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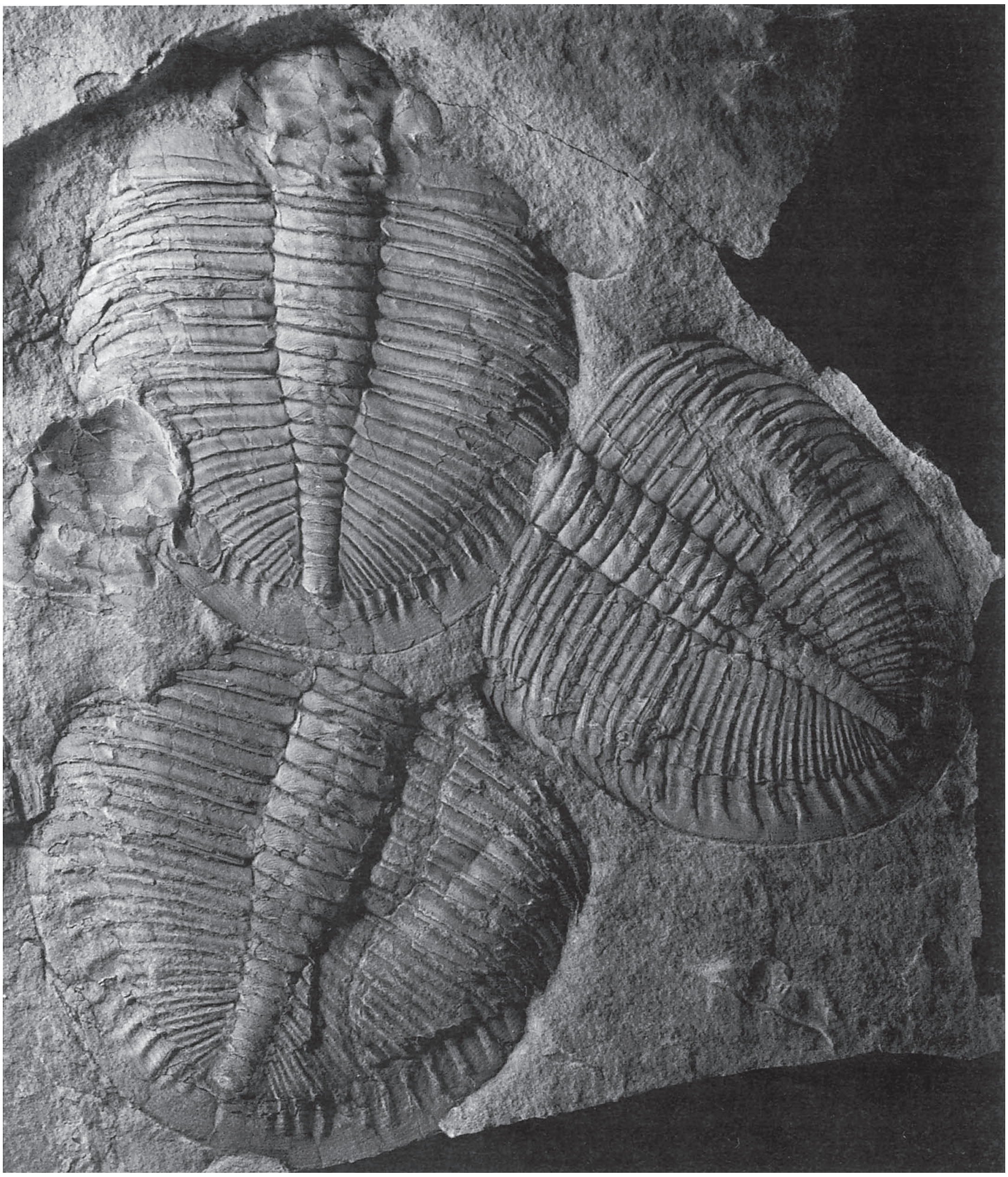
THE EVOLUTIONARY PROCESS AND THE FOSSIL RECORD



The Ordovician trilobite *Ogygiocarella*, × 1.35. (Photograph courtesy of P.R. Sheldon.)

2.1 Molecular Palaeontology

G. B. CURRY

Introduction

In its widest sense, molecular palaeontology embraces the study of intact molecules in living organisms, as well as the investigation of the variably decayed remnants of ancient molecules which occur in great abundance in rocks and fossils (Runnegar 1986). In extant molecules such as DNA or proteins, the nucleotide or amino acid sequences are reproduced accurately from generation to generation with only minor changes caused by genetic drift or natural selection. Because such molecules are ubiquitous in all life forms, homologous molecules can be extracted from a wide taxonomic range of living organisms and their sequences compared, either directly or indirectly, to provide information on the systematic interrelationships of their host organisms.

Using such techniques, phylogenetic history can be investigated on a scale ranging from phyla to subspecies. The molecular clock hypothesis further extends this approach by attempting to use molecular 'distances' to date divergent events between taxa (Thorpe 1982). To do this the molecular clock must first be calibrated using sequences from organisms which have well dated divergence events — in effect organisms which have a good fossil record. The molecular clock hypothesis is hotly debated even by molecular biologists, and it is clear that the rates of sequence change are highly variable both in different molecules and in identical molecules within different species. Nevertheless, the interest in the molecular clock does mean that molecular biologists will increasingly be drawing conclusions and making predictions about topics which previously have been the exclusive preserve of palaeontologists.

Fossilization of organic molecules

Despite the palaeontological importance of recovering the prodigious 'historical' information stored in extant molecules, it is undoubtedly the investigation of molecular fossils which has the greatest potential for the development of molecular technology in palaeontology. The fact that resistant organic molecules can survive for many millions of years has been one of the most remarkable geological discoveries of recent years (see also Section 3.2). The presence of large quantities of organic debris in rocks has long been recognized, but previously it had been widely assumed that these compounds contained no palaeontological or biological information because of the extensive degradation they had experienced. It is now clear that such an assumption is wrong, and that certain robust molecules can survive virtually intact, or at least in recognizable form, for many millions of years. The key to such discoveries lies in the application of technological advances in subjects such as organic geochemistry and molecular biology which allow the recovery, purification, and characterization of organic materials with a precision never before attainable (Curry 1987).

The raw material for molecular palaeontology is the accumulation of the variably decayed remains of ancient animals, plants, and micro-organisms which has built up in rocks over many millions of years (Section 3.2). This organic debris occurs both interstitially in sedimentary rocks and as inclusions within fossil shells and skeletons. The vast scale of such accumulations is perhaps not generally appreciated — enormous as they are, the reservoirs of fossil fuels such as oil, gas, and coal represent only the tip of the iceberg. To a greater or lesser extent all sedimentary rocks contain less apparent, highly dispersed, and generally less degraded, organic debris. On average about 2% of the volume of sedimentary rocks is composed of organic compounds, and conservative estimates suggest that there is about 10 000 times more organic material in rocks than in the present-day global biomass. One group of ubiquitous molecular fossils, the biohopanoids, is present in quantities which equal or exceed the total mass of organic carbon in all living organisms.

Most of this reservoir is thought to be useless for molecular palaeontology, because it has been so intensely altered as to be totally unrecognizable. In addition to the complications imposed by hydrolyzation and other physical, chemical, and biological processes of decay, investigations of molecular fossils have also to contend with the effects of a host of other geological phenomena such as diagenesis, vulcanism, and tectonism. As a result, fossil molecules can be exposed to an infinitely variable combination of heat, pressure, and percolating fluids, and can with time recombine into complex and intractable new structures by reacting with each other and with mobile components migrating from external sources. The possibility of contamination by molecules derived from extant organisms is an additional, and ever-present, complication.

In the face of all these problems, the extent to which molecules can survive fossilization is striking, most particularly in the well documented cases of molecules which are fully exposed to the ravages of geological processes. The commercial implications of accumulations of fossil molecules has provided a major stimulus for their study, and a wide range of molecular fossils have now been discovered in crude oils which have been intensely degraded. The great majority of fossil organic material has not been so intensely degraded, and hence should be particularly informative, although as yet such material has not been thoroughly investigated.

Analytical techniques

The major complications in investigating molecular palaeontology stem from the fact that raw samples contain extremely complex assemblages of molecular fossils, which occur in all stages of decay, from virtually unaltered to strongly degraded. Furthermore, most liberated fossil compounds readily combine into complex, heterogeneous agglutinations, which are often insoluble and hydrophobic and hence difficult to analyse. The first hurdle, therefore, is to separate the different constituents, and to recognize the various stages in the decay of a particular molecule, each of which will generally produce slightly different daughter products depending on its decay history. The development of chromatographic and electrophoretic techniques which can reliably separate and analyse samples of 1 μg or less provided a major stimulus to the study of organic debris within fossils, although the long-term survival of molecular fossils was first demonstrated using techniques from organic geochemistry.

Organic chemists now derive most of their information from computer-controlled combined gas chromatograph mass spectrometers (C-GC-MS) which first separate, and then analyse, the structure of fossil molecules at a resolution measured in nanograms (10^{-9} gm). These procedures can identify geochemical fossils because the carbon skeleton of the original biological molecule is characteristically preserved either unaltered or with minor rearrangements, substitutions, or the removal of side chains (Fig. 1). A significant recent technological advance is the recognition that large, highly reactive molecules, which are usually particularly susceptible to degradation, can be stabilized over geological time when incorporated into inert polymeric agglutinations. These relatively intact and extremely informative fossil molecules can be released by the partial chemical dissolution of fossil polymers prior to C-GC-MS analysis, and have now been isolated from well preserved 50 Ma compounds. The main drawback to the organic geochemical approach is that the analytical techniques are complex and require specialist skills and expensive equipment.

The major preoccupation of molecular palaeontology has been to demonstrate unambiguous links between intact living molecules and their resistant fossil remains. A classic example is the petroporphyrins, which are common constituents of crude oils. As early as 1934 it was proposed that vanadyl petroporphyrin represented degraded chlorophyll *A* from plants; the fossil molecule has essentially the same structure, but has lost its side chain and the central magnesium ion has been substituted by a vanadyl ion (Fig. 1).

Subsequently the decay pathways of a wide range of compounds have been traced from living organisms through to sediments and rocks, providing information both on the origins of fossil fuels and on the conditions which prevailed during their alteration (because the state of decay is closely related to temperature, pressure, etc.). Molecular fossils can also provide information about ancient environmental conditions, e.g. when the chemical composition of a group of marine phytoplankton is known to vary directly with ocean temperature, and such variations can be detected in their fossil remains. Mapping out the distribution of such compounds in rocks therefore provides some indication of oceanic temperature variations in the past. Investigations of fossil molecules have also led to the discovery of previously unrecognized living molecules; biohopanoids, an important group of membrane-forming lipids in extant bacteria, were first recognized by their ubiquitous fossil derivatives.

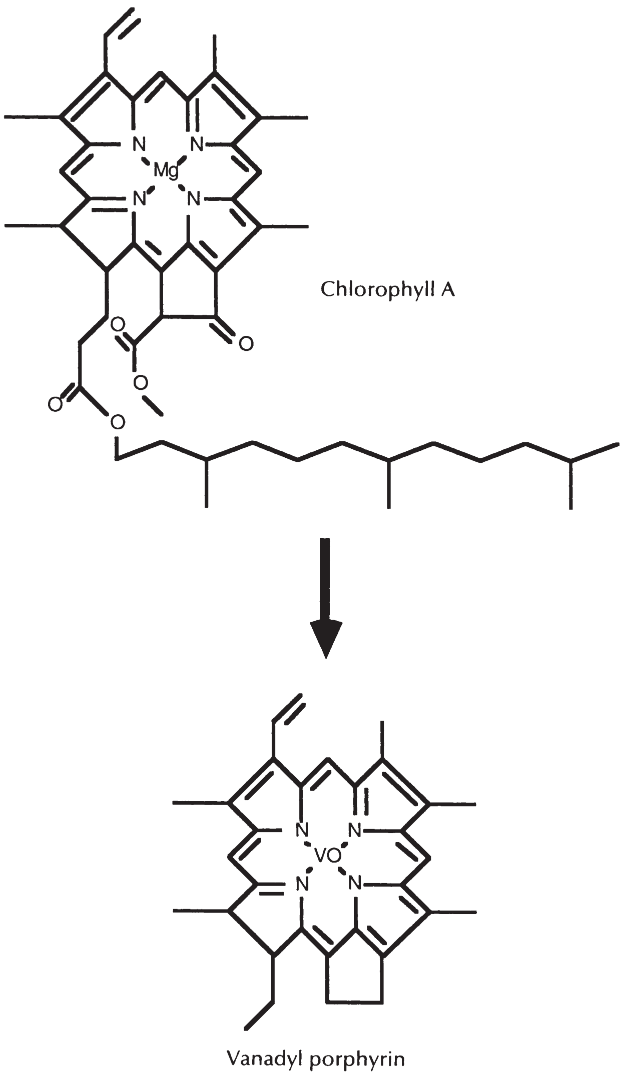


Fig. 1 A classic example of a geochemical fossil — vanadyl porphyrin, one of a suite of petroporphyrins (common constituents of crude oils), which is thought to be the breakdown product of the photosynthetic pigment chlorophyll *A* from plants. Over geological time the central magnesium ion has been replaced by a vanadyl ion, and the side chain has been stripped away. The side chains of chlorophyll are thought to give rise to other common geochemical fossils (phytanes and pristanes).

Organic compounds from biominerals

There is now considerable interest in the preservation of molecular fossils within the shells and skeletons of fossils (Wyckoff 1972; De Jong *et al.* 1974; Westbroek *et al.* 1979; Hare *et al.* 1980). Compared with free compounds in sediments and rocks, organic compounds from biominerals are relatively protected from decay and contamination — a kind of biological 'fluid-inclusion'. It is widely believed that this important group of molecular fossils represents the remains of original organic compounds which were incorporated into the skeletal fabric during shell growth as essential extra- or intracrystalline elements of 'organic-matrix-mediated' biomineralization. Although these entombed molecules do fragment over geological time, it is now clear that some of their breakdown products are often retained within skeletal fabrics (Figs 2, 3). The more porous mineralized matrices are obviously much more prone to contamination from percolating fluids, but the possibility of spurious results can be reduced by investigating the organic content of surrounding sediment, and by determining stable carbon isotope ratios which reveal the contamination of marine fossils by predominantly terrestrially-derived groundwater. Palaeontologists have long been interested in biomineralization processes, and an understanding of the intimate association between the organic matrix and the inorganic mineralized phase, which appears to be a major factor in the long-term stability of molecular fossils, is clearly crucial for the full exploitation of molecular palaeontology.

Organic compounds have now been isolated and characterized from a diverse taxonomic range of invertebrate and vertebrate fossils spanning the entire history of shelly faunas (i.e. 600 million years). The best results have been obtained with well preserved Mesozoic, Cenozoic, and Quaternary specimens (i.e. the past 250 million years). These data have mostly been presented in the form of amino acid mole percentages.

Detailed analyses of molecular remnants from living and fossil scallops spanning about 200 million years demonstrate the expected progressive decay in the total quantity, and percentage survival, of amino acids (Fig. 2). The rate of decay reaches a plateau at about the 1%–2% survival level during the Cretaceous (*c.* 100 million years), and thereafter the total quantities of molecular fossils remain relatively constant.

Free amino acids represent only one of three broad categories of molecular fossils recognized; insoluble organic residues and soluble peptides also display a similar decay profile (Fig. 3). Changes in the respective proportions of these components with time probably indicate some movement between categories. The consistency of amino acid profiles over geological time is remarkable, for example in nautiloids spanning almost 400 million years. Changes in relative abundance with time are generally thought to be a diagenetic effect, and such alteration phenomena are useful indicators of the

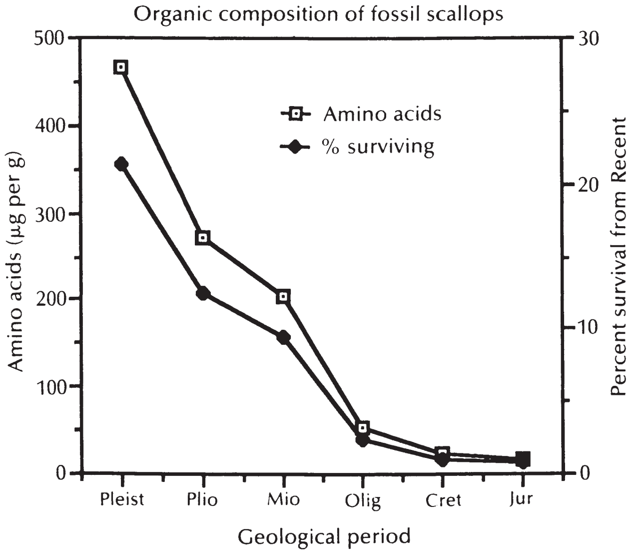


Fig. 2 The progressive decay of organic compounds from the shells of fossil scallops with time. Approximate ages, in millions of years, for the horizontal axes are Pleistocene (2), Pliocene (4), Miocene (15), Oligocene (30), Cretaceous (100), and Jurassic (175).

state of fossil preservation when coupled with isotopic data and laboratory experimentation on Recent shells.

Molecular fossils and systematics

Because of the ubiquitous distribution of amino acids in living tissues, the amino acid compositions of fossils have as yet had only limited use as taxonomic indicators. However, consistent differences between the amino acid compositions of living and fossil brachiopods appear to distinguish between brachiopod orders, with the chitinophosphatic-shelled inarticulate *Lingula* being characterized by higher concentrations of alanine and lower glycine. While such variations are probably related to different shell mineralogy, amino acid profiles also distinguish between different orders of calcareous-shelled articulate brachiopods. It seems highly probable that the crude systematic application of such data will be restricted to the higher levels of taxonomic classification (i.e. superfamily, order).

A more recent innovation has been the use of immunological techniques to investigate molecular fossils (De Jong *et al.* 1974; Westbroek *et al.* 1979; Muyzer *et al.* 1984; Lowenstein 1986). Such an application makes use of the major attribute of the immune system, namely that antibodies recognize their target molecule by detecting a small diagnostic region or regions known as determinants. Antibodies prepared against living tissues or a particular fundamental molecule such as collagen, can therefore detect the presence of that molecule in fossils, provided that fragments containing the determinants have survived. As determinants are much smaller than intact molecules, their survival potential is much greater. Antigenic determinants are known to survive for at least 70 million years (De Jong *et al.* 1974; Lowenstein 1986). The advantages of immunology are the high specificity of antibodies

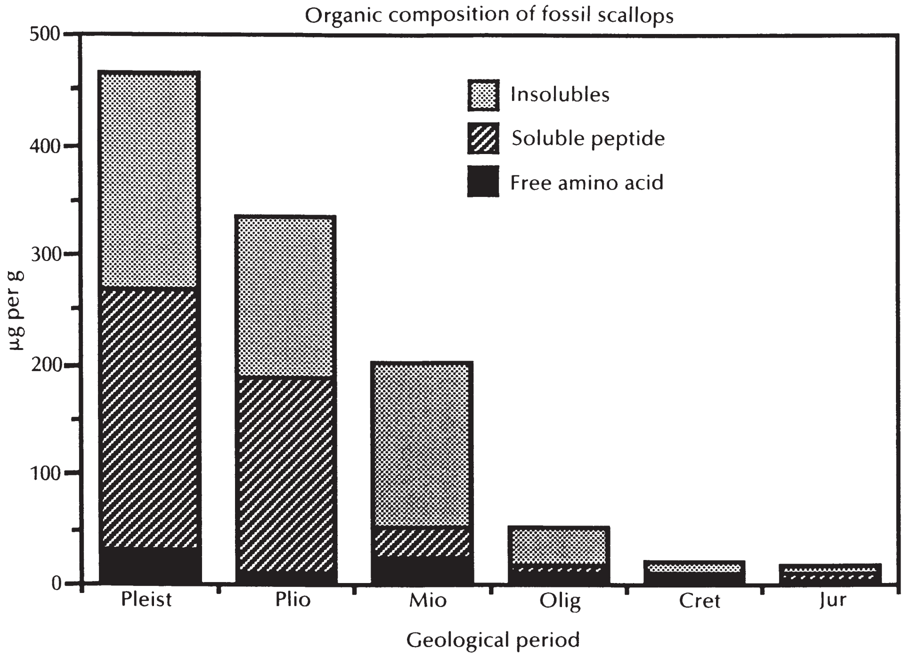


Fig. 3 Proportions of free amino acids, soluble peptide fragments, and insoluble organic residues in the shells of scallops of various ages. Horizontal axis as in Fig. 2.

(in particular monoclonal antibodies directed against a single molecule), and the ability to carry out large numbers of determinations once the antibody has been prepared, which allows rapid assessments of the extent of fossil organic preservation. The production of antibodies is, however, a complex and specialized field.

Immunological techniques potentially provide greater systematic resolution, at least to the generic and familial level, although species-specific reactions have been detected in relatively recent fossils (Lowenstein 1986). Such an application is in effect a variation of the widely used technique of reconstructing phylogeny from immunological distances, a procedure which can be justified on the grounds of the direct linear relationship between antigenicity and amino acid substitution rate. Experiments with living taxa have demonstrated the potential of immunology in this field, with antibodies against one bivalve species reacting with all but one of the other taxa in its family; the implication that the exceptional genus may be incorrectly assigned is apparently supported by other lines of evidence (Muyzer *et al.* 1984).

Full exploitation of the evolutionary and taxonomic applications of molecular palaeontology will require much more detailed information about the structure, composition, survival potential, and distribution of fossil molecules. Although there have been reports of the preservation of fragments of DNA in 2000 year old mummies and other relatively recent fossils, DNA molecules are relatively unstable, particularly susceptible to hydrolysation, and concentrated in vulnerable soft tissues rather than protective mineralized skeletons (Runnegar 1986). On present information, DNA is therefore likely to be very short-lived on a geological time-scale, although extant DNA is a potent source of information for palaeontologists. The search for molecular fossils must, at least for the present, concentrate on the more or less informative building blocks of organic molecules produced by DNA (e.g. protein residues) as a pathway to the partial understanding of the composition of ancient biochemical systems. Certainly the widespread preservation of amino acids, and the more restricted survival of appreciable portions of original molecular structure for at least 70 million years, has been demonstrated by immunology and organic geochemistry. The extent of such excellent preservation is unknown, however, and at the present time the field is one of considerable potential, tantalizingly glimpsed but with little hard data.

Reports of the preservation of characteristic original amino acid sequences of 80 Ma fossil shell proteins are particularly encouraging, as is the reported (but not published) sequencing of 15 amino acids at the N terminal end of a small Ca^{2+} binding protein from oyster shells of Recent, Middle Miocene (15 Ma), Middle Cretaceous (100 Ma), and Middle Jurassic (175 Ma) ages. However, it has so far proved extremely difficult to sequence segments of fossil molecules routinely, perhaps because of interference from co-existing dark polymeric compounds. Technological developments which are much more precisely tailored for the special conditions of the fossil record are clearly crucial, and palaeontologists may well have to become more familiar with the capabilities of existing equipment and possibly even involved in the design of new equipment.

Whatever the technique, it is clear that an integrated approach is necessary to avoid the many potential pitfalls in working with molecular fossils. Taxonomic studies should, in the first instance, concentrate on organisms which have a long and abundant fossil record and are still living today. This allows cross-checking of phylogenetic inferences against morphology, extant biochemical systematics, and geological history, and the tracing of organic preservation from living to fossil within single lineages. Large numbers of well preserved specimens of different ages are required, since the yield of organics per gram of fossil is low. A robust, non-porous, coarsely-crystalline, skeletal ultrastructure is also an obvious advantage because of the protection it provides for enclosed molecular fossils.

At the present state of knowledge only high level taxonomic indicators can realistically be anticipated from molecular fossils, and the most obvious and dramatic demonstration of such an application may well come from problematic groups whose morphology provides ambiguous clues as to their taxonomic affinities. In any event it is certainly now possible to begin utilizing fossil molecular data to augment or complement existing taxonomic methodology. All of the taxonomic tools available to the palaeontologist, including the study of morphology alone, have particular strengths and weaknesses; taken in combination, molecular and morphological, living and fossil, they will be a potent measure of taxonomic relationships.

Future developments

The assimilation of such complex and unfamiliar technology into geological investigations is necessarily a slow procedure, but the investigation of molecular palaeontology is now a blossoming field. Although molecular data from the fossil record is still beyond the grasp of most scientists, the speed of development, and of automation, is such that analyses of this kind may soon be routine. Current studies have clearly demonstrated that such work can significantly augment or complement a wide diversity of geological and biological research. In addition to taxonomy, there are, for example, indications that the remains of ancient molecules also contain important information on geochronology (i.e. amino acid dating), the origins of fossil fuels, palaeoenvironment reconstructions, and the processes which operate during diagenesis. For the biologists such organic remnants could well provide valuable insights into evolutionary processes at the molecular level.

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2.2 Speciation

B. CHARLESWORTH

Species concepts

Modern evolutionary biologists are generally agreed that the *biological species concept* provides the most satisfactory basis for discussing the problem of the origin of new species (*speciation*). According to the biological species concept, species are 'groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups' (Mayr 1942). This concept was arrived at during the nineteen-thirties, as a result of the recognition by systematists and geneticists that purely morphological definitions of species are unworkable, in view of phenomena such as the occurrence of intergrading sets of morphologically distinct populations over a geographical range, and of morphologically nearly indistinguishable but reproductively isolated populations coexisting in the same place. Under the biological species concept, the former situation is now treated as a case of a single *polytypic species* or *Rassenkreis*, and the latter as the existence of a number of *sibling* species.

Examples of polytypic species and sibling species abound (Mayr 1963), and demonstrate that there is no tight causal relation between the evolution of morphological differences of the kind that are detectable in the fossil record, and the evolution of reproductive isolation. A polytypic species is at least potentially capable of evolving as a unit, e.g. a selectively favourable mutation that arises at one end of its range is capable of diffusing throughout the whole species, as a result of migration, and replacing its alternative allele. Conversely, such a mutation has no prospect of spreading from one biological species to another under natural conditions.

In this sense, the biological species represents a natural unit of evolutionary change. Clearly, the concept applies only to sexually reproducing organisms. Furthermore, cases where it is difficult to apply are observed, and are indeed to be expected, since intermediate stages in the degree of reproductive isolation between geographically or ecologically separated populations must occur under almost any evolutionary hypothesis other than that of strictly saltatory evolution (Mayr 1963).

Modes of reproductive isolation

According to this view of the nature of biological species, the process of speciation is to be equated with the development of reproductive isolation between two populations that were formerly fully capable of interbreeding. This process is the ultimate source of the diversity of life on Earth, since sympatric populations that are not reproductively isolated will eventually lose their distinctness. Modes of reproductive isolation may be divided into the two broad categories of *prezygotic* and *postzygotic* barriers, referring to whether or not F1 hybrid individuals are produced by matings between members of the two species (Dobzhansky 1937; Mayr 1963). Prezygotic modes of isolation include differences in ecology, timing of breeding or flowering, and differences in mating behaviour or reproductive physiology, that prevent successful fertilization in interspecific matings. In many groups, such as *Drosophila*, behavioural prezygotic isolating barriers are the primary agents that prevent gene flow between sympatric species, which are often completely isolated genetically in spite of the absence of strong postzygotic barriers (Coyne & Orr 1989). Postzygotic isolating barriers include inviability or sterility of F1 individuals, or of subsequent hybrid generations.

Theoretical studies have shown that isolating barriers have to be extremely strong in order to prevent gene flow between two populations that are in contact. Neutral alleles will face no significant obstacles to diffusion from one population to the other unless there is nearly a 100% loss in fitness to F1 hybrids, or their probability of formation is near zero, except for loci which are very closely linked to genes involved in controlling the isolating mechanisms (Barton & Charlesworth 1984). The same applies to alleles that are selectively advantageous in both populations, but originally arise by mutation in only one of them. Studies of *hybrid zones*, where two genetically distinct geographical races come into contact along a linear transect, resulting in a relatively narrow region where hybrids are formed, have demonstrated empirically that such gene flow occurs at enzyme and protein loci detected by electrophoresis (Barton & Charlesworth 1984). These are probably close to being selectively neutral. Loci that are under natural selection that favours different alleles in the two populations (because of differences in environment or genetic background) may remain differentiated between populations in contact; the extent of such divergence depends on the balance between the strength of the selection pressure concerned and the amount of gene flow. *Clines*, where populations vary along a linear transect in response to an environmental gradient in selection pressure, are the product of such a balance (Endler 1977). There are numerous examples of clines maintained over very short geographical gradients by intense selection pressures, the classic example being the evolution of metal tolerance by plants living on polluted sites such as old mine spoils (Endler 1977). There is thus no difficulty in understanding how morphological and physiological differences can be maintained between populations that are more or less freely exchanging genes, and which show little differentiation with respect to protein loci. These populations do not constitute separate species.

Knowledge of the genetic basis of isolating barriers between species is clearly of crucial importance in understanding the ways in which they may evolve. In flowering plants, it seems that ecological differences between related species often prevent interbreeding between them, even if they inhabit the same general area; habitat disturbances may result in the mingling of populations isolated in this way. There is clearly no direct genetic control of reproductive isolation in these cases, other than via the characters that lead to the ecological differences between the species. Such differences seem to be under the same type of genetic control as similar within-species differences (Stebbins 1950). This is generally true of morphological and physiological differences between related species (Mayr 1963; Barton & Charlesworth 1984). Genetic analysis of behavioural isolating barriers has largely been confined to *Drosophila*. What little information is available indicates that these are usually polygenic in nature, with different loci controlling male and female courtship behaviour (Barton & Charlesworth 1984).

The genetic basis of sterility or inviability of interspecies hybrids has been much more thoroughly studied. Especially in plants, differences in chromosomal arrangements between related species often result in reduced pairing between chromosomes at meiosis in F1 hybrids, leading to the production of gametes containing abnormal numbers of chromosomes (Stebbins 1950). Zygotes resulting from these gametes suffer reduced viability, so that the effective fertility of the hybrid is low. Accidental doubling of the chromosome number in an interspecies hybrid can lead to restoration of fertility, in cases where failure of pairing of chromosomes in meiosis causes hybrid sterility in diploids, since tetraploidy allows pairing between homologous chromosomes derived from the same species (Fig. 1). Crosses between such tetraploid hybrids and the parental species result in the production of sterile triploid individuals, so that the former are effectively a new species. Polyploidy of this kind is an important mode of speciation in flowering plants (Stebbins 1950), and is the only known method of saltatory speciation other than by the spread of a parthenogenetic variant within an originally sexual population.

F1 sterility due to failure of proper development of the gonads or germ cells, rather than failure of chromosome pairing, is a common phenomenon in animals and plants. In animals with separate sexes and chromosomal sex determination, it has long been known that it is often the *heterogametic* sex (i.e. the sex that is heterozygous for the chromosome pair involved in sex determination) that is most severely affected (*Haldane's rule*). The same rule also applies to hybrid inviability. This provides an opportunity to study the genetic basis of the sterility by means of crosses involving the fertile sex. This has been extensively exploited in *Drosophila* (Dobzhansky 1937; Muller 1940; Coyne & Orr 1989). The results of these studies show that sterility (or inviability) is caused by interactions between several genes, such that combinations of alleles derived from the two different species result in sterility. The simplest situation of this kind is when one species has a genetic constitution A_1B_1/A_1B_1 and the other A_2B_2/A_2B_2, where A and B represent two different loci. Each species is, of course, perfectly fertile and viable; infertility or inviability results from adverse effects of interactions between the alleles A_2 and B_1 or A_1 and B_2. It is frequently observed that loci on the sex chromosomes themselves often contribute disproportionately to the fitness breakdown of hybrids. This is probably the causal basis of Haldane's rule; X-linked or Y-linked alleles from one of the two parental species are fully expressed in F1 hybrids of the heterogametic sex, and have the potential to interact adversely with alleles from the other species at loci on non-homologous chromosomes (Muller 1940; Coyne & Orr 1989).

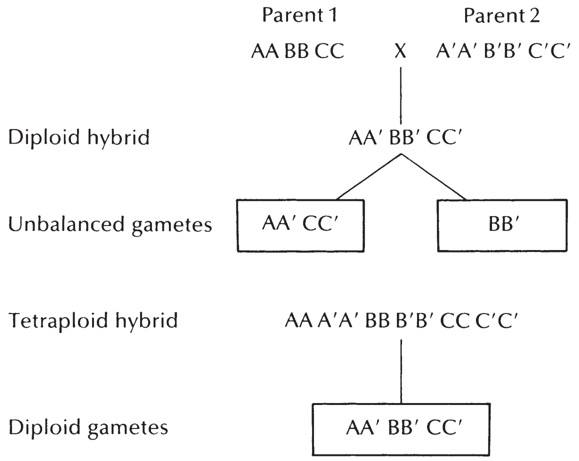

Fig. 1 The effect of polyploidy in restoring normal segregation in the F1 hybrid between two diploid species with three pairs of chromosomes. Note that a cross between the tetraploid hybrid (which produces diploid gametes) and either parental species will result in a triploid offspring. Such an individual will have low fertility, owing to the production of unbalanced gametes in meiosis.

The origin of reproductive isolation

These data indicate that changes at several gene loci are usually required for the achievement of reproductive isolation, other than by polyploidy or parthenogenesis. This is virtually a logical necessity, since it is most unlikely that a mutant allele at a single locus could both confer a high degree of infertility with individuals carrying the original allele, and become fixed in the population in opposition to this intense pressure of selection. The only faintly plausible mode of speciation by a single genetic change is through the chance fixation in a small population of a chromosomal rearrangement that causes drastic fertility loss to its heterozygous carriers. However, the chance of such a fixation event is very small in a random-mating population when the fertility loss to heterozygotes is high. Furthermore, even the most infertile rearrangement heterozygotes rarely suffer a fitness loss of more than 50% or so, and it has been shown that this reduction in fertility does not create much of an isolating barrier. Thus, even chromosomal speciation is most likely to occur as a result of a number of steps, each of which has a small impact on fertility (Barton & Charlesworth 1984).

The empirical evidence from the genetic analysis of species crosses is in good general agreement with these population genetic considerations. It should be stressed, however, that we have little idea in any individual case as to what has caused the genetic divergence between two populations that results in pre- or postzygotic isolation. A variety of theoretical models that can generate the evolution of such isolation have been proposed. As first pointed out by Darwin (1859), when criticizing the idea that hybrid sterility has evolved in order to prevent the fusion of species, post-zygotic isolation cannot be selected for directly, since natural selection can never favour lowered fitness. Dobzhansky (1937) and Muller (1940) proposed that the accumulation of independent evolutionary changes in two totally geographically isolated populations will very probably eventually result in the evolution of reproductive isolation. This can occur even if the populations are subject to identical environments, since different mutant alleles at different loci will arise by chance in the two populations, and become fixed by genetic drift or natural selection. The process is facilitated by the existence of environmental differences between the populations, to which they become adapted.

Alleles that get fixed in one population are not selected to interact well with the alleles from the other population, but have to perform well on the background of their own population. Thus, a sufficiently long process of divergence will result in the establishment of gene combinations that function perfectly well within the population in which they occur, but produce a breakdown in fitness when alleles from one species are combined with those from the other. The loss in fitness to species hybrids is no more surprising than the fact that a carburettor from a car manufactured in the U.S.A. does not function in an engine made in Japan. This model is entirely consistent with the genetic evidence described above. Furthermore, the predominant role of the sex chromosomes in contributing to the lack of fitness of F1 hybrids between closely related species is predicted by this model, if the genetic changes concerned are due to the fixation by natural selection of alleles that are favourable on the background of their own species (Coyne & Orr 1989).

Similarly, prezygotic isolating barriers can be understood as a product of the gradual divergence in male and female courtship behaviour (in animals), or in the biochemistry of fertilization, between two geographically isolated populations. The male and female functions within any single population are, of course, always selected to ensure efficient mating and fertilization, but there is no such selection to preserve the ability to mate with individuals from a geographically separate population. Sexual selection, acting on mutations affecting male characteristics of relevance to success in competition for females, may promote the divergence of isolated populations with respect to mating behaviour. An alternative possibility, first suggested by Dobzhansky (1937), is that prezygotic isolating barriers are the product of selection for behaviour patterns that prevent the gamete wastage which occurs because of matings between members of two populations that are in contact, and kept separate by postzygotic barriers (the process of *reinforcement*). While reinforcement is a theoretical possibility, it seems unlikely to be the only cause of the evolution of prezygotic isolation, since many cases are known where this occurs between populations that have never been in contact. Furthermore, unless postzygotic barriers are very strong, it is probable that two populations in contact will merge before they evolve behavioural differences, except in systems where narrow hybrid zones are maintained or where sharp ecological gradients maintain differentiation (Fisher 1930). None the less, there is some evidence that reinforcement plays a role in the evolution of behavioural isolation in the genus *Drosophila*, since pairs of closely related *Drosophila* species that are sympatric tend to have stronger degrees of behavioural isolation than pairs of allopatric relatives (Coyne & Orr 1989).

The possibility that speciation may be triggered by random drift during periods of restricted population size associated with the foundation of new, geographically isolated populations (*founder effect speciation*) has been the subject of considerable debate (Mayr 1963; Barton & Charlesworth 1984; Carson & Templeton 1984). The basic idea is that two alternative stable equilibria may occur under natural selection. The ancestral population is located at one of these equilibria, and passage through a small founding population causes random sampling of genotype frequencies that can sometimes result in a chance transition from one equilibrium to the other. Under appropriate circumstances, a hybrid population formed from crossing populations located at the two alternative equilibria will suffer a substantial fitness loss, and so the two populations will be at least partially isolated reproductively.

The original motivation for this theory was the observation that populations of a species are often relatively uniform over a wide geographical range, but peripheral isolates may deviate sharply in their characteristics from these. This led Mayr (1963) to propose that the potential for evolutionary change is restricted in large populations, because of the existence of genetic and developmental devices that prevent the manifestation of new variation on which selection could act. He claimed that these devices can be overcome by the random genetic changes that accompany the foundation of a new, isolated population. Later, Carson was stimulated to propose a related idea by the observation that inter-island migration of Hawaiian *Drosophila* is almost invariably accompanied by speciation (Carson & Templeton 1984). While theoretical models have shown that partial reproductive isolation can indeed evolve by this mechanism, the probability of producing anything approaching complete isolation by a single founder event is low. In addition, empirical and theoretical results of population genetics do not support the notion that evolutionary change is inhibited in large populations (Barton & Charlesworth 1984). Finally, alternative interpretations of the biogeographical data advanced in support of founder effect speciation have been proposed. For example, complete isolation permits two populations to differentiate with respect to favourable alleles, which would diffuse through both populations if they were connected by a chain of intermediate populations. This will produce an association between the foundation of new isolates and divergence or speciation. The role of founder events as causal agents of speciation thus remains controversial.

Sympatric and parapatric speciation

So far, the discussion of mechanisms of speciation has proceeded as though reproductive isolation takes place as a result of the genetic divergence of wholly isolated, geographically separate populations. This is the process of *allopatric speciation*, which can proceed by the mechanisms described above. There is little question that this is an important mode of speciation, perhaps the predominant one. This view has been vigorously championed by Mayr (1942), and there is indeed a wealth of distributional evidence which suggests that geographical isolation promotes genetic divergence and speciation. The most extreme alternative is *sympatric speciation*, the evolution of reproductive isolation between genotypes within a population that was originally mating randomly. Theoretical models of this process are reviewed by Seger (1985). The trigger for sympatric speciation is the maintenance of genetic polymorphism in a spatially heterogeneous population, where different genotypes are favoured in different patches. In such a system, selection can favour the evolution of preferential mating between like genotypes, thus preventing the production of segregant offspring that may be ill-adapted to all types of patch. The existence of races of phyotophagous insect species that are adapted to different host species is often quoted as an example of sympatric speciation, but it is not clear whether these are examples of true species (Futuyma & Mayer 1980). Since the theoretical conditions for the maintenance of genetic variation suitable for generating selection for preferential mating are rather severe (Seger 1985), the conclusion of Mayr (1963) that sympatric speciation is rare or non-existent seems likely to be essentially correct.

A more promising alternative is *parapatric speciation*, which involves the evolution of reproductive isolation between populations that are only partially isolated geographically. The classic model of this process is that of Fisher (1930), who suggested that a set of populations distributed along a geographical gradient of selection pressure would experience selection for mating preferences that would reduce the flow of genes between populations, and hence prevent the introduction of genotypes that are ill-adapted to the local environment. Later theoretical work has confirmed that this is, indeed, a mechanistically plausible process (Endler 1977; Barton & Charlesworth 1984). Of course, parapatric and allopatric speciation cannot be strictly distinguished, since populations at the extreme ends of a continental species range have very low probabilities of exchanging genes. There are several classic examples of reproductive isolation between populations located at the ends of such species ranges which have bent round on themselves, so that the extremes are now in contact (Mayr 1963). These represent cases in which reproductive isolation has evolved between populations that are connected by a series of other, adjacent populations between which gene flow may well be possible. If the intermediate populations were to become extinct, such cases would be open to misinterpretation as examples of strict allopatric speciation. Furthermore, the fact that the degree of geographical isolation tends to be correlated with divergence and speciation does not necessarily provide evidence for strict allopatric speciation, since (other things being equal) genetic divergence under the parapatric model will always be enhanced by restrictions on gene flow (Endler 1977). While it is always possible to interpret phenomena such as hybrid zones and geographically disjunct species ranges in terms of secondary contact between species that have diverged in allopatry, such interpretations are not necessarily demanded by the data. Thus, the biogeographical evidence does not seem to permit a clear-cut conclusion to be drawn concerning whether or not speciation usually requires strict allopatry.

Ecological aspects of speciation

Up to now, the ecological significance of speciation has not been mentioned. For two related species to coexist stably in the same area, it is necessary that they become adapted to somewhat different ecological niches, otherwise the competitively superior one will cause the rapid extinction of the other. Especially in birds, there is extensive evidence for ecological differences between close relatives. The Galapagos finches provide a well documented example of the ecological divergence of related species, which appears to have been driven largely by divergent adaptations of geographically separated populations to different food sources (Grant 1986). Without the evolution of such different ecologies, speciation would not result in any increase in biological diversity within a given geographical area. Sibling species show that such ecological differences may arise without any gross morphological changes (Mayr 1963), although they are often associated with morphological differences, as in the case of the bills of the Galapagos finches. Ecological opportunities provided by the invasion of new habitats, unoccupied by competitors, must play a major role in stimulating the rapid increase in the number of species during adaptive radiations. Natural selection is, needless to say, the primary causal agent in this aspect of speciation (Grant 1986).

Speciation and the fossil record

Speciation, in the sense used here, is simply a population genetic process that results in the acquisition of reproductive isolation between two formerly interbreeding populations. It thus cannot be directly observed in the fossil record. Indeed, it is important to recognize that, in a sense, there is no such thing as a speciation event, since all the evidence suggests that the process of acquiring total reproductive isolation is a multistep process that requires numerous intermediate stages, examples of which can be studied in contemporary species (Mayr 1942, 1963). Of course, the whole process of acquisition of specific status may occupy only a few thousand generations, as witnessed by examples of good species that are nearly identical at the molecular level (Barton & Charlesworth 1984; Coyne & Orr 1989). From the geological perspective, the time needed to develop complete reproductive isolation between two lineages may be effectively instantaneous. If no noticeable morphological differences evolve during the process, it will pass unnoticed in the fossil record, whereas morphological evolution in a single lineage might be counted as generating a new species, with the ancestral form A being replaced by a new form B. The fossil record thus provides a very incomplete picture of the process of speciation, particularly since subtle ecological, physiological and behavioural differences of the kind that frequently distinguish sibling species (Mayr 1963) will be missed. There are few cases in which it can be reasonably inferred that speciation has been observed in the record (Gingerich 1985; Section 2.3).

Of course, if form B appears in the record alongside A, it may be reasonable to infer that B originated in a speciation event elsewhere, and subsequently migrated into the range of A, which is unchanged morphologically. Patterns of this kind have been well documented by Cheetham (1987), for example. This kind of observation is the basis for the claim often made by supporters of the theory of punctuated equilibria, that morphological evolution usually only occurs in association with speciation (Gould & Eldredge 1977). As Turner (1986) has shown, it does not necessarily provide firm evidence for this claim. If speciation is often unaccompanied by detectable morphological change, then a progenitor of B with the same morphology as A could have coexisted alongside A, and only be distinguished by the palaeontologist as a result of evolutionary change that occurred well after speciation. Provided that evolutionary change in morphology is episodic, as is to be expected on most models of adaptive evolution, the punctuational mode of evolution can be explained without ascribing a special causal relation between speciation and morphological change. Such a causal relation does not seem to be consistent either with the evidence from present day organisms, where morphological change unaccompanied by reproductive isolation can be observed (as in polytypic species), or with population genetic theory (Turner 1986).

Nevertheless, the association of speciation with geographical isolation, and with new ecological opportunities, means that a correlation between episodes of rapid speciation and morphological evolution and diversification is to be expected. Island radiations provide small-scale examples of this that have been intensively studied (Carson & Templeton 1984; Grant 1986). Larger-scale events, such as the mammalian radiations of the Eocene, may be inferred to have the same causes (Wright 1949), the successive occupation of new major modes of life by speciating lineages providing the basis for the origin of the diverse combinations of characteristics distinguishing higher taxa (see also Section 3.6).

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2.3 Microevolution and the Fossil Record

P. R. SHELDON

Introduction

Despite its many imperfections, the fossil record gives us a historical perspective on evolution that cannot be obtained from a study of living organisms alone. A lifetime's research on, say, fruitflies in a laboratory or peppered moths in a wood, though indispensable, can only span a fleeting moment in a species' history. A crucial task for evolutionary biologists is to integrate results from an increasingly detailed analysis of the fossil record into a comprehensive synthetic theory, one which bridges the gap between the neontological and palaeontological scales of observation. This explains the growing attention paid by geneticists to high-resolution fossil data.

The term microevolution is taken here to mean all the evolutionary changes that occur within a species up to and including the formation of new species, either by lineage branching (i.e. cladogenesis or speciation) or by phyletic transformation (i.e. anagenesis).

Fossil species in practice

Although the fossil record of any species will always be deficient vertically (in time), laterally (in space), and morphologically, the hard-part record of some forms — especially shelly marine invertebrates — is rather better than sometimes asserted. Attempts to quantify completeness of stratigraphic sections have enabled palaeontologists to calibrate accessible levels of time resolution, and to define the kinds of evolutionary and palaeoecological questions that the fossil record is uniquely placed to answer (Section 3.12).

The acquisition of reproductive isolation can never be directly observed in the fossil record (Section 2.2). Nevertheless, many palaeontologists try to make the species they describe live up to a definition such as: 'Species are morphologically distinct groups within which variation is of the magnitude expected in interbreeding populations, and between which the differences are of the kind and degree expected to result from reproductive isolation of natural populations'. In practice, of course, such species can never be more than 'morphospecies' (units that embrace individuals of similar form), in which sibling species go undetected and from which truly conspecific variants and sexual dimorphs may be unwittingly excluded. Even greater conceptual problems arise if lineages undergo extensive anagenesis: some workers, especially biostratigraphers, divide such lineages into arbitrary chronospecies, whilst others, mostly theorists adopting a strict cladistic approach, would prefer to denote a single unbranching lineage with a single specific name, irrespective of the total change. The more continuous the record, the more problematic the nomenclature (e.g. Bown & Rose 1987; Sheldon 1987).

Patterns of evolution

The belief that many fossil species remained in morphological stasis throughout their existence prompted Eldredge and Gould (1972) to invoke a pattern of punctuated equilibrium as an alternative to the pervasive paradigm of phyletic gradualism. Previously, lack of intermediates between species had largely been accounted for by incompleteness of the record. Basing their proposition on Mayr's allopatric speciation model and on observations of Devonian trilobites and Pleistocene land snails, Eldredge and Gould argued that the rise of new species is expected to be episodic, local, and rapid (as opposed to continuous, widespread, and slow) and so the chance of finding intermediates in the fossil record is bound to be low. A speciation event would normally span less than 1% of the species' later existence in stasis. Fossil sequences should show stasis with sharp morphological breaks marking the migration of the descendant form from the peripheral, isolated area in which it developed. The presumed ancestor is then expected to persist for a while alongside its putative descendant. Thus, according to punctuated equilibrium theory, significant evolutionary change occurs at events of branching speciation and not during the *in toto* transformation of lineages. These contrasting patterns have provided a very useful framework for discussion and stimulated a more rigorous analysis of the fossil record.

Perception of patterns

It has often proved impossible to establish the validity of an evolutionary pattern to universal satisfaction. Many relevant hypotheses, such as ancestor–descendant relationships or genetic versus ecophenotypic change, are never truly verifiable. But here, as usual in palaeobiology, we are not in the business of proof but in assessing the relative probabilities of competing hypotheses.

Fortey (1988) discussed the biases that influence perception of patterns, showing how it is comparatively easy for the convinced punctuationist to 'see' gradualistic change as a series of punctuation events. However, as intervals without data become restricted to smaller and smaller timespans, so one pattern rather than another can be shown to be more probable by applying the principle of parsimony (though, of course, the most parsimonious explanation is not necessarily the correct one).

Many of the standard textbook examples of gradualism dissolved in the wake of the punctuated equilibrium hypothesis. Most such cases were shown to lack sufficient documentation, whilst some, like the phylogeny of horses, were reinterpreted as showing punctuations, if anything. The ideal recipe for establishing evolutionary patterns includes some ingredients that are very difficult to obtain: many complete specimens from successive, small stratigraphic intervals whose relative age is unequivocal; a framework of well-constrained absolute ages; samples spanning the entire geographical and temporal range of all closely-related lineages; as many ontogenetic stages as possible (in order to recognize heterochronic relationships) and statistical data on all available characters. To avoid generating artificial patterns, fossils should only be assigned to named species late in these procedures.

A knowledge of geographical variation is important because spurious vertical patterns of phyletic change could arise in local sections by waves of immigration and emigration of intraspecific variants tracking their favoured environment. Also, in theory, a peripheral isolate might evolve *gradually* to a new species which, on migration, appears abruptly alongside its parent species remaining in stasis. Geographical consistency of morphological change is not, however, a prerequisite for establishing the validity (i.e. genetic basis) of evolutionary trends. For example, dissimilar trends could occur in adjacent populations of a benthic species living in a tectonically unstable shelf area. The subpopulations might become isolated for a while in silled basins, each imposing different selection pressures, such as if one basin shallowed as another deepened. Eventually divergent strands of the lineage might be reunited if the physical barriers to gene exchange were removed whilst hybridization was still possible.

Examples from the fossil record

The case histories which follow have been selected to illustrate various aspects of the debate and for their implications for microevolutionary theory.

Williamson (1981) presented evidence for both stasis and punctuated speciation in many lineages of Cenozoic lacustrine molluscs from East Africa. The 'speciation events', which took 5000–50 000 years, were accompanied by an increase in morphological variance that Williamson interpreted as extreme developmental instability in transitional populations. The strong possibility remains, however, that the new short-lived forms were ecophenotypic variants induced by intense environmental stress.

Hallam (1982) concluded that the Jurassic oyster *Gryphaea* showed a step-like pattern of punctuated change, allied with morphological trends, some of which were paedomorphic. He found no evidence of gradualism or cladogenesis. Recently, however, Jonhson (*in* Fortey 1988) has reported gradual and continuous derivation of *Gryphaea* morphology in the Middle Jurassic from another oyster, *Catinula*.

Stanley and Yang (1987) documented stasis in shape for 19 lineages of Neogene bivalves, some spanning as much as 17 million years without taxonomically significant change. Populations millions of years old often resemble their Recent descendants almost as closely as geographically separated conspecific living populations resemble each other. Stanley and Yang emphasized that shape and size should be kept separate in all calculations of evolutionary rates, arguing that most reported trends relate to variables representing only some measure of body size.

Cheetham (1987), examining 46 characteristics in nine species of Neogene bryozoans, found overwhelming evidence for stasis and, by inference, punctuated speciation. The few within-species trends present related to features not used in species diagnoses and he cautioned against judging patterns from single morphologic characters.

Planktic foraminifera and radiolarians yield some of the best known lineages in the fossil record, because of their widespread distribution, abundance in DSDP cores, and commercial use in biostratigraphy. These micro-organisms display a wide variety of evolutionary tempos and modes (see papers in *Paleobiology* **9** (4), 1983, and Banner & Lowry *in* Cope & Skelton 1985 for reviews). Gradual changes seem relatively common. Malmgren and Kennett (1981) demonstrated persistent gradualism in a lineage of temperate foraminifera that spanned four successive chronospecies in 8 million years. Planktic foraminifera also show a pattern best described as punctuated anagenesis (e.g. Malmgren *et al.* 1983), which is probably common in other groups too, including ammonites (e.g. Callomon *in* Cope & Skelton 1985).

Sheldon (1987) reported parallel gradualistic evolution of benthic Ordovician trilobites from central Wales. Over a period of *c.* 3 million years eight lineages underwent a net increase in the number of pygidial ribs, a character used in species diagnosis (Fig. 1). The end members of most lineages had previously been assigned to different species and, in one case, to different genera. In view of intermediate morphologies and temporary trend reversals, practical taxonomic subdivision of each lineage proved impossible. The apparent success of earlier Linnean nomenclature (with its implications of discrete species) could easily have been misinterpreted as evidence of punctuation and stasis. Perception of many other gradualistic patterns equally may have been hindered by conventional descriptive procedures, particularly the requirement to apply binominal taxonomy to fossils and the practice of lumping together specimens collected from different horizons in order to amass enough material for full 'species' description.

Although vertebrate data are sparse, gradual evo-

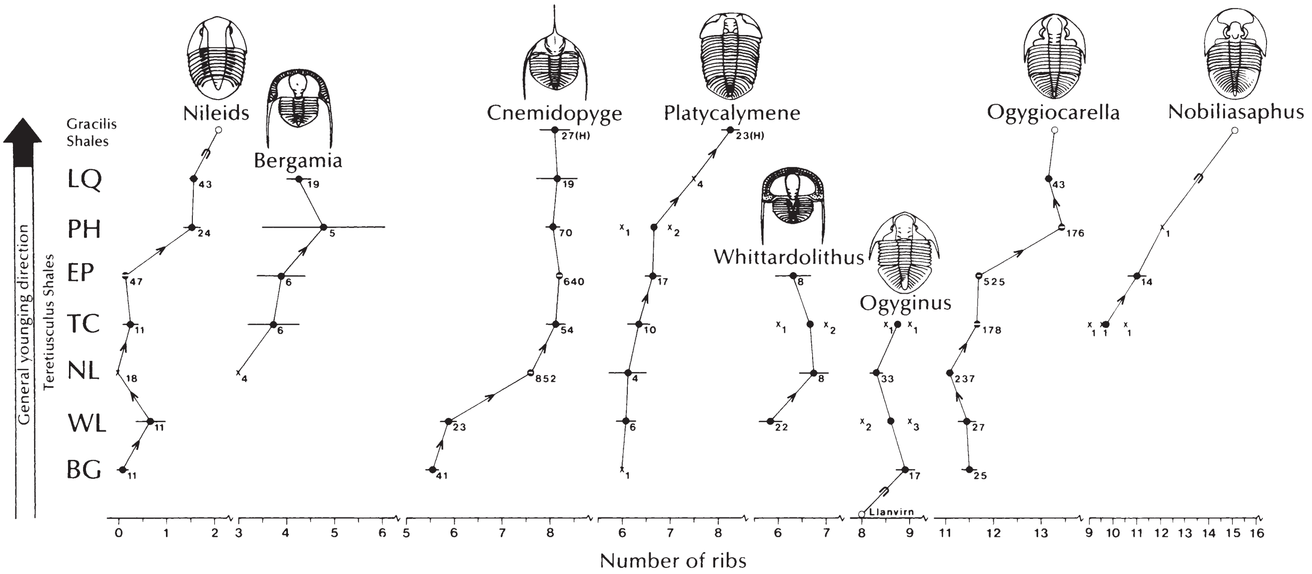

Fig. 1 Summary of changes in mean number of pygidial ribs for eight Ordovician trilobite lineages in the Builth inlier, central Wales. Means with 95% confidence interval and number of measurements are shown by -●-$_n$ and ⊖n. Approximate mean (○). Data from Hughes (see Sheldon 1987) (H). Individual measurements (X_n). Successive means (↑) are significantly different at the 95% confidence level. Successive means (⇑) are certain to be significantly different but full data are unavailable. Vertical spacing between sections (BG, etc. see Sheldon 1987) is not to scale. Reversible shifts in means are common *within* sections (not shown subdivided). Sections in the Teretiusculus Shales span *c.* 3 million years. (From Sheldon 1987.)

lution appears to be fairly common, particularly in Tertiary mammals (e.g. Gingerich 1985; Godinot *in* Cope & Skelton 1985). Bown & Rose (1987) saw no sign of stasis in Eocene primates from Wyoming, reporting both gradual anagenesis and cladogenesis in sharp contradiction to the predictions of the punctuated equilibrium model. They highlighted the problems that gradualism causes for systematic palaeontology and biostratigraphy. Bell *et al.* (1985), in a multicharacter study of a Miocene stickleback lineage, found that taxonomically significant morphological change was accomplished by protracted trends *and* by rapid bursts of evolution, without tight synchrony of change among characters (mosaic evolution).

Although there are some well attested examples of gradual cladogenesis in the fossil record (Gingerich 1985), the great rarity of branching points where nodes are known is consistent with common patterns of change in which cladogenesis is rapid and/or involves small, isolated populations.

Random change and trend reversals

There has been much interest in the possibility that some morphological trends seen in the fossil record may be the result of processes other than natural selection. The genetic drift hypothesis predicts that the morphology of selectively-neutral characters will vary through time as a random walk. Indeed, it has been argued that evolutionary rates exist only when the hypothesis of a symmetrical random walk can be refuted. However, Sheldon (1987) argued that temporary reversals of variable characters probably occur in all evolutionary lineages, and so many trends driven by selection may be indistinguishable from random walks. Reversals probably reflect times when some other attribute, genetically uncorrelated with the one under consideration, was selected. It would be unreasonable to expect that the one feature chosen for plotting was consistently the only one favoured by selection, or that it was always linked to every other favoured trait. In fact, long-sustained net trends in a single character may reflect genetic coupling to other characters having negative effects on fitness (see also Section 2.2).

The widespread tendency not to expect reversals, or to interpret them as ecophenotypic change or random drift, led to the unrealistic portrayal of phyletic gradualism as unidirectional change. Reversals have many consequences. For instance, they complicate the theoretical arguments (Fortey 1988) concerning differentiation between cases of gradualism and punctuated equilibria; they should not be automatically taken to indicate that the observed change is only ecophenotypic; and jumps in morphological trends cannot be used to estimate the amount of time missing at diastems.

Patterns of evolution in different environments

It is still inappropriate to estimate the relative importance of particular patterns of evolution in different environments. Given the immense range of attributes of living organisms (e.g. complex life cycles and reproductive strategies) it would not be surprising to find different patterns emerging from broadly similar environments. Benthic invertebrates, for instance, have a wide diversity of larval dispersal modes and these early stages, although rarely preserved, might profoundly influence patterns. There is some evidence, as might be expected, that abrupt speciation and extinction are commonly associated with benthic species living in shallow marine settings. However, Sheldon (1987) suggested that, almost paradoxically, stasis seems to prevail in these more widely fluctuating, rapidly changing environments, whereas species living in, or able to track, narrowly fluctuating, slowly changing environments show persistent phyletic evolution rather than stasis.

Some of the perceived punctuations in shallow benthic settings may simply reflect higher rates of short-term deposition and more hiatuses (less completeness) than in offshore, pelagic environments. But, although the most reliable evolutionary patterns will come from the most complete sequences, the depositional conditions promoting completeness might in themselves encourage gradual phyletic evolution, especially of benthos.

Conclusion

Studies of the fossil record have revealed a wide spectrum of microevolutionary patterns, from which can be inferred a variety of evolutionary processes. Punctuated equilibrium and phyletic gradualism should be viewed as just two theoretical versions of many possible evolutionary patterns and the temptation to force poorly documented cases to fit one or other of these models must be resisted. Often there is simply too little data to assess patterns of change as, for example, with the genus *Homo* (Section 1.12). We are not yet in a position to assess accurately the relative frequency of particular patterns and the domain of their expected settings.

Individual taxa probably exhibit different patterns at different times, and different morphological characters in the same species may evolve at different rates. Episodic changes need not be associated with branching events and demonstrating stasis in a species is not the same as demonstrating punctuated speciation.

Most geneticists believe that a punctuated appearance of species is consistent with neo-Darwinian theory. In many ways it is explaining stasis — which is certainly more prevalent than would have been predicted from studies of living organisms — that represents the greater challenge.

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