2.4 Heterochrony

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Introduction

Heterochrony is the phenomenon of changes through time in the appearance or rate of development of ancestral characters. While the recognition of a close relationship between ontogeny and phylogeny has a long history it was not until the late nineteenth century that it was formalized by E. Haeckel in his 'Biogenetic Law' (ontogeny recapitulates phylogeny). This involved a change in the timing of developmental events; but only in one direction — by terminal addition. Phylogenetically this meant that ancestral adult forms were encapsulated in the juvenile stages of their descendants. This became known as recapitulation.

Exceptions to this rule (known as 'degenerate' forms) were noted by the leading protagonists of recapitulation, particularly palaeontologists such as A. Hyatt (ammonites), R. Jackson (echinoids and bivalves), and C. E. Beecher (trilobites and brachiopods). With the awareness that these so-called degenerate forms were at least as common as examples of recapitulation, the Biogenetic Law began to slide into oblivion.

In the nineteen-twenties W. Garstang recognized that ontogeny did not always recapitulate phylogeny — it created it. Garstang believed that the retention of ancestral juvenile characters by descendant adults, which he termed *paedomorphosis*, was the key to understanding the evolution of many major groups of organisms, in particular the evolution of vertebrates from tunicate larvae. However, recent research has shown that both paedomorphosis and 'recapitulation' play important roles in evolution (Gould 1977; Alberch *et al*. 1979; McNamara 1986a; McKinney & McNamara 1991).

Nomenclature

Heterochrony involves the decoupling of the three fundamental elements of growth: size, shape, and time, or the extension or contraction of these elements. Temporal changes of size and shape relative to one another produce heterochrony, when either size or shape, or both, are affected by changes in their rate of ontogenetic development. Changes to the timing of onset or cessation of morphological development and size change can also produce heterochrony. If size alone changes between ancestor and descendant, *dwarfs* or *giants* are produced.

If the rate of shape change is increased, or its period of operation is extended, the descendant adult passes morphologically 'beyond' the ancestor: this is *peramorphosis* (this equates, to some degree, with the Haekelian 'recapitulation'). Conversely, if the rate of shape change is reduced, or its period of operation is contracted, the descendant adult passes through fewer growth stages, so resembling a juvenile stage of the ancestor: this is *paedomorphosis*.

These terms can be applied not only to the appearance of meristic characters (in other words, individual structures produced during an organism's ontogeny) but also to subsequent changes of shape of these structures during ontogeny. Thus not only may the rate of induction of structures vary, but the structures which are produced may show phylogenetic changes as they vary their rate of shape change. These two basic forms of heterochrony are known respectively as *differentiative heterochrony* and *growth heterochrony* (Figs 1, 2).

The relationship between size and shape is known as *allometry*. If the relative size and shape of a structure remain the same relative to overall body size during ontogeny, growth is *isometric*. However, if a particular structure increases in size relative to the whole organism, as well as changing its shape, growth shows *positive allometry*. Should a structure decrease in relative size, growth shows *negative allometry*. Increasing the degree of allometry is expressed phylogenetically as peramorphosis. Reducing it produces paedomorphosis. Similarly, extending or contracting the period of allometric growth produces peramorphic or paedomorphic descendants respectively.

Paedomorphosis and peramorphosis are morphological expressions of heterochronic processes. Paedomorphosis can occur by *progenesis, neoteny*, or *post-displacement* (Fig. 1). Peramorphosis can occur by *hypermorphosis, acceleration*, or *pre-displacement* (Fig. 2).
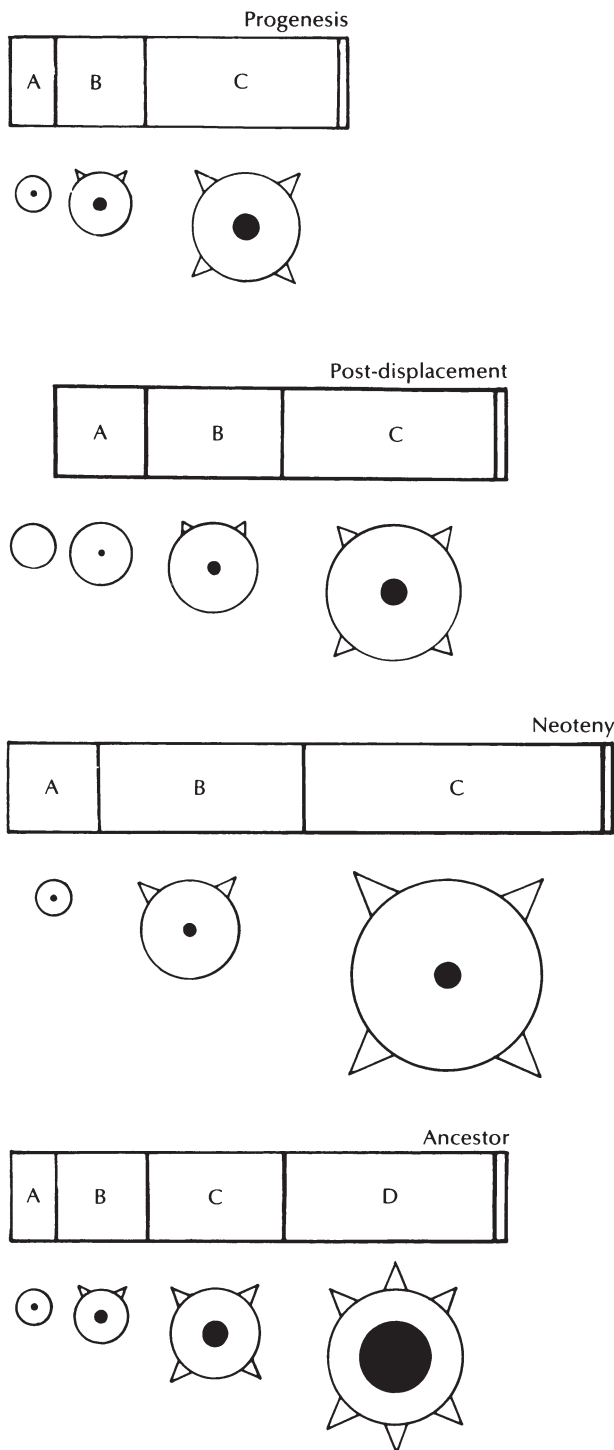
Fig. 1   The relationship of the three paedomorphic processes to the ancestor. *Progenesis* occurs by precocious maturation, *post-displacement* by the delayed onset of growth, and *neoteny* by reduced rate of morphological development. *Differentiative paedomorphosis* is shown by the spine production, *growth paedomorphosis* by the central spot. (From McNamara 1986a.)

Progenesis often occurs by precocious sexual maturation. Consequently morphological and size development is prematurely stopped, or severely retarded. The resultant adult paedomorph will be smaller than the ancestral adult. The prematuration morphological history of both the progenetic form and its ancestor will be identical. Progenesis is often global, affecting all structures, but it may also affect local growth fields. Some characters, however, are likely to have a more distinctly juvenile appearance than others. Thus, in the fossil record, it is generally possible to deduce the operation of progenesis: the morphotype is smaller than its presumed ancestor and resembles a juvenile stage of the ancestor. It will, however, be appreciably larger than the corresponding ancestral juvenile stage.

Neoteny is reduction in rate of morphological development during juvenile growth. If maturity occurs at the same age in both ancestor and descendant, they will be the same size. Often onset of sexual maturity is delayed in neotenic forms, consequently the neotenic forms attain a larger adult size. Neoteny may be global in its effects on the organism, or dissociated when it affects only certain morphological structures. Reduction in degree of allometry of specific structural elements will result in neoteny. Unlike progenesis, where the juvenile ontogenetic trajectories of ancestor and descendant are alike, juvenile growth trajectories are different between ancestors and descendants.

Post-displacement occurs by changes to the timing of onset of growth of particular morphological structures. Thus, by comparison with the ancestor, a structure commences development at a later stage, compared with other parts of the organism. Should subsequent development and cessation of growth be the same in the descendant as in the ancestor, the displaced structure will attain a shape at maturity resembling that found in a juvenile of the ancestral form. The displaced structure is also likely to be smaller than in the ancestor.

Hypermorphosis occurs by extending the juvenile growth period, by a delay in the onset of sexual maturation. Early juvenile development will progress at the same rate as in the ancestor. By extending growth allometries to a larger size, the hypermorphic adult can attain morphological characteristics quite distinct from those of the ancestral adult. Like progenesis, hypermorphosis is often global in its effects, but it too can affect only local growth fields.
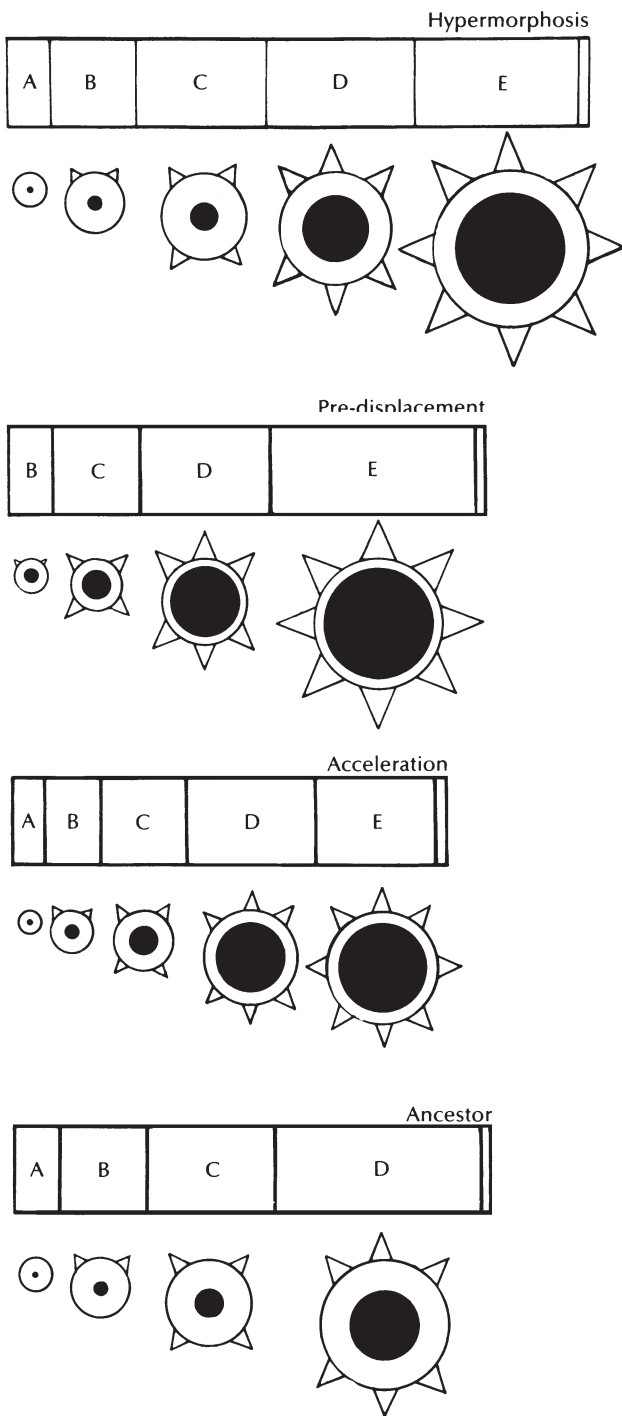
Fig. 2 The relationship of the three peramorphic processes to the ancestor. *Hypermorphosis* occurs by delayed sexual maturation, *pre-displacement* by earlier onset of growth, and *acceleration* by increasing the rate of morphological development. The spines and central spot demonstrate *differentiative* and *mitotic peramorphosis*, respectively. (From McNamara 1986a.)

Acceleration of rate of morphological development during ontogeny will produce a peramorphic descendant. In allometric terms, acceleration is an increase in the degree of allometry. For meristic characters it is an increase in the rate of production of structures. If acceleration is operating only on specific structures, then there need be no overall increase in body size. However, the particular structure is likely to be larger. As with neoteny, juvenile ontogenetic growth trajectories will be different in the ancestor and descendant.

Pre-displacement involves the earlier onset of growth of a specific structure. This allows a longer period of growth and development. Ancestral allometries will therefore, in effect, be extended. The resultant structure will be more advanced morphologically and larger than the equivalent structure in the ancestral adult, so long as cessation and rate of growth are identical in ancestor and descendant.

The identification of heterochronic processes in the fossil record is generally based on the precept that these processes can be characterized by the study of size and shape alone. The assumption is made that size is a proxy for time: the larger the organism, the longer period of time it took to reach that size. This assumption may not always be valid. Shea (1983) has suggested that two forms of progenesis and hypermorphosis can be recognized. In the first, time and size are not dissociated; thus smaller size correlates with shorter time, larger size with longer time. This Shea calls 'time hypomorphosis (= progenesis)'. The corresponding peramorphic process is time hypermorphosis. In the second case the progenetic form attained its reduced size and shape in the same amount of time that the ancestor took to attain maturity. This occurred because the rates of size and shape change were equally reduced through ontogeny compared with the ancestor. This Shea termed 'rate hypomorphosis (= progenesis)'. Time and rate progenesis or hypermorphosis can theoretically be distinguished in the fossil record. Early ancestral and descendant ontogenies will be the same when time progenesis has occurred, whereas they will differ in rate progenesis. Future emphasis on the study of growth lines in suitable invertebrate groups, such as molluscs, corals, and echinoids, will allow the true rates of growth of fossil organisms to be ascertained (McKinney 1988).

Heterochrony at different hierarchical levels

While most of the literature dealing with heterochrony as a factor in evolution concentrates on its role at the specific or supraspecific level, it needs to be stressed that much recognized intraspecific morphological variation in populations is, in fact, engendered by heterochronic processes. These act upon both meristic and allometric traits. For instance, intraspecific variation in ammonites often involves variation in the numbers of ribs or tubercles generated at a certain size. Similarly, in echinoids intraspecific variation often involves differences in the rate of production of meristic characters, such as the number of coronal plates and spines. Variation in numbers of these structures between two individuals of the same size may be accounted for either by variations in rates of development (neoteny or acceleration) or by onset and offset of growth (pre- or post-displacement and progenesis or hypermorphosis).

However, variations in rate of size increase may also produce such intraspecific differences. Thus if two individuals from a single population each 20 mm in length possess, in one case, six spines, and in the other eight, this may reflect a variation in rate of spine development (neoteny or acceleration), if both attained 20 mm in the same period of time. Alternatively, the individual with six spines may have increased in size at a faster rate through ontogeny, and thus only have had sufficient time to generate six spines. It is possible to test whether this latter mechanism has occurred by analysing the developmental patterns of other structures. For instance, if one of these organisms reached a length of 20 mm faster than the other, then all of its structures should appear relatively paedomorphic. However if, as is often the case, intrapopulational variation shows some characters to be paedomorphic and others peramorphic, then rates of structural development will have changed.

Selection of heterochronic morphotypes, and the resultant morphological evolution of a new species, is reflected in substantial shifts in the mean values of heritable phenotypic variation of shape or size of morphological structures. These occur by perturbations to the developmental programme. These may be under strong directional selection pressure (see below). Evolution of a substantial new heterochronic morphology may result in the evolution of new adaptive structures. These allow either geographical or ecological separation from the ancestral stock, and subsequent genetic isolation and estab-

lishment of a new species (see also Section 2.2).

In recent years documentation of heterochrony in the fossil record at the interspecific level has been undertaken in particular on ammonites (see McKinney 1988), echinoids (McNamara 1988), and trilobites (McNamara 1986b). It has been suggested (McNamara 1982) that heterochrony may be one of the factors responsible for rapid speciation events. This is particularly so where progenesis or hypermorphosis have occurred. However, gradual, phyletic changes may equally well be engendered by small modifications in growth rates between populations, resulting in subtle shifts in morphology through time.

Heterochrony has been proposed as a major factor in evolution at the supraspecific level. For instance, the orthodox view of the origin of vertebrates is that they may have arisen from the pelagic larva of a tunicate-like deuterostome invertebrate. This would have occurred by progenesis from an early larval stage. The free-swimming tunicate larva possesses all the fundamental chordate characters: a notochord, dorsal hollow nerve cord, gill slits, and post-anal propulsive tail. Attainment of precocious sexual maturation would have caused the retention of such ancestral larval characters into the adult phase and a consequent major adaptive breakthrough.

The earlier that perturbations to the embryological developmental system occur, the more profound the morphological consequence. Taxonomically, this is likely to be expressed at a high level. For instance, it has been suggested (McNamara *in* McKinney 1988) that progenesis at early developmental stages has been instrumental in the evolution of a number of higher taxa: saleniid, tiarechinid, neolampadoid, and clypeasteroid echinoids; edrioasteroids; baculitid ammonites; thecideidine and craniacean brachiopods; and branchiosaurid amphibians (Fig. 3).

Other heterochronic processes have also been instrumental in the evolution of higher taxa. For instance, it has been proposed that birds may have evolved from theropod dinosaurs. The very large orbits of birds, their inflated braincase, retarded dental development, and overall limb proportions indicate that early birds may have been paedomorphic theropods. Feathers are thought to have been present on juvenile theropods. The paedomorphic processes were probably neoteny and post-displacement.
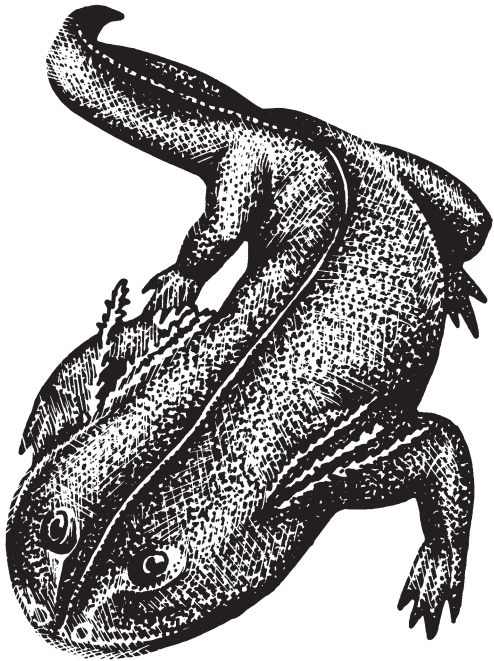
Fig. 3 Reconstruction of a paedomorphic branchiosaurid amphibian.

Heterochrony and directed speciation

The pattern that is emerging from studies of heterochrony in the fossil record is one of frequent directed heterochronic speciation. The direction of morphological evolution is strongly constrained by the nature of the organism's own ontogeny. Thus a number of characters in a lineage may show progressive paedomorphosis or peramorphosis. Provided that the descendant morphotypes are suitably adapted along an environmental gradient, a phylogenetic trend, in the form of a *paedomorphocline* or *peramorphocline*, may develop. The environmental and morphological directionality may be induced by the effects of either competition or predation. With induction of the heterochronic morphological gradient by competition, the persistence of the ancestral form constrains selection to one direction: along the environmental gradient away from the ancestral species. The phylogenetic pattern generated will be one of cladogenesis. Selective pressure from predation in one environment may induce the evolution of a paedo- or peramorphocline. In this case the phylogenetic pattern is one of anagenetic speciation.

Recent studies of echinoids, brachiopods, bivalves, ammonites, graptolites, and ammonites (see McNamara *in* McKinney 1988) indicate that the anagenetic pattern is common. Specific examples

include the evolution of a number of anagenetic paedo- and peramorphoclines in spatangoid echinoids, such as *Schizaster, Hemiaster, Lovenia, Pericosmus*, and *Protenaster* (Fig. 4). All show evolution from coarse to fine-grained sediments (probably shallow to deep water). Conversely, the Cenozoic brachiopod *Tegulorhynchia* evolved along a paedomorphocline from deep to shallow water into the genus *Notosaria* (Fig. 5). Similarly a number of trilobite lineages are thought to have evolved by heterochrony along the same environmental gradient (McNamara 1986b). In the marine environment changing water depth and sediment type are frequent environmental gradients along which paedo- and peramorphoclines develop.

Ecological causation of heterochrony

While many of the examples of directed heterochronic evolution have been interpreted as having arisen by selection of morphologically adaptive characters, it has also been argued that other factors, such as life history strategies, which affect elements such as size and time of maturation, may also be targets of selection. McKinney (1986) has suggested that for a suite of Tertiary echinoids selection favoured large forms along an environmental gradient from shallow to deep water (equating with unstable to stable environments) (Fig. 6). He argued that any subsequent morphological changes were incidental allometric by-products of the size change. The larger size was attained either by slower, neotenic growth or by extended, hypermorphic growth. This indicates that the target of selection was reproductive timing and/or body size. Such size increase along lineages (Cope's Rule; Section 2.10) may reflect *K*-selective pressure (large body size, delayed reproduction and development, and longer life spans in a stable environment).

While analyses of other echinoid lineages does not provide unequivocal corroboration of this pattern, there is ample evidence that many progenetic species are, conversely, *r*-selected (small body size, early maturation, high fecundity, and short life span in an unstable environment). Many so-called 'dwarfed' faunas may be *r*-strategists, inhabiting unstable, fluctuating environments. The small body size of progenetic Late Cretaceous oysters and ammonites may have been an adaptation to a soft, unstable substrate. The same is true for many progenetic brachiopods. High fecundity of progenetic species has been documented in edrioasteroids and trilobites (McNamara *in* McKinney
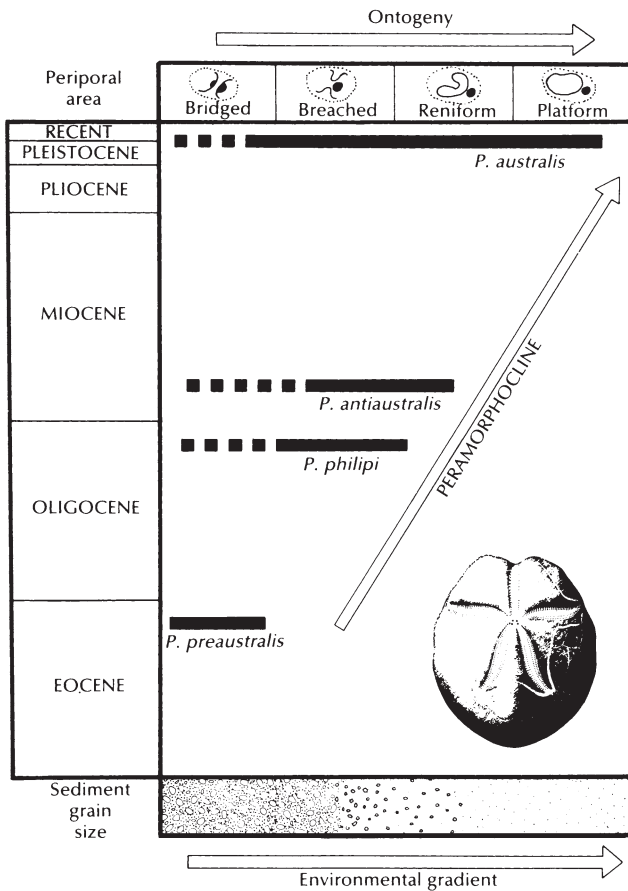
Fig. 4 Peramorphocline in the evolution of the periporal area in the Cenozoic spatangoid echinoid *Protenaster*. Later species underwent greater morphological change in this character than earlier species. This led to the ability of later species to feed from progressively finer grained sediments. (From McNamara 1985.)

Fig. 5 Paedomorphocline in the evolution of the umbonal region of the Cenozoic rhynchonellid brachiopods *Tegulorhynchia* and *Notosaria*, showing paedomorphic retention of larger foramen (and hence thicker pedicle) and smaller umbonal angle. The environmental gradient along which the paedomorphocline evolved was from deep to shallow water. (From McNamara 1983.)

1988). Although in these cases small size and precocious maturation may have been the principal targets of selection, unless the resultant progenetic morphology was also adaptively significant in the new environment, selection would not have occurred.

Most heterochronic changes occur as a result of changes to the internal developmental regulatory system. However, certain changes may actually be induced by environmental perturbations. The effect of changing environmental pressures may lead to facultative heterochrony within populations. For instance, the frequency of development of paedomorphs in living populations of salamanders is directly influenced by the population density. When low, a large proportion of individuals develop as neotenic paedomorphs, attaining maturity in their larval form, so remaining and reproducing in the aquatic environment. At high population densities
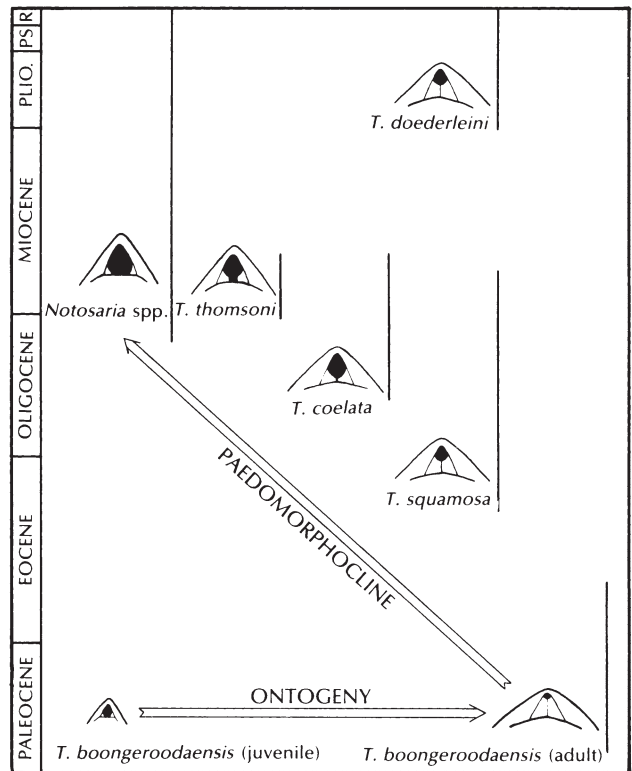
few individuals are paedomorphic, the high density levels inducing metamorphosis to the terrestrial form.

There is also indirect evidence from the fossil record (McNamara 1986b) that changes in water temperature at different water depths in the marine environment may have been a factor in inducing progenesis in a number of lineages of Cambrian trilobites. Experimental work has demonstrated the effect of higher temperatures in inducing premature maturation in some living arthropods.
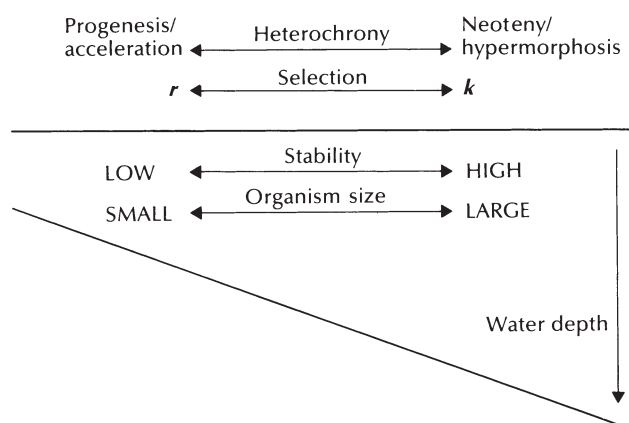
Progenesis/ acceleration ← Heterochrony → Neoteny/ hypermorphosis

r ← Selection → k

LOW ← Stability → HIGH

SMALL ← Organism size → LARGE

Water depth

Fig. 6 Diagrammatic summary of McKinney's (1986) proposed relationship between water depth, ecological stability, selection, organism size and heterochronic process, based on a suite of Tertiary echinoids from southeastern U.S.A.

Frequency of heterochrony in the fossil record

Any attempt to assess the frequency of heterochrony or of the heterochronic processes is fraught with problems, not the least of which are historical prejudices. While the Haeckelian school were blinkered to the existence of paedomorphosis, the Garstang/de Beer school were equally contemptuous of peramorphosis. In a recent survey of palaeontological literature from 1976 to 1985, McNamara (in McKinney 1988) documented 272 examples of heterochrony; of these, 179 were of paedomorphosis, the remaining 93 were of peramorphosis.

The most comprehensive recent analyses of heterochrony in the fossil record have centred on trilobites, echinoids, ammonites, bryozoans, and graptolites. These studies have shown both paedomorphosis and peramorphosis to be important factors, but paedomorphosis still predominates. The greater frequency of paedomorphosis, if true, may occur because existing developmental programmes are utilized. Peramorphosis always requires the production of novel bauplans by extending the pre-existing developmental pathways.

Trilobites show a changing relative frequency of paedomorphosis and peramorphosis. During the Cambrian paedomorphosis, particularly that induced by progenesis, was predominant. Post-Cambrian forms, however, show a marked decline in the incidence of progenesis and a greater frequency of peramorphosis. It has been argued (McNamara 1986b) that this change may reflect an improvement in regulation of the developmental system in later trilobites.

Recent analysis of heterochrony in irregular echinoids (McNamara 1988) has highlighted the complex activity of heterochrony in single lineages, some characters being paedomorphic, others peramorphic. Furthermore, one paedomorphic structure might have evolved by neoteny, whilst another might have formed by post-displacement. The operation of a complex array of heterochronic processes has been termed *mosaic heterochrony*. With each structural element of an organism essentially following its own ontogenetic trajectory, and each being potentially subject to changes in developmental regulation, there is the possibility of the evolution of a multitude of heterochronic morphotypes. Any one of these may potentially form a new species, with the target of selection being the resultant morphotypes, size, or life history strategies.

Ammonites have featured prominently in studies of heterochrony for over 100 years. They were used initially as examples of 'recapitulation', by Hyatt and co-workers; while to O. Schindewolf and other workers in the first half of this century they showed evidence only of paedomorphosis. Recent research (see McKinney 1988) has shown the ubiquity of both phenomena, but peramorphosis, particularly of the septa, appears more common than paedomorphosis.

Colonial organisms, such as bryozoans and graptolites, show a two-tiered heterochronic pattern. Both the individual animals and the colony as a whole may be affected by heterochrony. The former is known as *ontogenetic heterochrony*, the latter as *astogenetic heterochrony*. This two-tiered structure is comparable with the two-tiered structure of diffentiative and mitotic heterochrony present in non-colonial organisms. Astogenetic heterochrony has been reported more often than ontogenetic heterochrony (McKinney 1988), perhaps because astogenetic changes reflect developmental modification of ontogenetic characters, so reflecting the individuality of the colony as a whole. Heterochrony in colonial organisms may have been important in macroevolution. Ontogenetic heterochrony in highly integrated colonies may result in large morphological differences between ancestor and descendant. It would appear that periods of reef building correspond to periods of high integration in colonial animals. It is likely, therefore, that astogenetic heterochrony will predominate during periods of reef building.

Many of the examples of heterochrony involving vertebrates occur in amphibians. Most of these show paedomorphosis, akin to that seen in living

salamanders. Many of the interspecific and inter-generic differences in allometry of skull plates in Palaeozoic fishes are the result of mitotic hetero-chrony, though few studies have actually couched it in these terms. Similarly, phylogenetic changes in limb allometries in mammals are due to hetero-chrony. The limited evidence from studies of mammals seems to suggest a predominance of peramorphosis over paedomorphosis. This may occur because of the frequent operation of Cope's Rule in mammal lineages, suggesting size as being an important target of selection. For example, exten-sion of ancestral allometries by increased size in horses through the Tertiary resulted in peramorphic descendants by hypermorphosis. However, some characters, such as development of the foot, show paedomorphic reduction in some digits.

Developmental processes underlying heterochrony

Changes to the onset, offset and rate of growth of morphological characters are essentially under three interactive levels of control: genetic, hormonal, and cellular. Perturbations to the genetic regulation of hormonal and cellular development, particularly at early embryological stages, are likely to be critical factors in heterochrony.

Developmental regulation is not simply a matter of discrete entities called 'regulatory genes' acting upon 'structural genes'. It involves a complex inter-action between active sites or structural components of proteins, combined with cell–cell interactions (Campbell & Day 1987). Developmental processes are controlled by highly organized, dynamically structured multigene families. The manner in which the genome is encoded and expressed in develop-ment is far from clear, although it would seem that only a small area of the highly dynamic, constantly changing genome is occupied by genes for development.

The region involved in regulation in a typical eukaryote gene is the promotor region. This contains DNA binding proteins specific to the gene, and capable of controlling the level of transcription. The role of the promoter sequence in gene control, and its effect on growth, highlights the activity of hor-mones in growth, and how perturbations to the genetic control of hormone production can have a strong phenotypic expression.

Growth, moulting, and sexual reproduction in arthropods, for instance, are all under hormonal control. It has been suggested (Campbell & Day 1987) that hexapods evolved from a myriapodous ancestor by progenesis: a small change in the genetic control of the hormone responsible for the incep-tion of maturation, and of the hormone controlling post-larval development, had a profound effect on the phenotype. Even within fossil lineages the activity of genes controlling hormone production can be inferred. Two forms of progenesis in trilo-bites have been identified: *sequential* and *terminal* (McNamara 1986b). Terminal progenesis is likely to have occurred by a premature cessation in pro-duction of a juvenile hormone. Sequential pro-genesis, where each intermoult period is shortened, is thought to have occurred by premature pro-duction of an ecdysone-like moulting hormone during each intermoult period. This premature hormonal activity will have been under direct genetic control.

The third factor in the developmental processes that cause heterochrony is activity at the cellular level. Hall (1984) has stressed the importance of the number and mitotic activity of the cells in the initial skeletal condensation in vertebrates. Thus onset of growth is determined by the number of stem cells that start condensation, the proportion that divides, rate of cell division, and amount of cell death. These parameters all act early in development and deter-mine the time of onset of growth. The rate of growth of skeletal elements is influenced by adjacent tissues, hormones, and allometric factors. Muscle action, tendon insertion, blood flow, innervation, and growth of adjacent tissues modulate the growth rate. Cessation of growth is partially determined very early in development by the number of growth plate cells and the number of times they divide. Timing of development of secondary ossification centres also affects the offset signal. Metabolic inhibition by production of a growth inhibitor to suppress cell proliferation and protein synthesis also stops growth.

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2.5 Red Queen Hypothesis

M. J. BENTON

Introduction

Palaeontologists have long argued that the distinctive features of the evolution of life were produced by changes in the physical environment. Changes in climate, or in sea-level, for instance, might explain why certain groups died out, or why an adaptive radiation took place at a particular time. This trend has continued in recent research into mass extinctions (Section 2.12), whether their cause is said to be changes in the earthbound physical environment, or the impact of asteroids.

On the other hand, many ecologists have viewed the large-scale aspects of evolution (macroevolution) as simply a scaled-up version of microevolution. Evolutionary change, they argue, can be produced by competition between organisms, and by interactions between predators and prey. This ecological view stresses the influence of the biotic environment, that is, other plants and animals, on evolution.

Van Valen's Law

The ecological view of macroevolution was codified by Van Valen (1973), who presented palaeontological and ecological evidence for a model of evolution that depended on the biotic environment, and termed the model the *Red Queen Hypothesis*. The palaeontological evidence was based on a study of the rates at which different groups of plants and animals go extinct through time. Van Valen used plots of species survivorship (Fig. 1) which showed the proportions of an original sample of organisms that survive for various intervals. He found, contrary to his expectations, that the probability of extinction within any group remained constant through time — his *Law of Constant Extinction*. For example, families or species of modern mammals are just as likely to become extinct as were their Mesozoic ancestors living 200 Ma. A species might disappear at any time, irrespective of how long it has already existed. Evolutionary biologists might have intuitively expected species within any group to become longer-lived over time on average. Van Valen's startling discovery seemed to deny some basic assumptions of evolution. If evolution is taken to mean improvement in the adaptation of a species to its environment through time, why is it that modern mammals are not better at surviving than their Mesozoic forebears?

Van Valen's explanation for the Law of Constant Extinction was that the various species within a community maintain constant ecological relationships relative to each other, and that these interactions are themselves evolving. Thus, the antelope on an African savanna, for example, evolves greater speed in order to escape from the lion, but the lion
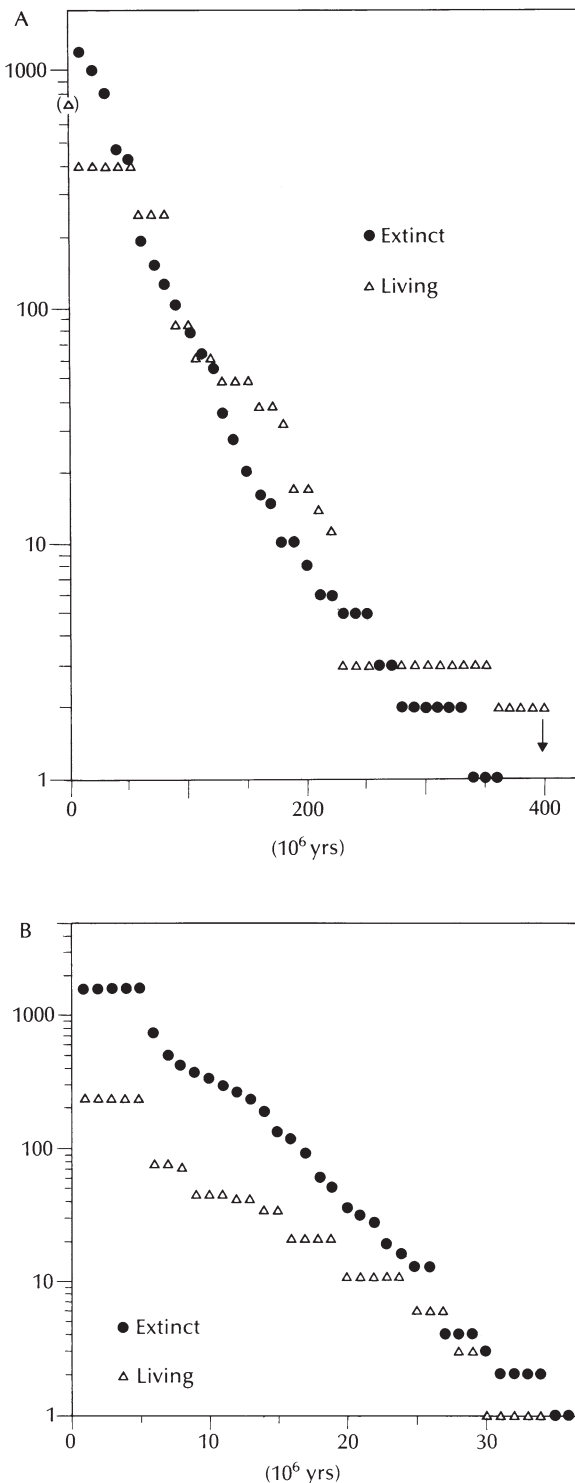
also evolves greater speed in order to catch its dinner. The status quo is maintained. If biotic interactions did not follow a pattern of ever-moving dynamic equilibrium, the community would be shattered. Were all antelopes to achieve a quantum improvement in their running speed, lions would starve and populations of antelope might outstrip the carrying capacity of the environment. This balance is the Red Queen Hypothesis. [In Lewis Carroll's *Through the Looking Glass*, the Red Queen told Alice, 'Now here, you see, it takes all the running you can do, to keep in the same place'.]

After 1973, many biologists accepted the Red Queen model, while others were critical. The main problem was simply the counter-intuitive claim that species do not improve their chances of survival through time. If organisms are continuously evolving and adapting, why do they not get any better, on average, at avoiding extinction? There were problems also with Van Valen's particular formulation of the Red Queen model. He explicitly made a zero-sum assumption: that there were fixed amounts of energy available to communities, and that any gain by one species was exactly offset by equal losses to others. It is not at all clear, however, that the amounts of energy, or resources in general, have remained constant through time. It is equally probable that the total global biomass has increased markedly many times as major new habitats were exploited (e.g. the move onto land (Section 1.8), the evolution of 'trees', the origin of flight (Section 1.9), and the evolution of deep-burrowing habits by various marine groups (Section 1.7.1)). The increase in biomass is possible by pulling more of the global carbon into the biotic part of the biogeochemical cycle, and/or by speeding up the rate at which carbon, and other essential elements, are cycled through the system (Benton 1987).

Problems with 'progress', and the Stationary Model

Although the Red Queen model does not predict improvements in the ability to avoid extinction, it does explicitly assume that, within any lineage, later members will be competitively superior to earlier ones: that a present-day antelope can run faster than its Pliocene forebear, that modern mammals are clearly competitively superior to their Palaeocene ancestors. This notion of progress is frequently assumed by biologists and palaeontologists, but is probably impossible to test directly. Nevertheless, simple assumptions of progress of this kind have

Fig. 1 Taxonomic survivorship curves for A, pelecypod (bivalve) and B, mammalian genera (major Therian orders). These graphs show roughly linear trends, and indicate constant probabilities of extinction for genera of any duration. (After Van Valen 1973.)

been criticized recently (Benton 1987). There seems to be no adequate way yet of demonstrating 'progress' in macroevolution, least of all competitive improvement. The evolution of horses can be taken as a well known example of an adaptive trend, or record of improvement through time. The early small leaf-eating horses of Eocene times gave way to larger animals with fewer toes (greater running speed) and deeper teeth (for grinding up the new silica-bearing grasses) in the Miocene (Section 1.11). However, if the fossil record were reversed, we could equally well demonstrate how the horses adapted to the diminishing grasslands by becoming smaller forest-dwellers, living a cryptic life and switching to a diet of tree leaves. Where is the progressive improvement of competitive ability? The whole question seems to hinge on how macroevolution is viewed. If organisms are generally very well adapted, finely tuned by natural selection, and if the physical environment has only minor effects, the Red Queen Hypothesis has to hold. If, on the other hand, organisms are viewed as only moderately well adapted, natural selection as only a sporadic force for evolutionary change, and the physical environment as an important influence through local and global extinction, and radiation events, then the Red Queen Hypothesis cannot be correct.

In 1984 Stenseth and Maynard Smith formalized an alternative to the Red Queen model, termed the *Stationary Model*. This model assumes that evolution is driven mainly by abiotic factors, and that it will cease in the absence of changes in the physical environment. The two models make very different predictions and, as Stenseth and Maynard Smith (1984) wrote, 'the choice between the Red Queen and Stationary Models will have to depend primarily on paleontological evidence'.

The Red Queen model predicts that the rates of speciation, extinction, and phyletic evolution will remain constant in ecosystems, even when the diversity of species has reached equilibrium so that the numbers of species do not change. The Stationary Model, however, predicts that at equilibrium no evolution will occur. Bursts of evolution, extinction, and speciation will happen only in response to changes in the physical environment. These two models can be visualized by plots of species survivorship over time, which gives a measure of the rate of extinction (Fig. 2A, B).

Testing the models

Hoffman and Kitchell (1984) applied a palaeonto-

logical test. The first problem they encountered was to find an example spanning several million years in which no environmental change had occurred. Such a case is highly unlikely, and it proved necessary to make allowances for episodic perturbations in the physical environment. The modified patterns are still distinctive (Fig. 2C, D). The Red Queen model predicts an approximately regular decline in the number of species surviving (that is, constant extinction), with occasional changes of slope that correspond to major environmental perturbations. The Stationary Model predicts a distinctly stepped pattern, with constant numbers of species at equilibrium, and sudden extinctions at times of environmental change.

Hoffman and Kitchell (1984) also examined the records of microfossils (coccoliths, foraminiferans, radiolarians, diatoms, and others) from 111 deep-sea boreholes through the past 50 million years of sediments of the Pacific Ocean floor. The species survivorship curves obtained from these data (Fig. 3) are more or less smooth, rather than stepped, and they seem to support the Red Queen model. An analysis of the cumulative appearance of new species also gave general support to the Red Queen model, although there was some evidence of stepping.

Further analysis shows there to be considerable variation in the probability of extinction over geological time: for example, there seem to have been particular periods in which all the microfossil groups had high extinction rates. These indicate plankton extinction events which would normally be attributed to sharp changes in the physical environment. When Hoffman & Kitchell (1984) made allowances for these events, the various analyses again pointed to the Red Queen model.

Another test, also using the plankton record, was carried out by Wei & Kennett (1983). Their study was based on the fossil record throughout the world of 149 species of foraminifera over the past 24 million years. They found that major changes in rates of extinction and speciation corresponded to palaeoceanographic perturbations (Fig. 4), and they regarded their data as consistent with the Stationary Model.

These two studies illustrate some of the practical difficulties involved in testing the Red Queen model. One serious problem is in separating biotic from abiotic factors in order to assess their relative significance: it is probably impossible to pigeon-hole both kinds of phenomena as independent factors. Secondly, in many real situations, and pos-
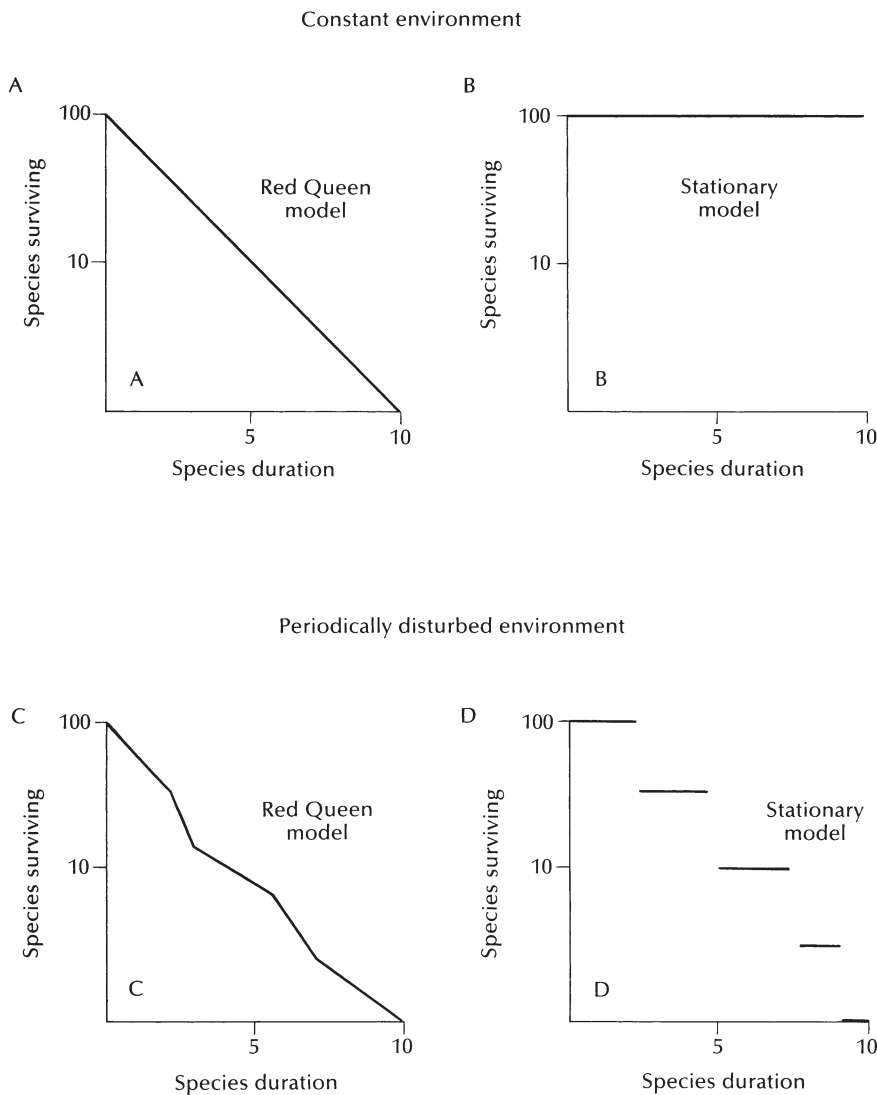
Fig. 2   Predictions of the Red Queen and Stationary models for species survivorship in constant (A, B), and periodically disturbed (C, D) environments. (After Hoffman & Kitchell 1984.)

sibly including the two described above, the test would be inconclusive. For example, it would be hard to distinguish between two predicted patterns if both curves were stepped as a result of rapid changes in the physical environment. At the other extreme, continuous small changes in environmental conditions might give similar gently sloping graphs for both models.

Furthermore, as Hoffman and Kitchell (1984) pointed out, both the Red Queen and Stationary models assume that ecosystems tend towards a diversity of species that is at equilibrium. Both hypotheses predict that the total number of species is constant: the addition of one species to the system causes the loss of another. Yet models that do not assume such an equilibrium could also account for the Law of Constant Extinction and for the other palaeontological data. In these models, there would

be no necessary limit to diversity, and the rates at which species arise or go extinct would not be correlated with each other, nor with total diversity. The data so far are equivocal on these points.

Other research seems to count against the Red Queen Hypothesis. Kitchell et al. (1989) studied a simple predator–prey relationship: naticid gastropods and bivalves. The naticid gastropods prey on bivalves by boring through their shells and extracting the flesh. Both groups are plentiful as fossils, and such predation has left identifiable borings in fossilized bivalve shells. Kitchell and her colleagues modelled the predator–prey system mathematically and found that, whatever the starting point, the system tended to a static position. The bivalves evolved either to reproduce early (before they were eaten) or to devote all of their energy to building a thick shell to minimize the chance of successful
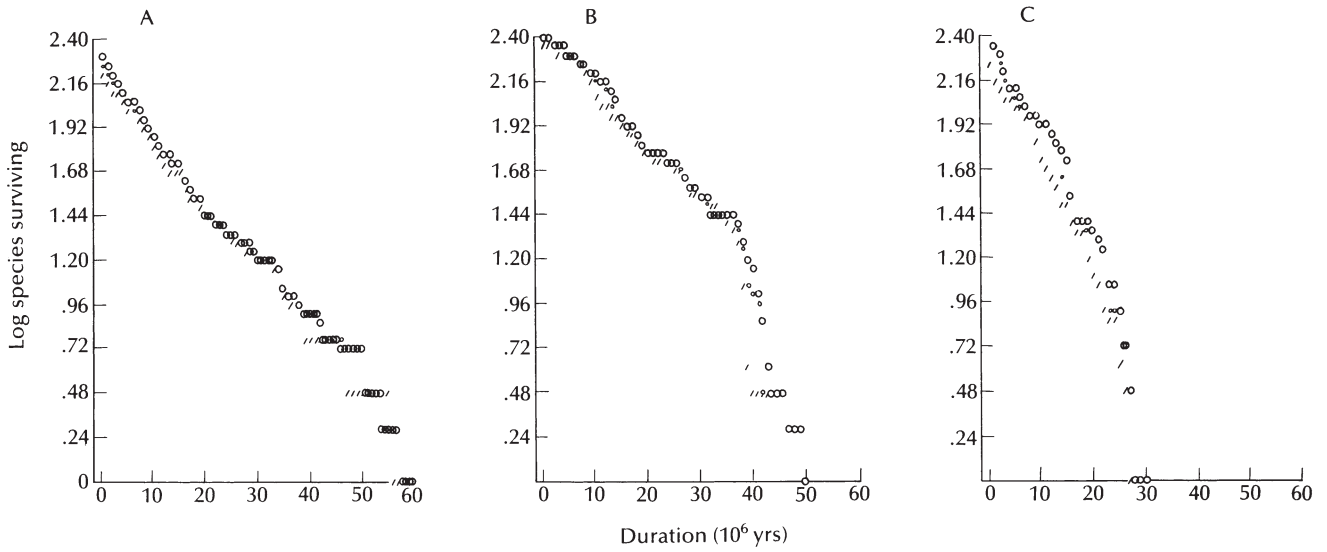
A

B

C

Log species surviving

2.40
2.16
1.92
1.68
1.44
1.20
.96
.72
.48
.24
0

2.40
2.16
1.92
1.68
1.44
1.20
.96
.72
.48
.24

2.40
2.16
1.92
1.68
1.44
1.20
.96
.72
.48
.24

0 10 20 30 40 50 60

0 10 20 30 40 50 60

0 10 20 30 40 50 60

Duration (10^6 yrs)

Fig. 3 Species survivorship curves for A, coccoliths; B, radiolarians; and C, planktic foraminifera. Each graph contains data for three cohorts — taxa arising in the earliest Pliocene, in the latest Pliocene, and in the Holocene, and each is represented by a different symbol. (After Hoffman & Kitchell 1984.)
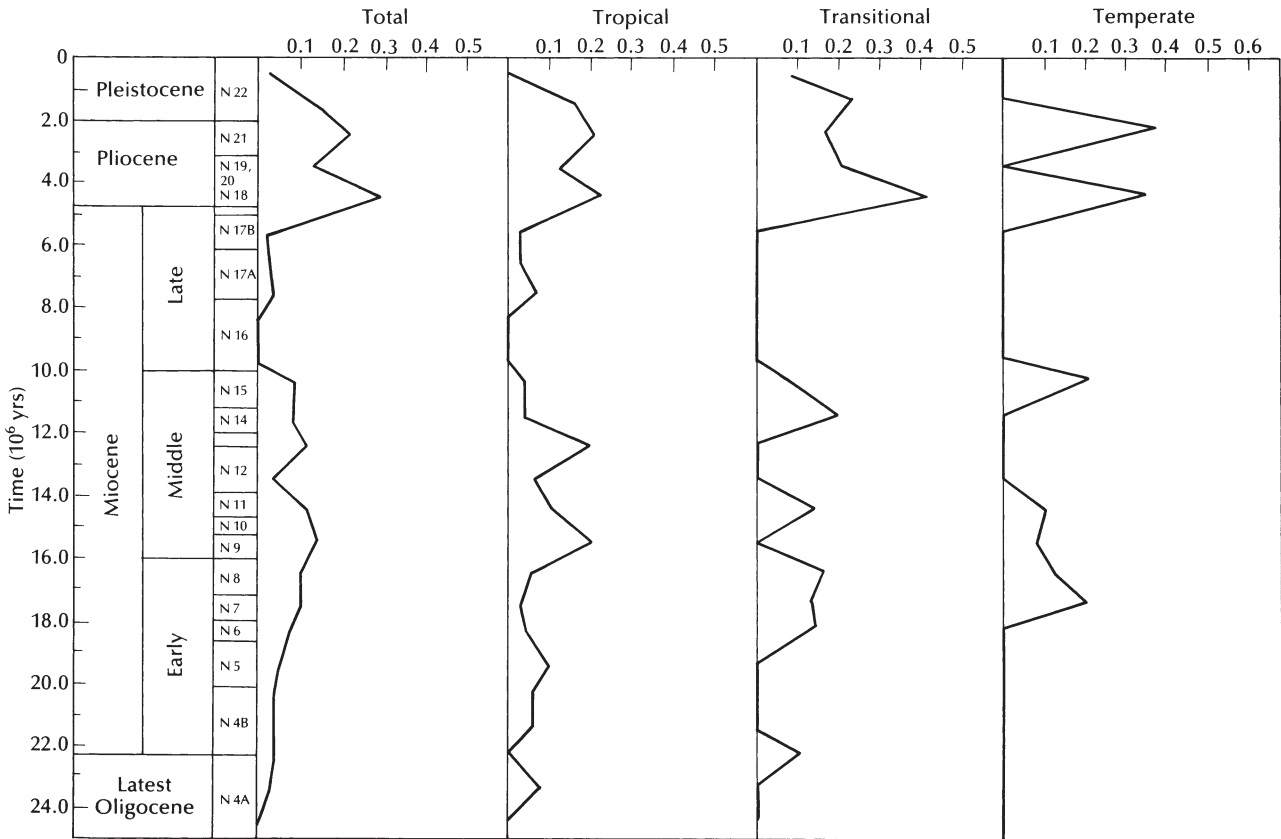
Total   Tropical   Transitional   Temperate

0.1 0.2 0.3 0.4 0.5   0.1 0.2 0.3 0.4 0.5   0.1 0.2 0.3 0.4 0.5   0.1 0.2 0.3 0.4 0.5 0.6

Time (10^6 yrs)

0

2.0

4.0

6.0

8.0

10.0

12.0

14.0

16.0

18.0

20.0

22.0

24.0

Pleistocene — N 22

Pliocene — N 21 / N 19, 20 / N 18

Miocene — Late — N 17B / N 17A / N 16

Middle — N 15 / N 14 / N 12 / N 11 / N 10 / N 9

Early — N 8 / N 7 / N 6 / N 5 / N 4B

Latest Oligocene — N 4A

Fig. 4 Extinction rates for species of Neogene foraminifera for the whole of the oceans ('total'), and for tropical, transitional, and temperate assemblages, for the past 25 million years (latest Oligocene to Recent). The 'N' zones are standard Neogene planktic foraminiferal zones. Peaks in extinction are correlated globally, and linked to major changes in the physical environment. (After Wei & Kennett 1983.)

boring attacks. This result speaks against the Red Queen model, which would require constant evolution in a particular direction.

Other biologists have argued that species probably do not keep running towards unattainable goals, as the Red Queen Hypothesis predicts. Each species is faced with the need to make compromises. Many bivalves, for example, have to balance the need for a strong shell against the costs of a heavy shell. The compromise solution is to have a thin corrugated shell. 'Constant running' in one direction is often not possible in a lineage, and the simplistic view of the Red Queen model as continuous and endless evolution in one direction may be denied by the limitations of genetic variation, development, and mechanical design factors.

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2.6 Hierarchy and Macroevolution

N. ELDREDGE

Introduction

Evolution is the scientific explanation of the design apparent in organismic nature. Natural selection is generally seen to be the principal cause of deterministic modification of the phenotypic properties of organisms through time. Macroevolution most commonly connotes the degree of such modification, and thus in its most general sense is simply 'large-scale genotypic/phenotypic change'. Microevolution, in contrast, refers to the relatively slight amount of change that occurs on a generation-by-generation basis through natural selection and genetic drift. A connotation of elapsed time is often implicit in the distinction between micro- and macroevolution: microevolution takes place in relatively short amounts of time (e.g. 'ecological time,' over a few generations), while macroevolution is generally held to occur in geological time. Yet some theories of macroevolution (e.g. saltation theories of the geneticist R. Goldschmidt, or the palaeontologist O. Schindewolf) invoke brief (even single generation) genotypic and phenotypic transformation. A further distinction commonly drawn between 'microevolution' and 'macroevolution' sees the former as a within-species or perhaps within-genus level phenomenon, in contrast with the degree of change associated more typically with the emergence of taxa of higher categorical rank (i.e. in the Linnaean hierarchy — families, orders, classes, etc.).

The 'evolutionary synthesis', dating from the mid nineteen-thirties, forms the core of modern evolutionary theory. The synthesis followed the successful fusion of Darwinian selection with an emerging understanding of the principles of heredity (achieved primarily through the efforts of geneticists R.A. Fisher, J.B.S. Haldane and S. Wright). This neo-Darwinian paradigm of drift- and selection-mediated dynamics of genetic stasis and change was then integrated with the data of systematics, palaeontology, and other biological subdisciplines to form what was widely heralded as a unified theory of evolution. It is the general position of the synthesis that 'macroevolution' is simply microevolution summed over geological time. Specifically, generation-by-generation stability and transformation, mediated by natural selection and genetic

drift, were held to be *both necessary and sufficient* to account for all aspects of the evolutionary history of life. Though the geneticist Dobzhansky (1937) and the systematist Mayr (1942) both sketched versions of macroevolutionary theory, it was left primarily to the palaeontologist Simpson (1944, 1953) to formulate the principles of macroevolution within the synthetic theory.

The assumption that microevolution yields a complete account of the evolutionary process when projected over evolutionary (geological) time restricts the study of evolutionary mechanics to laboratory and field investigations of living organisms. The role of palaeobiology in such a scheme, however, is by no means thereby rendered trivial: as Simpson (1944), for example, endeavoured to show, the integration of evolutionary theory with patterns of evolutionary events drawn from the fossil record is no simple matter. In particular, Simpson was concerned to show that it is the task of palaeontology to determine the relative intensities, and importance, of various microevolutionary processes (e.g. mutation rate, selection, population size, etc.) required to explain various evolutionary patterns of the fossil record. In that spirit, Simpson developed his model of 'quantum evolution' (rapid, 'all-or-nothing' modification of adaptive features of organisms in relatively small populations) to explain the relatively abrupt appearance so typical of many higher taxa.

Recent years have seen an alternative view emerge on the relationship between palaeontological data, geological time, and theories of the evolutionary process. In traditional evolutionary biology, it is the phenotypic (and underlying genetic) properties of organisms that are of central interest, and which 'evolve'. Organisms vary in these respects within local populations; populations are aggregated into species (Section 2.2). Natural selection 'sorts' the phenotypic attributes of organisms within populations to yield (1) stasis or change in phenotypes, and (2) the emergence of new species (and, by simple extension, higher taxa).

'Hierarchy theory' accepts the neo-Darwinian paradigm of within-population variation, selection, and drift, but seeks to extend the list of evolutionary entities beyond genes, organisms, and populations. Specifically, species, monophyletic (higher) taxa, and ecosystems have come to be viewed as having real existence, and are variously termed 'systems', 'entities', or even 'individuals'. The goal of hierarchy analysis is to elucidate the nature of each kind of large-scale entity, and thus to determine their pos-

sible role(s) in the evolutionary process.

If large-scale systems such as species, higher taxa, and ecosystems are real entities, they exist on a spatiotemporal scale which is too large to be encompassed in laboratory and field experimental studies of the Recent biota. It is the fossil record that reveals the actual dimensions of such systems, and thus it falls in large measure to palaeobiology to examine how they can be integrated with existing theories of the evolutionary process. Such work has two aspects: (1) the determination of any relevance of such large-scale systems to the original problem of evolution — that is, the origin, maintenance, and further transformation of adaptive phenotypic features of organisms; and (2) the recognition of other effects on the general history of life that may result from the existence of such larger-scale entities.

Specifically, the concept that large-scale systems such as species, taxa, and ecosystems are themselves entities, not merely epiphenomena or simple (and perhaps arbitrarily delineated) collectivities of organisms, has led to several palaeobiological theories that allege a degree of additional process to macroevolution, over and above — and in some instances 'decoupled' from — microevolutionary processes.

Hierarchies in evolutionary biology

Several meanings of the term 'hierarchy' are in general use in biology (Grene 1987). In the context of evolutionary theory, however, only two hierarchical systems are generally recognized: the *genealogical* and *ecological* (economic) hierarchies (Table 1). Both are thought to be implicated in the evolutionary process (Eldredge 1985, 1986, 1989; Salthe 1985), though some authors recognize one hierarchy and not the other. Both hierarchies consist of nested sets of entities forming distinct levels. Each level constitutes a class (or category — e.g. 'species'), specific examples of which are entities or 'individuals' (e.g. *Archaeopteryx lithographica*). The entities of any given level have as parts the entities of the adjacent lower level and form, in turn, parts of the adjacent higher level: demes have organisms as parts; in turn, demes are parts of species.

The entities at each level interact or behave in specific ways that unite them to form the entities of the next higher level. In the genealogical hierarchy the activity is 'reproduction' in the most general sense; thus, speciation is seen as the production of more entities (i.e. species) of like kind — an activity ultimately responsible for the ongoing existence of

Table 1. The genealogical and ecological hierarchies.

Genealogical hierarchy	Ecological hierarchy
Monophyletic taxa	Biosphere
Species	Ecosystems
Demes	Avatars (populations)
Organisms	Organisms
Germ line[a]	Soma[b]

[a] Composed of hierarchically nested chromosomes, genes, codons and base pairs.
[b] Composed of hierarchically nested organ systems, organs, tissues, cells and proteins.

higher taxa. In the economic hierarchy, direct inter-action among entities of any given level cohere the entities of the adjacent higher level; thus it is the interaction among local populations of non-conspecifics (as in predator–prey interactions) that unites them into local ecosystems.

The two hierarchies arise out of the two types of organismic activity, that is reproduction, on the one hand, and processes related to matter–energy trans-fer on the other. Viewed in this light, Darwin's distinction between *sexual* and *natural selection* is clear. In sexual selection, relative reproductive success arises strictly from among-population vari-ation in some aspect of reproductive behaviour, physiology, or anatomy. In natural selection, an organism's relative success in economic (matter–energy transfer) activities has an effect on that organisms's probability of successful reproduction.

The two hierarchies are direct outgrowths of these two distinct categories of adaptation that arise under sexual and natural selection. In sexual organisms, reproduction implies a local pool of suitable partners — a 'deme'. In most instances, there will be pools of suitable partners elsewhere; thus local demes form regional 'species'. Most modern treat-ments of species recognize them as reproductive communities, within which mating occurs, outside which it does not. Paterson (e.g. 1985) recently suggested that species are reproductive com-munities composed of organisms sharing a particu-lar set of reproductive adaptations, or 'specific mate recognition system' ('SMRS'). His concept obviates the ambiguity of disjunct distributions, where potential mates never meet. Moreover, because the SMRS is an adaptive system subject to (sexual) selection (favouring mate recognition in isolation) speciation minimally must entail (presumably allo-patric) divergence of the SMRS. Speciation is seen

as an outgrowth simply of continued reproduction in isolation, leading to modification of the SMRS. Because new (sexual) species arise in this fashion as a matter of course, higher taxa are maintained (as long as speciation rate exceeds extinction rate). Higher taxa are seen strictly as lineages of species; they are recognized (just as are clones of strictly asexual organisms) only when new adaptations ('synapomorphies' of phylogenetic systematics; Section 5.2.2) arise and serve as markers for the lineage. As such, monophyletic taxa do not 'repro-duce', that is, they do not produce additional entities of like kind. Genera do not give rise to new genera, the way that new species arise from old.

The economic activities of organisms of a species lead them to form local populations ('avatars') which may, but need not, be coextensive with local demes of the same species. But above this level (Table 1), a crucial distinction between the genealogical and economic hierarchies arises. Whereas the repro-ductive adaptations of organisms are shared by organisms in other demes elsewhere, the economic adaptations of organisms lead to *cross-genealogical* interactions between local populations belonging to different species. Local ecosystems interact with other such systems on a regional scale, but maps of genealogical systems and economic systems simply do not coincide. It is especially significant that *species are not parts of economic systems*. Thus, by sheer dint of the existence of two classes of organ-ismic activity — hence adaptations — organisms are simultaneously parts of two separate, hierarchi-cally arranged systems. And in particular, inter-action within and between entities of the two different hierarchies is of the greatest importance in elucidating a full causal theory of the evolutionary process.

The evolutionary process: role of the genealogical and economic hierarchies

Discussions of macroevolution traditionally empha-size the origin of higher taxa in the context of large-scale adaptive change. Under this synthesis, linear trends are often said to be generated by 'orthoselec-tion', i.e. long-term, predominantly directional natural selection, as distinct from 'orthogenesis', or linear phyletic change through unspecified causes internal to organisms. In general, the accumulation of significant amounts of adaptive transformation within a lineage has been termed *anagenesis*, which is commonly, if not invariably, held to be a process distinct from *cladogenesis*, or lineage splitting. Thus

much, if not all, macroevolutionary change has traditionally been considered to occur without any (or any significant) degree of speciation. A major exception to this generalization is the theme of *adaptive radiations*, in which morphological transformation proceeds rapidly and independently in several or many different directions, and lineage-splitting is directly invoked as part of the process. Simpson's (1944) earliest formulation of 'quantum evolution' also invoked lineage splitting (though not expressly termed 'speciation'); later (Simpson 1953) modified in favour of a purely phyletic conceptualization of quantum evolution.

The hypothesis of *punctuated equilibria* (Eldredge & Gould 1972) is based, in part, on the empirical claim that most species exhibit relative morphological stability throughout the bulk of their stratigraphic ranges (see also Section 2.3). Thus most anatomical change appears to occur along with speciation. Such species stability facilitates recognition of species as spatiotemporally-bounded entities; it further leads to the postulate that linear trends in macroevolution may reflect processes of *species sorting* in addition to directional natural selection. In general terms, such a model proposes that actual transformation of morphology occurs *via* directional natural selection (plus, perhaps, genetic drift) on a standard generation-by-generation basis. But the linearity of the trend through long periods of time — when the species remain morphologically stable and vary among themselves with respect to the evolving trait — arises through sorting of variation among species through a variety of potential causes.

The term 'species selection' itself embraces a number of variant conceptualizations. As developed as an outgrowth of punctuated equilibria (Eldredge & Gould 1972; the term itself was introduced by Stanley 1975; see also Stanley 1979), 'species selection' was virtually synonymous with the more general term 'species sorting' used here. Subsequent authors, seeking more precise parallel usage between organismic and higher-level selection, contend that 'species selection' is applicable only to species-level properties of species (*cf.* Vrba 1984). This argument holds that phenotypic (and underlying genotypic) properties of organisms are the focus of organismic selection. True species selection should be invoked only to explain species-level adaptations; it cannot logically be applied to the situation in which species differ merely in the frequencies of one or more *organismic phenotypic* traits. Williams (1966) was the first to argue this

point, claiming that 'group selection' can pertain only to group-level adaptations. Jablonski (1987) argued that geographical ranges are species-level properties, and show high heritability in his data on Cretaceous molluscs; he concluded that species ranges are therefore subject to true 'species selection'.

Hull (1980) has discussed two components that must be present for selection to occur at any level; these two components serve in addition as criteria for evaluating claims of species-level selection. According to Hull (1980), among entities involved in any instance of selection, there must be an *interactor* as well as a *replicator*. The relative success of interactors is recorded in the subsequent representation of their underlying replicators. Thus, in natural selection, relative economic success of organisms will affect their relative reproductive success, and hence the frequencies of the underlying genotypes. Organisms in this instance are both interactors and 'reproducers', with replicative fidelity supplied by their genes.

Hull's (1980) selection criteria imply that species selection cannot be directly analogous to natural selection. If species are genealogical entities (if, in other words, it is the reproductive activities of organisms that lead to the formation and continued existence of species), species are causally connected to the replicative activities of genes; but if it is further true that species, as whole entities, do not play direct roles in ecological systems, species cannot be said to be interactors, and Hull's criteria for selection are not met *by definition* for species. 'Species selection' appears to be most analogous to Darwin's *sexual selection* — because factors affecting rates of speciation and species extinction are involved.

Species sorting is a function of differential extinction and origination of species within a monophyletic clade. It is the goal of macroevolutionary theory to specify the causal processes underlying such sorting. In addition to processes at work *within* a given level, the entities above and below in the hierarchy provide constraints (initial, or boundary conditions) on processes occurring within any given level — the 'upward and downward causation' of many hierarchy theorists. Vrba's (1980) 'effect hypothesis' is an example of *upward* causation within the genealogical hierarchy. The effect hypothesis postulates that macroevolutionary patterns (for example, linear trends in one or more morphological attributes within a clade over geological time) may arise simply as an outgrowth (side effect) of the

biology of the organisms themselves. Nothing more — specifically, no selection at the species level — need be invoked as an explanation of such patterns.

Palaeontologists have sought links between characteristic speciation and extinction rates in lineages (macroevolutionary patterns), on the one hand, and aspects of organismic biology on the other — at least since Williams (1910) noted the apparent correlation between variation, niche width, and stratigraphic duration. Williams claimed that broadly niched (eurytopic) species, in addition to their characteristically wider geographical (habitat) occurrence, tend to display greater morphological variability (both within and certainly among populations) and longer stratigraphic durations than more narrowly niched stenotopes. Focusing especially on aspects of niche-width, macroevolutionary theorists have attempted to account for rates of both speciation and extinction. It seems, for example, that lineages comprised predominantly of eurytopic species show lower rates of species extinction and origination than lineages comprised of predominantly stenotopic species (see Eldredge & Cracraft 1980). The contrast is especially clear in sister-lineages. Indeed, Vrba (1980) used the Miocene—Recent sister lineages of Aepycerotini (impalas) and Alcelaphini (wildebeests, hartebeests, topis, etc.), the former species-poor and eurytopic, the latter speciose, with short-ranging stenotopic species, to illustrate one possible cause underlying the 'effect hypothesis' (see also Section 2.10). Vrba postulated that the trends in alcelaphine evolution were simply aggregates of higher rates of speciation and the accumulation of adaptive modification in the lineage of stenotopes — while little significant evolutionary transformation accumulated within the co-ordinate lineage of eurytopes, the aepycerotines.

Interhierarchic interaction and macroevolution

Darwin's (1859) original formulation of natural selection (where relative economic success affects relative reproductive success within a local population of a species) serves as a model of the mechanics of interaction between the two hierarchies in the evolutionary process. Organisms, as members simultaneously in both the economic and genealogical hierarchies, patently stand as the prime causal link between the two (although some hierarchy theorists (notably Salthe 1985) see direct causal interaction between entities at various levels of the two hierarchical systems).

Under the synthesis, species and higher taxa are generally depicted as having niches (or 'adaptive zones' in the case of higher taxa); further, in a widely used extension of Wright's (1932) metaphor of 'adaptive peaks', species and higher taxa are generally depicted as occupying peaks, or series of adjacent peaks (i.e. in an 'adaptive range'). Thus the most general approach to macroevolution under the synthesis holds that species and higher taxa are distinctly *economic* entities — effectively collapsing the dual hierarchy system into a single scheme.

Yet, following arguments outlined above, it has seemed to recent theorists that species and higher taxa are different sorts of entities from those that form complex biotic economic systems. Species are aggregates of local demes, all of which share a common fertilization system. From an ecological point of view, species are typically integrated into a variety of different ecosystems. Yet organisms within a species, as a rule, retain sufficient similarity in terms of economic adaptations that local populations are, to a great degree, redundant from one another. That is to say, the actual ecological role played by species is to serve as a reservoir of genetic information. Local populations are notoriously ephemeral; local extinction, on several geographical and temporal scales, is often counteracted by recruitment from neighbouring demes. An important consequence of the mere existence of species is that local parts of ecosystems are continually replenished from demes elsewhere. Recent studies of larval recruitment in intertidal communities — after events that range from slight to total disruption — amply bear out the role that species play as reservoirs of genetic information.

Darwin (1871) called species 'permanent varieties'. The expression is apt in the context of macroevolution, because the complexion of ecosystems is forever modified upon the final extinction of a species; the possibility of replacing local populations with conspecifics is forever lost. In general, just as species display a within-species pattern of supply of organisms to replace local populations, following extinction events that result in the loss of many higher taxa, the identities of the surviving taxa determine the natures of the subsequently founded ecosystems. Disruption of ecosystems results in extinction — the more severe the disruption, the higher the characteristic level of disappearance of taxa, from species on up; and the higher the average level of taxonomic extinction,

the greater the change in economic systems.

Theories (e.g. the 'Red Queen Hypothesis', Section 2.5) often depict evolution as a process of inexorable adaptive change. Recent empirical and theoretical work in palaeobiology suggests rather a different picture: the ecological systems of which all organisms are parts, are formed from whatever organisms are extant at any given moment. With normal, small-scale fluctuations in composition and relative abundance of organisms, ecological systems appear to be quite stable. Speciation and extinction do occur, and so affect the composition of ecosystems. Some phyletic modification may accrue within species, but, because most demes are ephemeral, little net change typically accumulates within species throughout most of their histories. Little in the way of concerted evolutionary change, either within species or among species within lineages, tends to occur unless and until external perturbation disrupts ecosystems to the point where entire species — and higher taxa — become extinct, rendering impossible the resumption of ecosystems of the same composition as before. Thus, although the presence of genealogical entities (species and higher taxa — as packages of genetic information) are indispensable to the formation and ongoing existence of ecosystems, it appears that it is primarily the disruption of such economic systems that leads to significant amounts of change within entities of the genealogical hierarchy. Hence mass extinction appears to be an important causal cornerstone of macroevolution.

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2.7 Patterns of Diversification

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Introduction

The past 3.5 billion years have witnessed substantial change in the numbers of protist, animal, and plant taxa on Earth. The magnitude of that net change is evident from comparison of the lush biological diversity present in so many modern habitats with Archaean sediments seemingly barren of fossils. But reconstructing the geological history of organic diversity has proved difficult. Biases in the preservation, collection, and study of fossils have combined to obscure patterns of change in diversity. Despite the difficulties, a variety of different patterns of diversification has now been documented at scales ranging from local communities to the entire biosphere. These patterns indicate that the net accumulation of taxa through time has been quite unsteady.

Biases in the fossil record

The geological history of taxonomic and ecological diversification is obscured by a variety of time-dependent and time-independent filters. Most of these are various sorts of sampling biases, which cause the observed fossil record to differ from the actual history of the biosphere (see also Section 3.12). The most severe of the time-dependent biases is the loss of sedimentary rock volume and area with increasing age (Raup 1976b). Both sedimentary rock area and rock volume correlate strongly with the numbers of animal species described from that stratigraphic interval (Raup 1972, 1976b). Rock volume and area affect apparent species richness by influencing the likelihood that a given species is preserved, discovered, and described (Raup 1976b). Similar biases have been documented in the fossil record of vascular plants on land (Knoll *et al*. 1979). The quality of preservation of fossils within sedimentary rock also tends to deteriorate with increasing age, because of extended exposure to diagenesis (Raup 1972). The kinds of sedimentary rock and, by implication, the environments preserved in the stratigraphic record have varied greatly through time. Variability in the representation of palaeoenvironments in the stratigraphic record must in-

fluence the composition of the fossil record. Sea-level, which largely controls epicontinental marine deposition and preservation of fossils therein, has varied throughout the geological past. Low sea stands are usually represented in the stratigraphic record as diastems, disconformities, or unconformities, and lack any fossil record of shelf faunas. Other time-dependent biases include monographic effects (Raup 1972) and the distribution of systematists' labour (Sheehan 1977).

There are significant time-independent biases. For example, terrestrial environments (and the organisms that inhabit them) are not well represented in the stratigraphic record, in comparison to marine habitats (e.g. Padian & Clemens *in* Valentine 1985). Among marine organisms, heavily skeletonized forms are preserved far more frequently than lightly or non-skeletonized forms. Palaeobiologists often presume that the ratio of heavily skeletonized to non-skeletonized species has been approximately constant, at least since the early Phanerozoic, but no data or arguments to support that contention have been advanced. On the contrary, there is some evidence that skeletons have become more robust in time in response to newly evolving predators (Section 4.13).

The net result of these biases is quite severe, amply justifying the ancient laments about the incompleteness of the fossil record. Only approximately 10% of the skeletonized marine species of the geological past and far fewer of the soft-bodied species are known (Sepkoski *et al*. 1981; Signor *in* Valentine 1985). No doubt whole clades and communities of the past remain to be discovered. More importantly, these biases continue to obscure all but the most fundamental patterns in the history of diversification.

A brief aside on the semantics of diversity might prevent confusion. The term *diversity* has been used in two senses. Unfortunately, the two usages are rather different, and treating the term carelessly confounds an important concept. In the palaeontological literature, diversity is often used to mean richness, or the number of taxa present. Diversity also has a second meaning, incorporating both rich-