij, 1973), and thus to diversify and fill a wider range of niches (? e.g. bivalves vs. brachiopods archosaurs vs. mammal-like reptiles). However, this capacity is not an 'adaptation for success', but a boundary condition that becomes evident in terms of the diversity of shapes and sizes within a particular taxon after a radiation has taken place.

A third problem of the scaling of 'competition' concerns the amount of time involved. Most so-called competitive replacements lasted over millions of generations, and it is hard to envisage a constant competitive advantage that lasted so long and persistently favoured all of the species of one large taxon against all of the species of another in all environments. In the cases described above, the process of replacement lasted from 2–100 Ma, and even in the shortest of these time spans, the differential competitive advantages would have been so miniscule that it is hard to envisage how they could have been maintained for so long in the face of random environmental changes. In this respect, long-term patterns of replacement could just as well be stochastic as the result of prolonged one-way competition. The problem is akin to that cited by Gould (1980, p. 103) as a drawback of an extreme form of gradualism: '... to see gradualism at all in the fossil record implies such an excruciatingly slow rate of per-generation change that we must seriously consider its invisibility to natural selection in the conventional mode – changes that confer momentary adaptive advantages' (see also Dawkins, 1982, p. 103; Stanley, 1985, p. 21).

VII. SUMMARY

(1) Progressive improvement and competition have been seen by many biologists and palaeontologists as appropriate models of macroevolution, but that view is challenged here.

(2) Evolutionary progress (improvement in competitive ability through time) is hard to reconcile with the neodarwinian view of evolution. Orthogenesis and finalism must be excluded from any definition of progress, but these modern definitions are still *ad hoc*, and inevitably place *Homo sapiens* at the top of the pile. It has not been demonstrated that increases in morphological complexity correspond to better adaptation, that life has expanded in anything but an opportunistic way, that evolutionary trends show improving competitive ability, or that adaptations become increasingly effective through time.

(3) Many studies of modern communities have shown that interspecific competition plays a smaller evolutionary role than has been assumed, and alternatives have been proposed. Predation, abiotic factors, and chance may be just as important for many communities.

(4) Competition is a mainstay of several general macroevolutionary theories. The assumption that most species extinctions have been caused by competition is based on the probably incorrect assumptions that there is a fixed number of niches on the Earth, and that evolution is necessarily progressive. The Red Queen hypothesis, that species evolve as a result of biotic interactions ('diffuse competition'), has been hard to test: the available data from the fossil record could equally well be explained by static or

stationary models in which adaptations do not constantly track a deteriorating biotic environment. The community paradigm assumes that communities are real evolutionary units, moulded by biotic interactions, but it makes assumptions that ecologists now question. Finally, it has been proposed that evolutionary rates are determined by the levels of interspecific competition within different groups, but there are problems in defining evolutionary rates, and in determining levels of competition in specific taxonomic groups.

(5) In macroevolutionary studies, 'competition' between families, orders, classes or phyla is often cited as an explanation for major replacements in the past. However, there is a two-stage problem here. The relevant pattern (the 'double-wedge' pattern, in which the shapes of two clades are negatively correlated) must first be demonstrated from the fossil record, and only then can competition be considered as the mechanism.

(6) Most examples of supposed large-scale competition in the fossil record turn out to be nothing of the sort (Raup, 1981). In many cases the true pattern seems to be 'mass-extinction', rather than 'double-wedge'. Thus, competition is not indicated as the cause of extinction, but rather opportunistic replacement after an abiotically induced extinction event.

(7) Competition may be involved in the subsequent radiation of the replacing group: it could have a key adaptation that enables it to resist extinction, or which assists the adaptive radiation into empty ecospace. In other cases, both the extinction of one group, and its replacement by another, might involve no key adaptation, and no competition. There are five key adaptation models for major ecological replacements, and they ought to be tested before long-term competition is assumed.

(8) If a 'double-wedge' pattern is demonstrated in the fossil record, it could be a chance association of two taxa that never interacted, or it could be caused by selective predation, by differential response to a slowly changing environment, or by competition.

(9) The term 'competition' has frequently been misused in studies of macroevolution. It has often been an unproven assumption, patterns and mechanisms have been confused, and competition scenarios tend to be highly simplified explanations of what were probably complex processes. These are also problems of scaling, in applying concepts such as competition, adaptation and selection pressure to large-scale and long-term aspects of evolution, when they are currently only applicable to ecology and microevolution. If 'competition' exists at supraspecific levels, a new theory of competition in macroevolution will have to be developed.

VIII. ACKNOWLEDGEMENTS

I thank the President and Fellows of Trinity College, Oxford, for financial support during the earlier part of this work, and G. R. Chancellor, K. A. Joysey, T. S. Kemp, and W. I. Montgomery for their helpful and stimulating comments on different versions of the manuscript.

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