

PATTERNS AND RATES OF SPECIES EVOLUTION

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Contents

1. Introduction
2. Biological and morphological species concepts
3. Evidence from ecology and palaeobiology
4. Fossil evidence of speciation.
5. Species diversification through time
6. Evolutionary patterns and processes

Related Chapters

Glossary

Bibliography

Biographical Sketch

Summary

Species, and speciation, the process of the formation of species, are critical topics for evolutionary biologists. Biologists have long debated the meaning of species, and many philosophical stances have been adopted. Charles Darwin devoted his *Origin of species* to the topic, but famously failed to resolve the question. One hundred and fifty years of intense research by evolutionary ecologists, geneticists, molecular biologists, and palaeobiologists have led to the proposition of many models for the origin of species. The problem in studying species is that much of what is interesting happens on timescales midway between the short intervals available for study during human lifetimes, and the longer timescales available to palaeobiologists. The most likely, and probably the commonest, mode of speciation is according to the allopatric, or geographic model. An existing species becomes divided in some way, usually by a geographic barrier, and the two segments of the population evolve apart. After some time (hundreds of years), reproductive barriers set in, and the two populations become two species. However, it is clear also that speciation may occur sympatrically, without the need for geographic barriers. Studies of modern ecological situations give hints of how speciation has happened in the past tens or hundreds of years. Palaeobiological studies of the Neogene, the past 40 million years, can now show patterns of lineage division in some detail. Speciation in terrestrial plants and animals may generally occur after geographic separation, and relatively rapidly, following a punctuated pattern. However, speciation of widespread marine forms, especially plankton, may take longer, perhaps 100,000 years or more, and the process is sympatric. In other cases, however, speciation of lake fishes clearly occurred enormously rapidly, but possibly sympatrically.

1. Introduction

Patterns and rates of species evolution may be inferred from studies of modern biology and from the fossil record. Neither approach is perfect, but in conjunction, and with the careful choice of case studies, some useful generalities about the evolution and duration of species may be established. Studies of modern biology allow intensely detailed studies of large populations over their full geographic range, but the analyst has to guess what happened in the past. Studies of fossils may offer the time dimension, so that the evolution of a species may be followed step-by-step, but there may be problems in recovering a complete record that has no gaps, and it is hard to obtain detailed geographic coverage.

The biologist who is interested in speciation may examine the distributions of living species, and use studies of their relationships to infer past events. For example, Charles Darwin was able to establish that the various finches on the Galapagos islands were all related to each other, and had all presumably derived from a single ancestor on the nearest mainland, South America. He could work out the pattern of relationships among the various finches, and hence infer how they had migrated from island to island. More recent work has established in much more detail the exact patterns of relationships of the finches (based on both morphological and molecular phylogenetic evidence), and geological evidence has set a limit on the age of the Galapagos islands, so it is known that the 14 species of Darwin's finches diverged from a single common ancestor that reached the Galapagos some time after 5 million years ago, when the islands emerged from the waters of the Pacific.

In classical palaeontological studies, specimens may be collected centimetre-by-centimetre through a succession of rocks. In the case of classic studies of marine invertebrates, for example the asymmetric bivalve *Gryphaea*, known from the Lower Jurassic of Europe, large population samples may be taken, and the waxing and waning of individual species may be tracked through hundreds of metres of rock, representing millions of years. Simple statistical studies show that mean measurements of the populations vary through time, presumably as the species responds to minor environmental changes. But, in general, fossil species clearly show stasis, long-term stability of form. It is harder, however, to establish just what happens at speciation in most fossil examples since the stratigraphical acuity (the precision of dating individual sedimentary layers) is usually greater than the time interval of interest (i.e. > 50,000 years). Only in rare cases (see below) can palaeontologists document speciation events adequately.

2. Biological and morphological species concepts

The biological species concept is the dominant definition of species. In its simplest form, the biological species concept, as presented by Ernst Mayr in the 1940s, states that a species consists of all those individual organisms that normally interbreed and produce viable offspring. Speciation is usually accepted as being marked by the onset of permanent reproductive isolation in the descendants of once-interbreeding populations. It is assumed also that, although morphological differentiation need not form part of this model, nonetheless, populations will drift apart genetically and that this will be reflected in divergence of phenotypes rapidly enough that the point of splitting and detectable morphological differentiation essentially coincide.

Of course there are difficulties with the biological species concept, and many exceptions. For example, asexual organisms (clones) have to be defined differently. In nature, also, certain animals, and many plants, may readily hybridize, and even more examples of separate species may be induced to hybridize in laboratory conditions.

Palaeontologists have always adopted a morphological species concept in which species (morphospecies) are discerned by differences in the shape of their bodies or of parts of their bodies. This concept had been applied instinctively from the earliest days of palaeontology, when specimens were compared, and distinguished as separate species if they differed sufficiently in form. Indeed, this pre-evolutionary procedure for species distinction was no different among palaeontologists or systematists of extant forms.

Again, like systematists of modern forms, many palaeontologists became enthusiasts for populational thinking in the mid twentieth century: large collections of fossils were made, and everything measurable was measured. Species were distinguished, where specimens were abundant, by distance measures between the centroids of multivariate clusters of points. These approaches are common today, but obviously cannot be applied to forms that are rare or unlikely to fossilize.

The biological species concept, and variants, have never been applicable to the fossil record, although the related concept of allopatric speciation has been influential on palaeontological thinking. Clearly any tests of viable offspring from interbreeding of fossil taxa (equally tests of species recognition, genetic distinction, and the like) cannot be made. But it ought to be noted that systematists of modern taxa rarely set up regimes of interbreeding tests to solve a taxonomic problem of species definition. Most modern systematic work is based on morphological distinctions among dead museum specimens. What the fossil clearly lack, however, is the potential for molecular and genetic studies, a rapidly growing field in species-level systematics.

The 'biological' view of species lineages adopted by most investigators fits well with the concepts of modern phylogenetic systematics (cladistics). However, it conflicts fundamentally with the original use of the term 'species' as a fixed entity of classification. It also conflicts to some extent with the formal process of species naming in biological taxonomy. For example, some palaeontologists might argue that if a species lineage has evolved sufficiently in form (by anagenesis) to be entirely distinct from its ancestor, then it should constitute a different species; but by the definitions normally adopted, that can only be admitted if a cladogenetic (lineage splitting) event has occurred.

3. Evidence from ecology and palaeobiology

The confidence of biologists and palaeontologists in their attempts to discern patterns and processes of speciation has waxed and waned over the years. Darwin hoped for great improvements in knowledge of fossil lineages, especially through the Tertiary, so that all the discrete living species might be linked, through fossil forms, into their true phylogenetic patterns. At the same time, he famously drew attention to the great imperfections of the fossil record. These two thoughts have continued to dominate thinking about the palaeontological contribution to a knowledge of evolution.

In his *Origin of species*, Charles Darwin drew the important parallel between historical and spatial patterns of species distributions. He compared the propinquity of species in time (from the fossil record) and in space (from modern geographical distributions). Darwin had seen how the modern fauna of South America, for example, showed a range of unusual forms that compared closely with Pleistocene fossils from the same regions. He used this as strong evidence that the species had evolved on the spot from the fossil to the living form. Likewise, his studies on the Galapagos archipelago, and elsewhere, showed, on the whole, that geographically close forms were more similar than geographically distant forms, and hence that this was further evidence for evolutionary relationship.

Despite these suggestions, most palaeontologists and most biologists in the early twentieth century ignored the fossil record in their debates about species and speciation, mainly because of its perceived inadequacies. Attention focused on ever more detailed field-based studies of modern species.

A question of considerable interest has been the duration of the process of speciation. The example of Darwin's finches, mentioned above, indicated that the present 14 species must have diverged from their common ancestor within the five million years of the existence of the Galapagos islands. This observation simply places an upper limit on the time-scale of speciation: species splitting could indeed have taken a much shorter time.

3.1. The cichlid fishes of the African rift valleys

The cichlid fishes (Fig. 1) of the rift-valley lakes of East Africa provide a well-studied case of speciation in action, this time demonstrably much more rapid than Darwin's finches. The cichlids are often cited as examples where explosive evolution has occurred. The lakes are all relatively young in geological terms, and yet each contains large numbers of endemic species. For example, Lake Victoria is less than one million years old, and most of its 200 species of cichlids are endemic. These 200 species vary to some extent in external morphology, but much more in ecological and trophic specializations. There are algae grazers, plankton and detritus feeders, pharyngeal snail crushers, and insect and fish predators. Some of the cichlids have even more bizarre specializations: one of them feeds on hatchling fishes, grasping the snout of a mouth-brooding female, and forcing her to disgorge her young; another rasps the scales from the tail fins of other cichlids, and a third (in Lake Malawi) plucks the eyes from dead fishes.

Genetic studies on the mitochondrial DNA of cichlids from Lake Victoria show almost no differentiation among the species, which suggests that all 200 species diverged within the past 200,000 years, and perhaps within as little as 12,400 years. Comparisons of cichlids from different lakes show greater differentiation: fishes from Lake Malawi differ by more than 50 base substitutions from those from Lake Victoria. Within Lake Malawi, molecular genetic analysis revealed two distinct mtDNA lineages, but these were more closely related to each other than to cichlids from any other lake. The molecular studies confirm that speciation was rapid, and that speciation was contained within each lake.

EOLSS - PATTERNS AND RATES OF SPECIES EVOLUTION

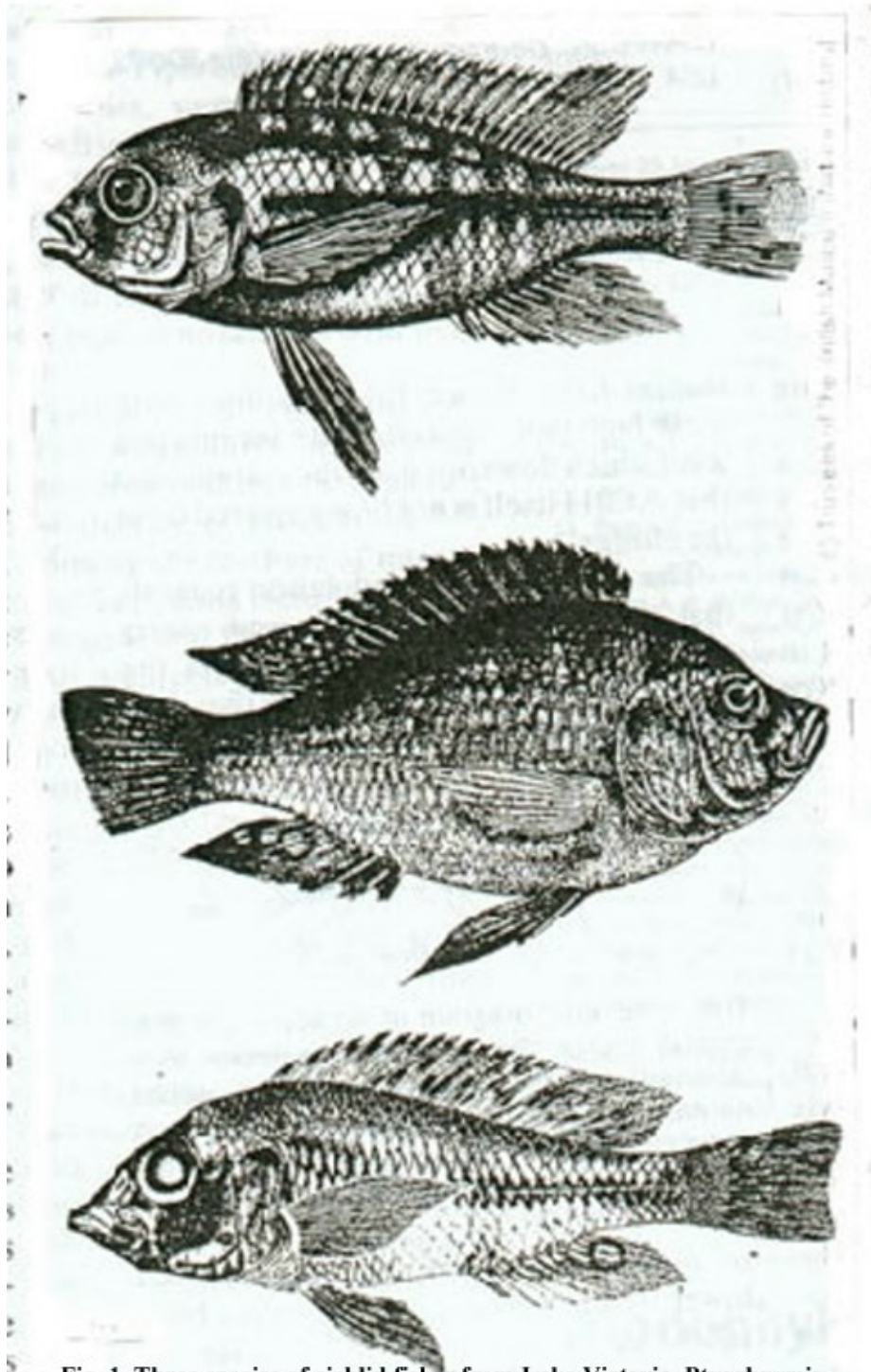


Fig. 1. Three species of cichlid fishes from Lake Victoria, *Ptyochromis sauvagei* (top), *Lipochromis obesus* (middle), and *Astatotilapia piceatus* (bottom), showing the diversity of form. These species evolved from a single common ancestor within less than one million years. Based on several sources.

Was speciation of the African cichlids sympatric or allopatric? The huge numbers of species packed into each lake, and the relatively limited areas of distribution of many of

the species in each lake, might suggest sympatric speciation, where genetic splitting has occurred without geographic isolation. However, the present distribution patterns, and the history of the lakes, suggests that most of the speciation events may have been allopatric, although this is debated. Along sections of the shores of the African lakes, individual species often occur in single small inlets separated from neighbouring sections of shore by minor barriers of rocks or vegetation. Throughout the history of the lakes, they have varied enormously in size, drying up substantially several times, and re-flooding. Perhaps, during drying episodes, when each of the great lakes divided into numerous small pools, evolution proceeded rapidly. On re-fusing, the fish faunas of each lakelet retained their genetic identity, and survived to the present as distinct species.

3.2. Sticklebacks and speciation by natural selection

But what actually triggers speciation? Perhaps species diverge genetically somewhat at random by a build-up of genetic differences (genetic drift), and then come to look and behave differently. Or perhaps species diverge as a result of natural selection acting on the habits and appearances of different sections of a single population. The latter may be the usual model. In a study of sticklebacks in three isolated freshwater lakes on the Pacific coast of British Columbia, Rundle and colleagues found that essentially the same two species had evolved in each case. Each lake contains one hefty, bottom-living species and one streamlined form that feeds in open water. The species have diverged in parallel in each lake very rapidly.

The stickleback pairs all evolved from the marine stickleback *Gasterosteus aculeatus* when they were trapped in the coastal lakes 10,000 years ago by a retreating glacier. The sticklebacks adapted to the new freshwater regime, and speciated apparently rapidly, and in parallel, into a bottom-liver and a swimmer in each of the three lakes. Speciation appears to have been sympatric and, importantly, driven by natural selection: the two major niches were available, and the sticklebacks diverged independently in each of the three lakes to exploit the two trophic and ecological modes (Fig. 2).

3.3. Ice ages and species migrations

Glacial conditions during the Pleistocene have apparently driven speciation in many other northern hemisphere organisms. Indeed, the recent retreat of the ice sheets from North America and Europe provided a major change in life conditions, and hence the possibility of determining speciation events on relatively short, measurable time scales. The general model is that, as ice sheets advanced southwards from the north polar regions, temperate and warm-adapted species of plants and animals fled south until they reached refugia, safe living spaces that retained their preferred life conditions. These glacial refugia lay in the southern United States and in south Europe (north Africa, southern Spain, south of France, Italy, Greece, Turkey).

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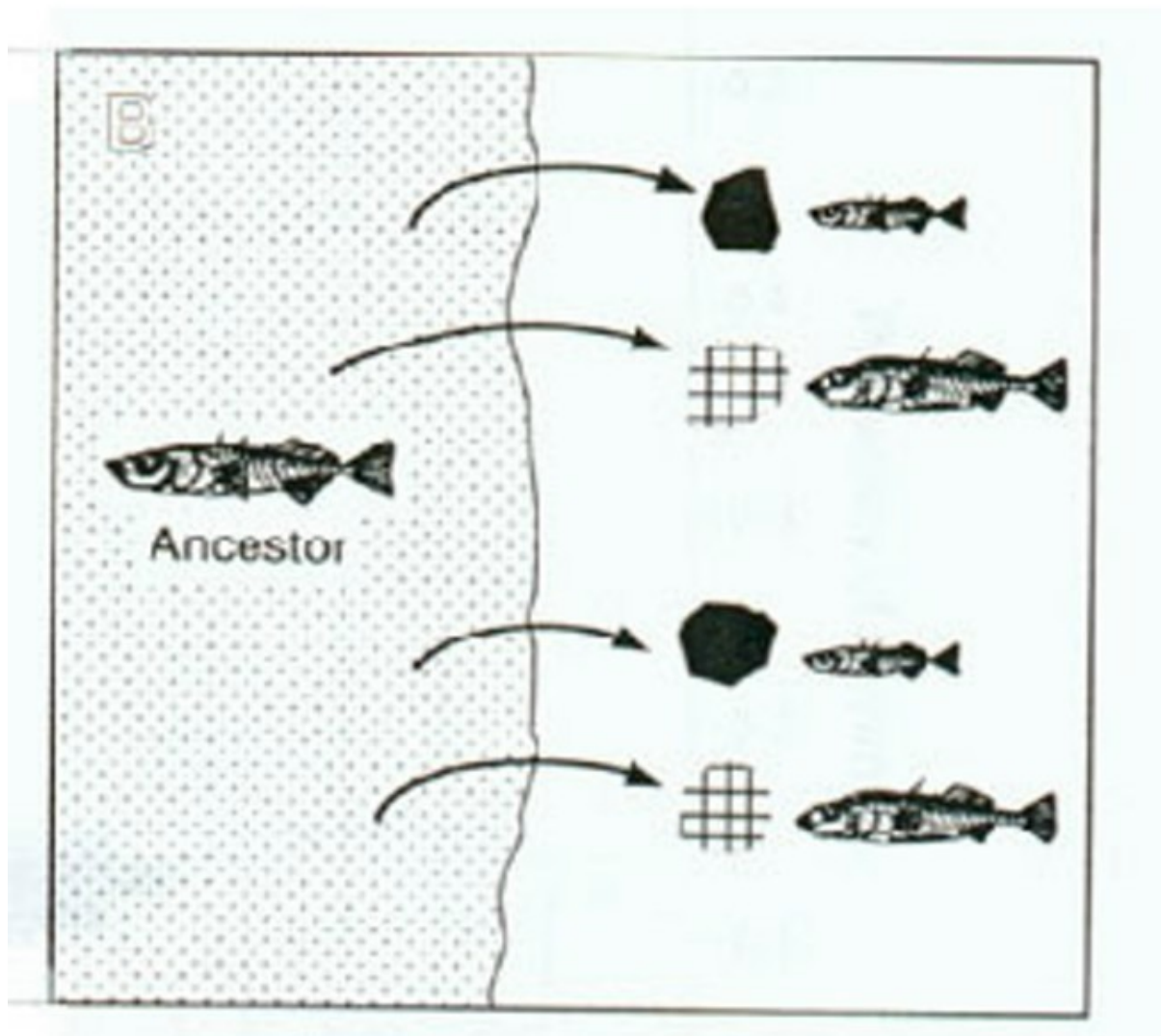


Fig. 2. Model for parallel speciation of sticklebacks. The ancestral species (left) colonizes a variety of different habitats (right). Ecological conditions in the new habitats lead to divergence in body size and other characters by natural selection, but the environmental factors cause parallel evolution of similar species independently in different geographic settings. Based on the work of Dolph Schluter.

As the ice sheets retreated 10,000 years ago, the temperate-adapted organisms moved north from the refugia, and recolonized North America and Europe. The key point is that the populations of what had perhaps been a single species before the advance of the ice, had had time to diverge in their separate southern refugia, and when they marched north again, they had, in many cases, become distinctive populations or even species that retained their separate identities. There are many examples.

The distribution of the European hedgehog, *Erinaceus*, is divided into an Iberian clade (that migrated from Spain over France, the low countries, and England), a German clade

(found in north Germany and Denmark), an Italian clade (that migrated in a straight line north over Switzerland, Germany, and southern Scandinavia), and a Balkan clade (that migrated from Greece and the Balkans northwards over eastern Europe). Similar splits in clades of the brown bear (*Ursus arctos*) and the beech (*Fagus sylvatica*) may also be attributed to refugia, divergence, and glacial retreat.

The African cichlids and the glacial refugia suggest that speciation can be rapid among certain groups of plants and animals, occurring perhaps in as little as a few hundred or thousand years. Once genetic divergence and differentiation in habits have occurred, species seem to retain their distinctness in nature. Much more fruitful work on modern organisms is possible, and can shed further light on processes of speciation in action. Extending to longer time scales is important as well, since individual species typically persist for a million years or more, and it is important to track how species change over those intervals.

3.4. The punctuated equilibrium revolution

Palaeontological work on species and speciation did not progress very far in the earlier part of the twentieth century. The time scales seemed too long, and the quality of the dating seemed too poor. However, a major impetus to studies on speciation in the fossil record came with the publication by Eldredge and Gould in 1972 of their theory of speciation by punctuated equilibria. This led to an active search for well-documented examples of speciation in the fossil record, although, in retrospect, most of the published examples from the 1970s and 1980s were not adequate to document speciation in action.

Eldredge and Gould termed the standard palaeontological and biological viewpoint 'phyletic gradualism'. According to this (Fig. 3A), it was assumed that evolving lineages were changing at variable rates, but changing pretty well continuously (anagenesis). Speciation was often seen as a by-product of this process of change: sometimes lineages had become so different from their starting points that they had evolved into a new species (the chronospecies concept). Speciation by splitting (cladogenesis) could also happen, but the process was no slower or faster than normal rates of lineage evolution.

The opposing viewpoint, evolution by punctuated equilibria (Fig. 3B), was quite different, both in pattern and process. Anagenesis was unimportant, and rapid morphological change at cladogenesis was all. The normal state of a lineage was stasis, essentially an absence of change for long periods. From time to time, speciation happens, but such speciation events are rapid and revolutionary. The pattern of punctuated equilibria is rectangular, and virtually all of evolution happens at speciation.

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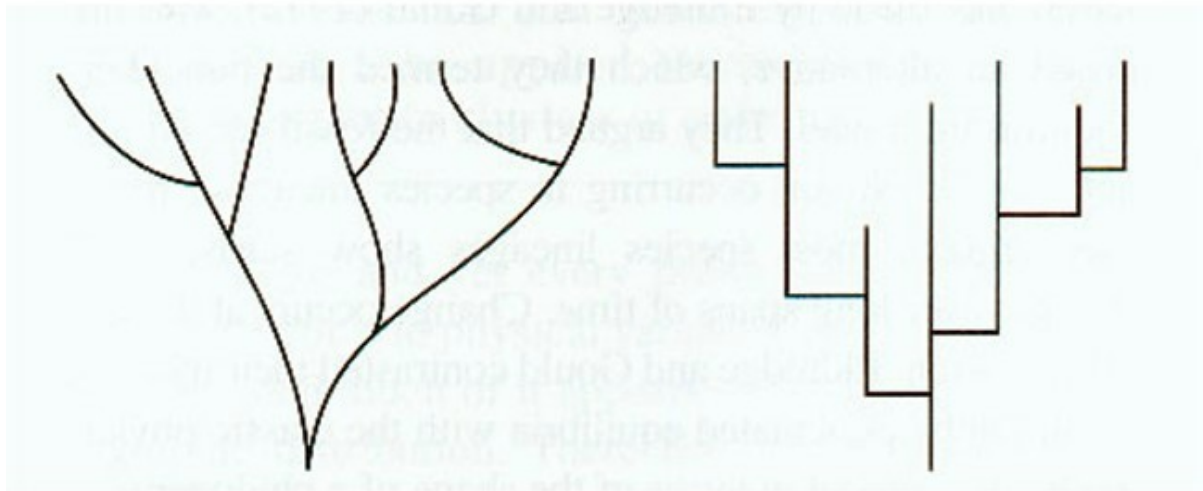


Fig. 3. Contrasting expectations of species-level evolution, the classic phyletic gradualism model (A), and the punctuated equilibrium model (B). Modified from various sources.

Eldredge and Gould based their new model on two well-established observations from the fossils and from the modern day. Stasis was actually what palaeontologists had known for years, but had not articulated. In fact, even in the very best of fossil records, it is rare to be able to see long episodes of gradual change. If anything, fossils may remain pretty constant in appearance through many metres or tens of metres of sediment (i.e. thousands or millions of years), and then everything seems to change. The second insight was that, if most speciation happened according to Mayr's allopatric model, then this would appear as a rapid event in the fossil record. The detail of the gradual divergence of two isolated populations would not be seen. This would be particularly true of peripheral isolates, small isolated marginal populations that might be expected to evolve most rapidly.

The key novelty of the model of punctuated equilibria is stasis. Stasis formed no part of Mayr's allopatric speciation model. Indeed, most evolutionists expect that anagenetic evolution is important, but the concept of widespread stasis essentially denies the existence of any kind of lineage evolution. The concept of stasis was at first immensely controversial, but quantitative genetic models have been found to explain it.

3.5. Stasis

Eldredge and Gould's emphasis on the evolutionary importance of cladogenesis over anagenesis may be the most significant contribution of palaeobiology to the question of species and speciation. If lineages are not constantly evolving, but in fact remain stable for hundreds of thousands, or millions, of years, there are wide implications for many areas of evolutionary biology, from models of community evolution to debates about the role of competition, from population genetics to phylogenetics.

Many hundreds of case studies of segments of the fossil record have now been published in an attempt to determine whether evolution happens by traditional phyletic gradualism or by punctuated equilibria. Early efforts were often inadequately documented, and did

not provide enough evidence about the accuracy of dating, and about the possibility of migrations of taxa in and out of the study area. Indeed, it soon became clear that what was a gradual anagenetic pattern to one person, was an obviously stepped, punctuational pattern to another. Larger-scale studies from the 1980s and 1990s involved in some cases tens of thousands of assessed specimens, very fine-scale stratigraphies, and subtle attempts to determine the nature of the species involved. Even in these massive exercises in data documentation, the quibble could be raised that apparent speciations might sometimes be simply ecophenotypic changes, nothing evolutionary at all. With morphospecies, it is clearly hard to distinguish ecophenotypic changes from true evolutionary changes. Perhaps, palaeontological studies can be convincing only if they involve both living and extinct forms.

3.6. Speciation and ecophenotypic change: the rift valley snails

In detailed studies of lake-living gastropods and bivalves through the past 4 million years, Peter Williamson in 1981 was able to show the prevalence of stasis. His study was especially strong in terms of the quality of dating and the sizes of his samples. Lake Turkana lies in the East African Rift Valley, on a tectonically active line where the continent of Africa is unzipping to form two major plates. Lake muds and sands accumulated in thick deposits as the rift opened, and volcanic ash (tuff) beds occur sporadically throughout the sequence. These tuffs can be dated radiometrically, and they provide accurate time fixes, showing that the sequence of sediments he studied ranged in age from 1.3 to 4.5 million years ago. The succession is 300 m thick and represents more-or-less continuous deposition, so it is possible to interpolate finer-scale dating throughout.

Williamson collected and measured hundreds of thousands of specimens of some 19 species of gastropods and bivalves through this time interval. Based on multivariate analyses, he was able to follow all these lineages up through the sequence, and to seek any evidence for variation from the mean within each lineage (Fig. 4). Stasis was the normal state of affairs, but rapid morphological shifts took place three times, two of which correspond to substantial lake-level rises. Williamson interpreted this as evidence for punctuated speciation events, arguing that rapid environmental changes had caused major evolutionary change. The new species were short-lived, he argued, because the parental stock had survived in neighbouring unstressed lakes, and returned to colonize Lake Turkana after the lake-level changes had taken place.

However, these conclusions were controversial. Critics argued that the supposed speciation events were merely short-term ecophenotypic responses to particular environmental stresses; once the stress was removed, the shell morphologies reverted to normal. Hence, they suggested that Williamson had failed to detect any speciation events. Such ecophenotypic effects are common among molluscs. For example, when a limpet larva settles, its shell starts to form, but the ultimate shape depends on where it ends up on the shore. If the limpet is low on the shore, the shell is low and broad, to resist wave-battering. If it is high on the shore, the shell becomes high and pointed, to allow for water storage in the apex. Despite the very different adult shell morphologies, no genetic change has taken place, and hence no evolution.

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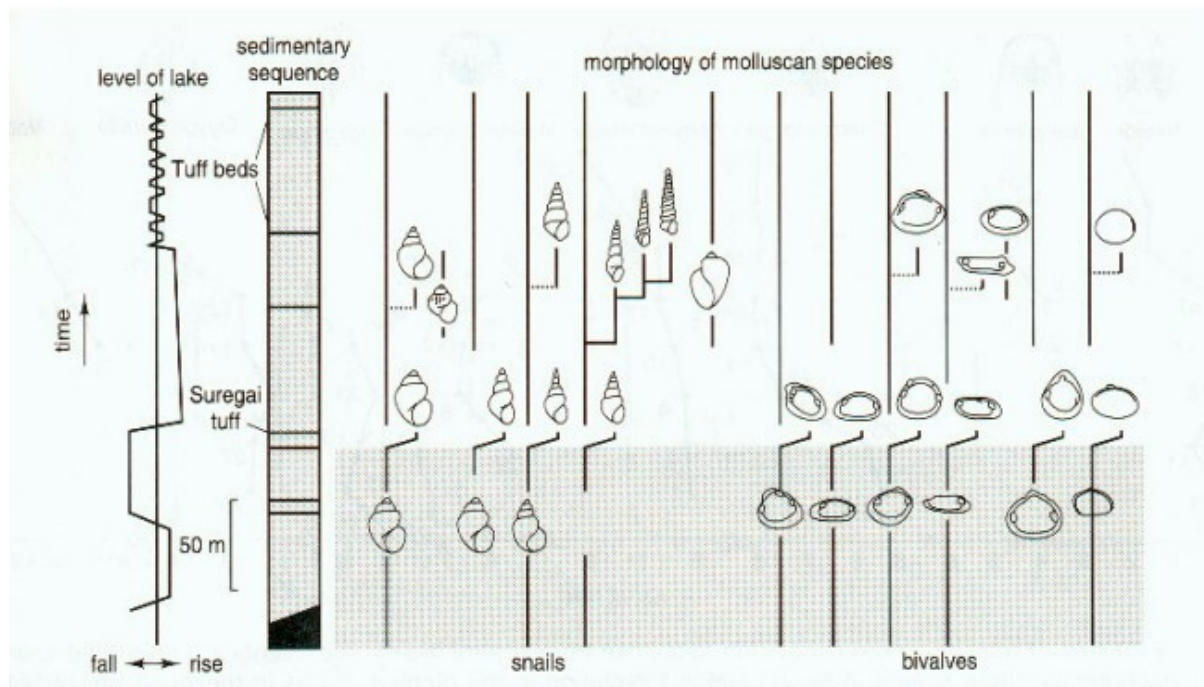


Fig. 4. Stasis in Pliocene molluscs. Ten evolving lineages of gastropods and bivalves in sediments of Lake Turkana, plotted through the past 4 million years. At times of major changes in lake level (shown on the left-hand scale), there appears to be a flurry of speciation events in most lineages: shell shape and size change. However, after the physical environmental crisis, shell form reverts to the pre-crisis morphology. It seems likely that the changes are ecophenotypic changes, non-evolutionary shifts in morphology in response to stress. More important is the demonstration of long-term stasis of all ten lineages, for over 3 million years. Based on the work of P. G. Williamson.

Despite this debate, Williamson's work did demonstrate the ubiquity of stasis. Here were 19 mollusc lineages evolving through 4 million years of fluctuating and stressful conditions, and not changing their phenotypes detectably.

4. Fossil evidence of speciation

The fossil record demonstrates the widespread occurrence of stasis. In a review of 58 published studies on speciation patterns in the fossil record, with organisms ranging from radiolaria and foraminifera to ammonites and mammals, and stratigraphic ages ranging from the Cambrian to the Neogene, 41 (71%) showed stasis, associated either with gradualism (15 cases; 37%) and with punctuated patterns (26 cases; 63%). It seems clear, then, that stasis is common, and that had not been predicted from modern genetic studies. But what of speciation: does the fossil evidence point to gradual or punctuated patterns?

Only 16 of the 58 palaeontological studies involved lineage branching (the others did not document speciation), and all but two of these showed punctuation and stasis. However, it would be wrong to assume from this small sample that punctuated speciation is necessarily the norm. Perhaps there are various patterns of speciation, and perhaps speciation style depends on the organisms in question.

4.1. Microfossils

Microfossil groups such as radiolaria, diatoms, and foraminifera frequently show gradualistic patterns of evolution and speciation. The microscopic skeletons of pelagic (open ocean) plankton can often be recovered in large numbers from sedimentary deposits that can be shown to have accumulated continuously over vast periods of time. The study by Sorhannus and colleagues in 1998 on the diatom *Rhizosolenia* is probably the most detailed of recent work on speciation in planktonic organisms.

Rhizosolenia is a planktonic diatom that occurs today in huge abundance in the highly productive waters of the equatorial Pacific. The siliceous valves of this genus rain on to the sea floor, where they accumulate in thick piles, mixed with other types of sediment. The morphological evolution of *Rhizosolenia* can be traced by sampling cores of this sediment, which have been taken in several places in the equatorial current system. Relative depths within each core provide a relative chronology, and this chronology can be tied to an absolute age scale using magnetic field reversals in the sediment. Sorhannus and colleagues used this technique to study several million years' worth of evolution of *Rhizosolenia*, which encompasses a well-marked speciation event (Fig. 5).

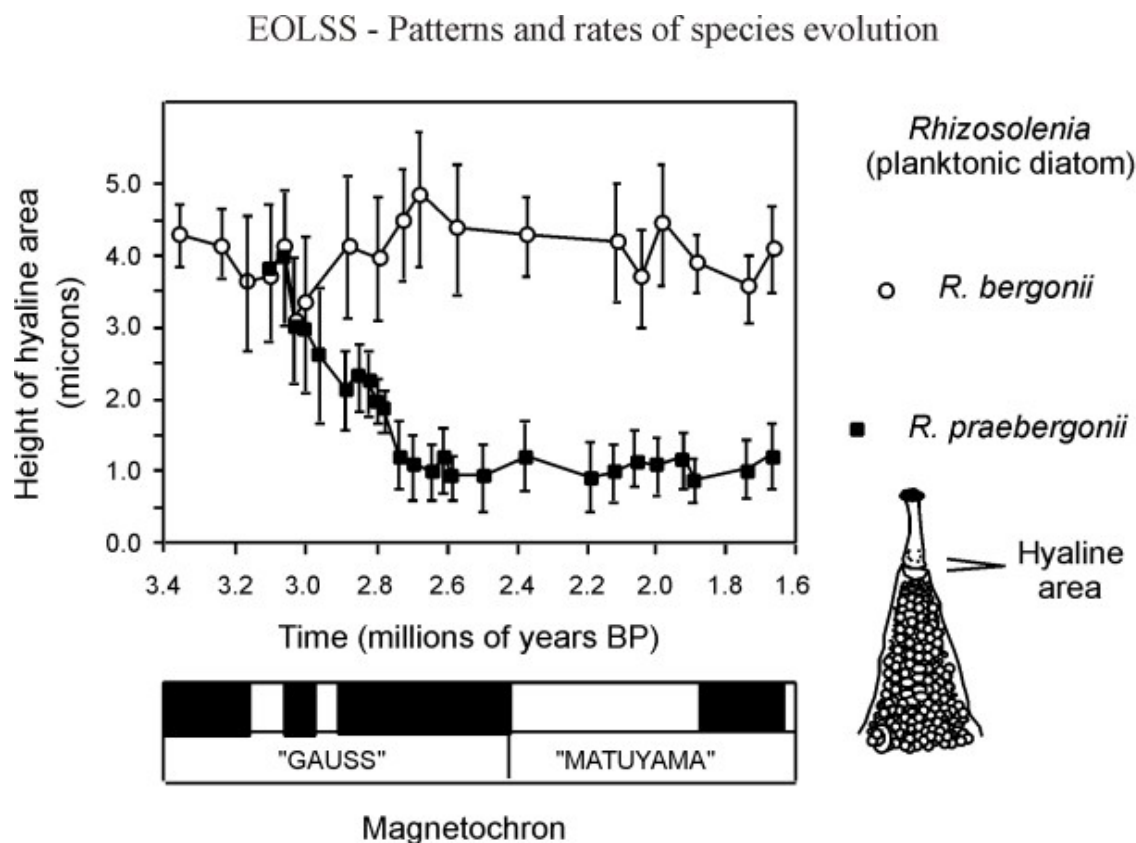


Figure 5. Gradual speciation in *Rhizosolenia*, a planktonic diatom from the equatorial Pacific. One species split into two some 3 million years ago, and the split can be detected in all deep-sea sediment cores so far studied. This was evidently a sympatric speciation event, and one that took some 300,000 years for definitive separation of the two species. Redrawn from Sorhannus et al. (1998).

The valves of *Rhizosolenia* are conical in shape, terminating in an apical process which is rooted in an annular structure known as the hyaline area. The valves are usually broken

at their distal ends, but Sorhannus and his colleagues were able to measure three distinct biometric variables: the length of the apical process, the height of the hyaline area, and the width of the valve at an arbitrary 8 microns from its apex. The first two characters are related to the overall size of the valve; the third is a shape parameter related to both size and the conical angle of the valve. These measurements were conducted on 5000 specimens in a number of populations in eight different cores, spanning two million years of evolution and about 60 degrees of longitude.

Planktonic diatoms generally reproduce asexually, but like many predominantly asexual organisms they occasionally produce sexual offspring, probably to counteract the buildup of deleterious mutations. This sexual reproduction means that the large populations of *Rhizosolenia* can be considered as biological species, and speciation must be effected by a permanent barrier to reproduction.

The morphometric data provide convincing evidence that speciation occurred at or before about 3 million years ago. Prior to this, there is only one discernible population, but afterwards, two morphologically distinct populations occur, within which there is a range of intergrading variation, but between which there is a morphological gap. The distinction is visible in all three measured parameters. The descendant species (*R. praebergonii*) later invaded the Indian Ocean where it appears abruptly in the sediment record.

In this case, speciation is evidently sympatric, since the same splitting event is seen in most of the cores around the equatorial belt of the Pacific. There is no evidence of an invasion of one species from an isolated population elsewhere; indeed, it is difficult to imagine where that population might have hidden and yet remained viable. Second, it is clear that most morphological evolution was not associated with speciation, but occurred afterwards, over about 500,000 years after the morphological distinction first becomes visible. Third, one of the new biological species evolved more rapidly than the other, becoming gradually smaller and evolving a markedly diminished hyaline area, whereas the other retained a morphology more like the ancestral species. Finally, the two species must have evolved slightly different environmental tolerances, for although their geographic ranges overlap for all their evolution, one of the two daughter species is entirely absent in one of the cores.

Other detailed studies of speciation in marine microfossils bear out some of these points. An early study on radiolaria and a more recent study on the planktonic foraminifer *Globorotalia* have yielded similar patterns of speciation: gradual divergence of two sister species over hundreds of thousands of years (hence refuting one of the expectations of the punctuated equilibrium model), and speciation by a 'budding' pattern, in which one of the daughter species is similar to the parent, and the other daughter species diverges away from this ancestral pattern.

4.2. Shallow marine invertebrates

Sympatric speciation and gradual evolution are probably much rarer among marine invertebrates and continental vertebrates, where there are many more possibilities for the establishment of physical barriers to interbreeding. In the open ocean, such barriers

are rare, and speciation among planktonic micro-organisms may be quite different from that among larger organisms living in diverse and evolving habitats.

Studies of lineage evolution among marine invertebrates from shallow waters suggest punctuational patterns of speciation. Such studies are much harder to make than those of deep-sea microfossils since continental shelf sediments accumulate sporadically, and this makes it harder to acquire information at high sampling precision. Nonetheless, immensely detailed studies have been carried out. For example, in long-term studies Alan Cheetham and Jeremy Jackson have sampled various genera of bryozoans in the past ten million years of sediments in the Caribbean, and their studies suggest punctuational patterns of speciation (Fig. 6).

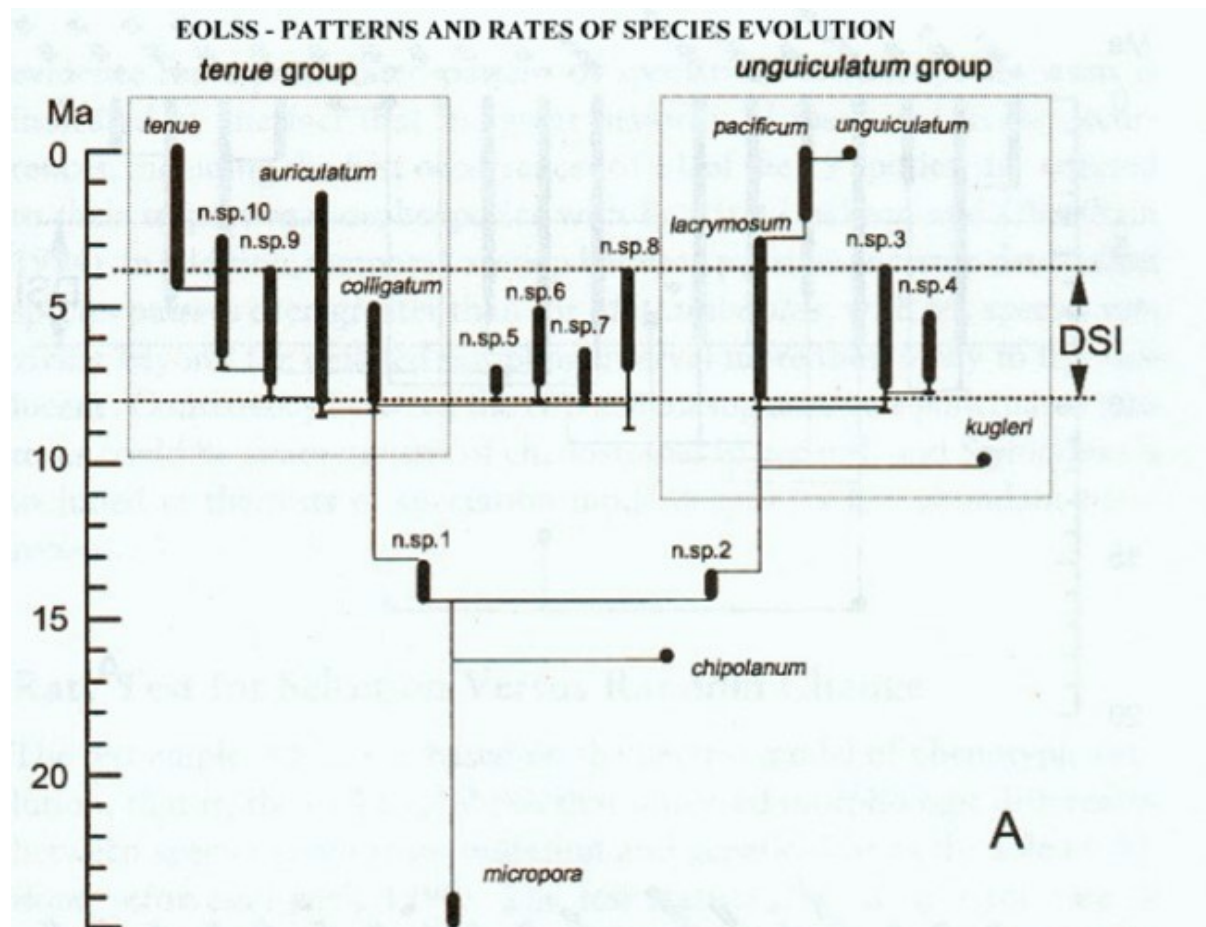


Fig. 6. Punctuational speciation in the bryozoan *Metrarabdotos*. The fossils show that *Metrarabdotos* radiated dramatically between 8 and 4 million years ago, and several species arose apparently rapidly, within the Dominican Sampling Interval (DSI), a particularly well sampled sequence. Based on the work of Cheetham and Jackson.

Metrarabdotos is an ascophoran cheilostome bryozoan that is represented today in the Caribbean by three species. Coastal rocks on Dominica and on other islands document the past 10 million years of sedimentation in shallow seas, and they yield abundant fossils of this bryozoan. The fossils show that *Metrarabdotos* radiated dramatically from 8 to 4 million years ago, splitting into some 12 species, most of which then died out by the Quaternary. Studies by Cheetham and Jackson have established a variety of protocols for distinguishing species within *Metrarabdotos*, taking into account the genetics of related extant species, and their amount of morphological differentiation, and then extending

comparable statistical tests of morphological differentiation to the fossil forms (they demonstrated highly significant correlations between genetic and morphometric differences among the modern forms). Based on 46 morphometric characters, the authors established a mechanism for distinguishing lineages among the fossils.

Lineage splitting in *Metrarabdotos* seems to have been rapid and punctuational in character (cf. Fig. 3A). Speciation was especially rapid in the interval from 8 to 7 million years ago, with nine new species appearing in that interval. There is some question about sampling quality here, since sampling is poor in the preceding interval, and so some of these nine new species might have appeared earlier. However, the interval from 8 to 4 million years ago, represented largely by information from Dominica, has been intensely sampled (DSI, Dominican Sampling Interval). So, although there are questions over the origins of the nine basal species within this interval, the origins of the remainder (*tenue*, n. sp. 10, and n. sp. 8) are more confidently documented as punctuational. The same kind of punctuational pattern of speciation has been found also in virtually all other studies on fossil marine invertebrates that have been carried out.

4.3. Terrestrial vertebrates

Problems that have been identified in the completeness of the fossil record of marine invertebrates are even more substantial for terrestrial vertebrates. Sediments are deposited sporadically on land, in rivers and lakes, and as soils, and there are generally enormous gaps of time between adjacent beds of rock. Inevitably, a literal reading of much of the continental rock record would give an apparently punctuational pattern of species appearances, but the sudden origins could be little more than an illustration of the huge gaps. At high taxonomic and stratigraphic scales (e.g. genera or families per 5 Myr time unit), the continental fossil record is no worse than the marine and there is no evidence for diminution of quality backwards in time. However, the common assumptions that the rock record on land is poorer than the marine, and that the quality of the fossil record declines sharply the further back in time one goes, are both clearly true at the taxonomic and stratigraphic scales necessary to study speciation in action.

Such considerations should not, however, lead one to despair of good evidence for speciation among vertebrates. The most recent parts of the fossil record, particularly those of the past five million years, in which the evolution of extant taxa is recorded, can document speciation patterns. Small mammals, such as insectivores, rodents, and bats are represented in some rock sequences by abundant fossils, particularly their tiny teeth, and these are ideal for morphometric studies of speciation. The fossil record of small mammals shows a wide variety of patterns of evolution. However, detailed records of gradual speciation events do not exist, suggesting that allopatric speciation may be the norm. With respect to morphological evolution, the prevalent theme is a complex mosaic pattern with different features evolving at vastly different rates in different species, and morphological evolution is not necessarily related to speciation.

5. Species diversification through time

It is clearly hard to document styles and patterns of speciation among living and extinct organisms. For similar reasons, it is also hard to document the pattern of species diversification through time. It is, however, more pressing than ever to understand how

diverse life is today, and how the current high biodiversity was achieved. These issues are not merely of interest to evolutionary biologists and palaeobiologists, but they clearly have an impact on conservation and political decision-making.

5.1. Biodiversity today

Estimates of the present diversity of life range over at least an order of magnitude, from perhaps 2-3 million species at the lower end, to 30-100 million at the upper end. The lower estimates represent summaries of the number of species that have actually been documented. It is estimated, for example, that some 1.9 million species of modern microbes, plants, and animals have been named so far by systematists, and that figure must be a minimum estimate of current biodiversity.

The constant accretion of newly described species shows that systematists have a long way to go in documenting modern biodiversity. Each year, on average, systematists add one or two new species of mammals and one or fewer new species of birds to the lists (based on estimates of taxonomic activity from 1900-1975) as well as dozens of newly named microbes, fungi, plants, and marine animals, and some 7,250 new species of insects.

If the additions of new species are the same each year, it might be possible to predict ahead how many species will, in the end, be described, perhaps 3 million species. However, a little reflection suggests that this comfortable impression is probably very far from the truth. It is wrong to extrapolate from the groups of living organisms that are most fully documented, such as birds and mammals. For insects, microbes, fungi, parasites, meiofauna, deep-sea organisms, and many others, taxonomists find new species wherever they look. If a taxonomist of bacteria takes a random soil sample, he finds many hundreds of previously unrecognized species; if a marine biologist scans a sample of mud scraped from the deep ocean floor, she may find dozens of undescribed species. For these groups, the rates of discovery and description depend only on the time and effort expended by taxonomists. This means that it is impossible to predict ahead just how many species are to be found.

For highly speciose groups, it might be more appropriate to carry out a detailed survey in one spot on Earth, find the maximum diversity, and then extrapolate worldwide. A well-known experiment concerns tropical rainforest beetles, carried out by the entomologist Terry Erwin. He sampled the entire arthropod fauna from the canopy of the tree *Luehea seemannii* in Central and South America. Erwin estimated that there are 163 species of beetles living exclusively in the canopies of *Luehea seemanni*. There are about 50,000 tropical tree species around the world, and if the numbers of endemic beetle species in *Luehea seemanni* is typical, this implies a total of 8.15 million canopy-dwelling tropical beetle species in all. This figure excludes forms that live in several tree species. Beetles typically represent about 40% of all arthropod species, and this leads to an estimate of about 20 million tropical canopy-living arthropod species. In tropical areas, there are typically twice as many arthropods in the canopy as on the ground, giving an estimate of 30 million species of tropical arthropods worldwide. This estimate came as a considerable surprise when it was published: 30 million species of tropical arthropods must imply a global diversity of all life in the region of 50 million.

So, estimates of modern biodiversity range from 3-5 million species at the low end, to 50-100 species at the high end. Many biologists and conservationist accept a middle figure of perhaps 20-30 million species.

5.2. Biodiversity through time - patterns of increase

It is evident that all living organisms, and all organisms known as fossils, derive from a single common ancestor (based on the evidence of shared complex characters, such as the DNA-RNA system of inheritance, homeobox genes, and the like). That common ancestor, the single species that gave rise to all of life, existed some 3,500 - 3,800 million years ago. Biodiversity has, then, expanded from one species to some 5-50 million species.

There are many ways to go from one species to many, and these can be expressed simply in terms of three mathematical models, represented by a straight line, an exponential curve, and a logistic curve, firstly as an uninterrupted increase (Fig. 7A), and secondly with some mass extinctions superimposed (Fig. 7B).

The linear model represents additive increase: simply the addition of a fixed number of new species in each unit of time. (The increase in this example, and the others, is a net increase, i.e. true increase minus extinctions.) In terms of an evolutionary branching model, additive increase would mean that, through time, speciation rates have declined, or extinction rates have increased regularly at a rate sufficient to mop up the excess speciations. The implied decline in the rate of evolution in the linear model comes about simply because the total number of species is increasing regularly, and yet the *rate* of increase across the board remains fixed; hence, for any individual evolutionary line, the rate or probability of splitting (speciating) must decline. Such a model has generally been rejected as improbable.

The exponential model is more consistent with a branching mode of evolution. If speciation and extinction rates remain roughly constant, then there will be regular doubling of diversity within fixed units of time. A steady rate of evolution at the level of individual evolutionary lines scales up to an exponential rate of increase overall since total diversity is ever-increasing. This model has been applied to the diversification rates of individual clades, and to the diversification of life in general.

The logistic model involves one or more classic S-shaped curves, each consisting of an initial period of slow diversity increase, a rapid rise, a slowing of the rate of increase as a result of diversity-dependent damping factors, and then a plateau corresponding to a limiting or equilibrium value. The logistic model has been used to explain patterns of diversification of marine organisms and of plants.

There is clearly no consensus on which model best explains the diversification of major sectors of life through time, nor on whether all patterns of diversification adhere to the same model of increase. The choice of model is important since each makes profoundly different claims about evolution.

EOLSS - PATTERNS AND RATES OF SPECIES EVOLUTION

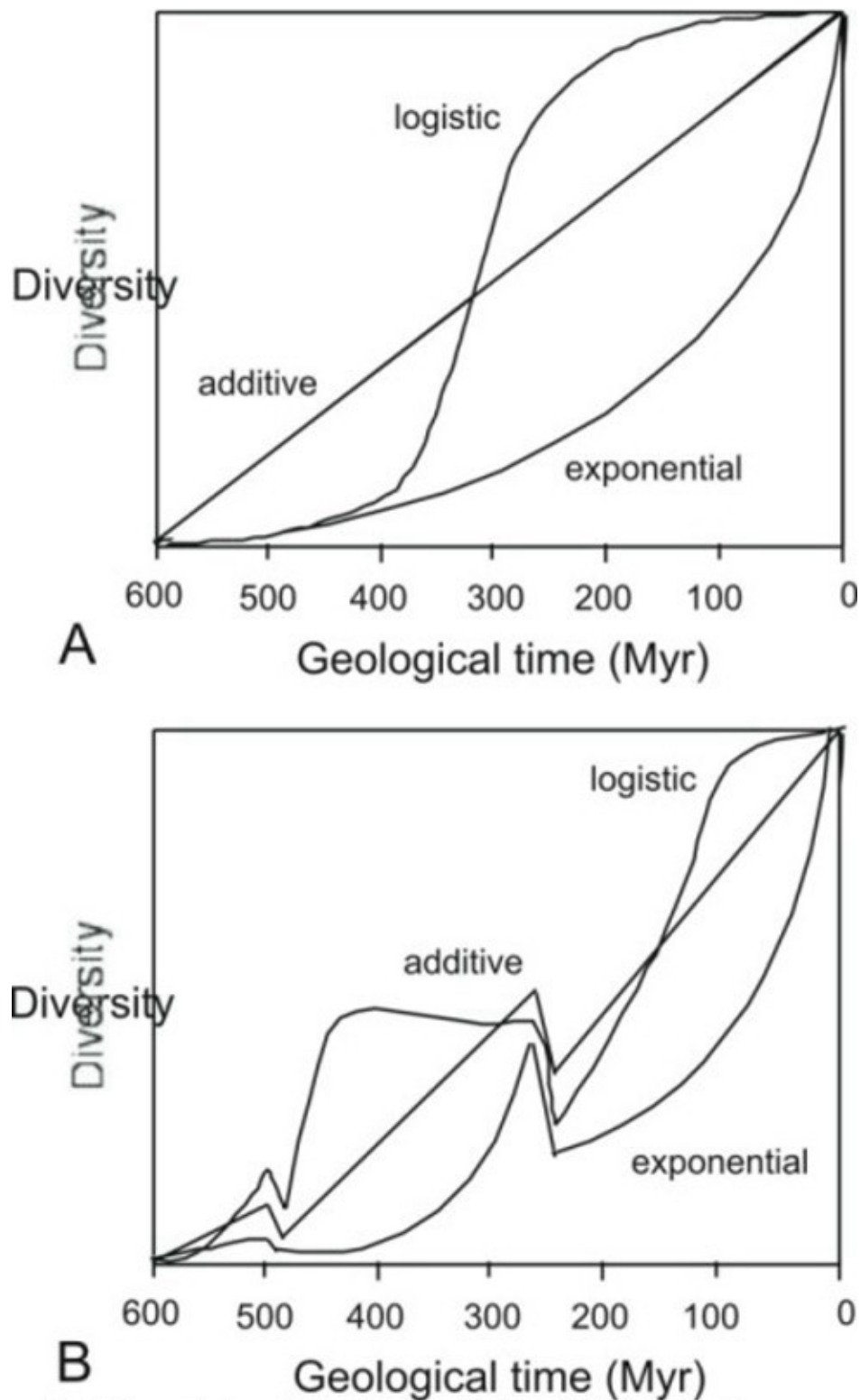


Fig. 7. Theoretical models for the diversification of life: A, in the absence of major perturbation; and B, with two mass extinctions superimposed. In each case, the upper curve is the logistic or equilibrium model, the middle curve is the additive or linear model, and the lower curve is the exponential model.

5.3. Biodiversity through time - land and sea compared

There are major differences between the patterns of diversification on land and in the sea, and the history of life in each realm may have been rather different. Today, about 85% of described species of plants and animals live on land, and the main groups (plants, arthropods, vertebrates) have reached their present great diversity in the past 450 million years. Plants and animals have been evolving in the sea since at least 600 Ma, and the fossil record is dominated by marine species, which make up some 95% of all described forms. This dominance of marine forms is partly accounted for by the fact that virtually the only organisms known from the Vendian and early Palaeozoic (600-450 Ma) are marine, and that the early history of life on land appears to have occurred at relatively low diversities. Also, fossils in certain marine environments are more likely to be preserved than those in many continental settings. The observation that life on land today is apparently five to six times as diverse as life in the sea, largely because of the insects, could be an artefact reflecting the greater amount of time devoted by systematists to continental than to marine organisms. However, if this difference is even partly correct, then it would imply a much more rapid diversification on land than in the sea.

In studies of the diversification of marine animal families (Fig. 8A), there is evidence for a short plateau in the Cambrian (lasting *c.* 40 million years), and a longer one from the Ordovician to the Permian (*c.* 250 Myr). This is followed by a long phase (250 million years) of near-exponential increase in diversity through the Mesozoic and Cenozoic, the rising element of a third logistic curve, which shows a hint of a slow-down in the last 25 million years or so, suggesting that a third plateau level may be achieved 125 million years in the future.

Marine invertebrate diversification has been explained in classical work by Jack Sepkoski, as the succession of three major phases of evolution, in which broad assemblages of different phyla ('evolutionary faunas') dominated the oceans, and were then replaced. The Cambrian fauna diversified exponentially at first, and then diversification slowed as the equilibrium level of 85 families was approached. The exponential diversification of the Palaeozoic fauna then began in the early Ordovician, reaching an equilibrium diversity of 350 families, and largely supplanting the Cambrian fauna. Finally, after the end-Permian mass extinction, which reduced the global diversity of the Palaeozoic fauna dramatically, the Modern fauna continued and accelerated its long-term rise in diversity.

In studies of the diversification of vascular plants (Fig. 8B), an equilibrium interpretation has also been given. There was a succession of major forms of plant types: early vascular plants in the Devonian; lycopods, ferns, conifers and others in the Carboniferous to Permian; gymnosperms in the Triassic to Jurassic; and angiosperms from the Cretaceous onwards. There was evidence for declining speciation rates and increasing species durations during each of the first three radiations, as the new set of clades partially replaced the old. Each new radiation led to an increase in total global diversity, while the diversity of the preceding floras declined. Angiosperms apparently continue to diversify at a high rate. It is hard to identify plateaux in land-plant species diversification, and it is hard to find evidence for logistic models of diversification. Equally, the total curve of species diversities through time is not obviously exponential and, if anything, the pattern appears to suggest linear increase in diversity through time.

The diversification of continental tetrapod families (Fig. 8C) appears to correspond to an exponential model of increase. Diversity levels remained low, at some 30-40 families, during the late Palaeozoic and much of the Mesozoic. They then rose to about 100 families at the end of the Cretaceous and, after recovery from the end-Cretaceous (K-T) extinction event, familial diversity increased rapidly towards 330 families, and it shows no sign of a slow-down. The pattern of diversification may be dissected into successive radiations of three global clade associations: basal tetrapods (formerly termed 'labyrinthodont' amphibians) and synapsids ('mammal-like reptiles') in the late Palaeozoic; archosaurs (dinosaurs, pterosaurs, crocodilians) in the Mesozoic; and lissamphibians (frogs and salamanders), lepidosaurs (lizards and snakes), birds, and mammals from the late Cretaceous to the present-day. These clade associations replace each other, and are associated with ever-higher global familial diversity levels, but it is difficult to fit logistic curves to any of the associations.

The diversification of insects (Fig. 8D) was also apparently exponential, especially in the Mesozoic portion of the curve. This suggests that insects have had a long and continuous pattern of expansion, perhaps slowing somewhat during the Tertiary, which may indicate that insect diversity is approaching an equilibrium level now.

EOLSS - Patterns and rates of species evolution

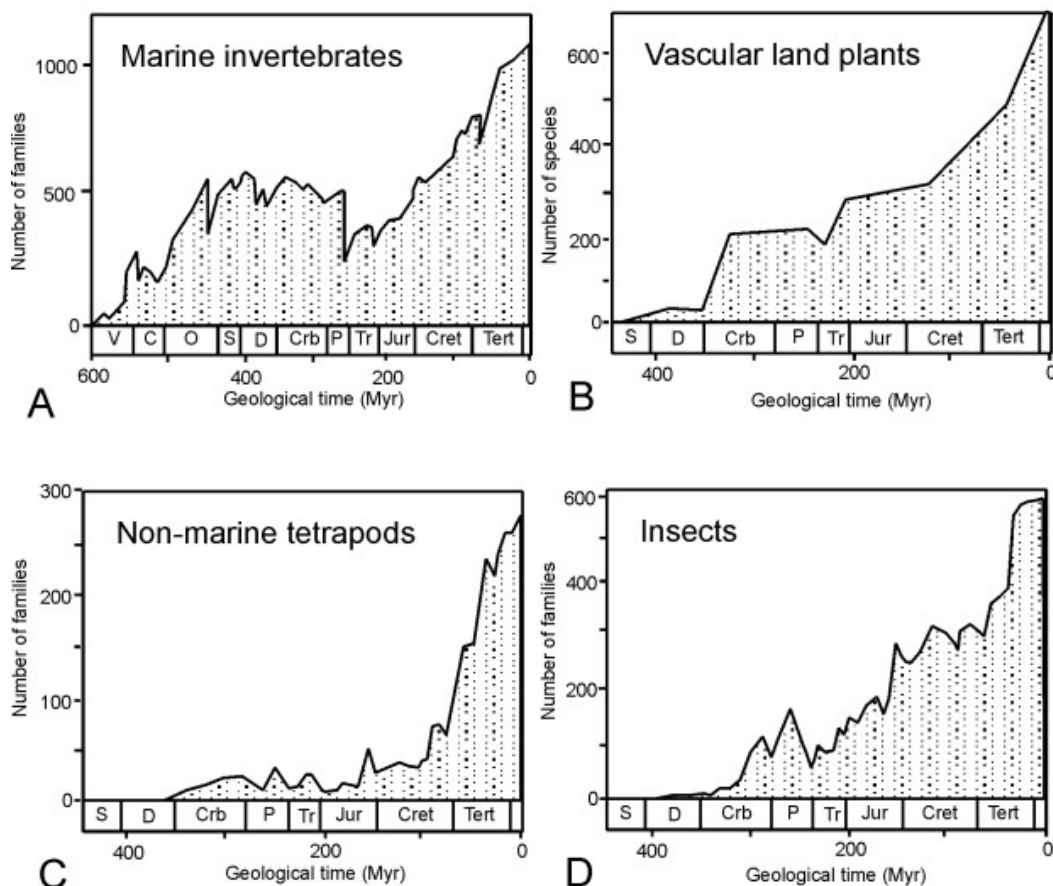


Figure 8. Patterns of diversification of families of: A, marine invertebrates; B, vascular land plants; C, non-marine tetrapods, and D, insects. (Based on Sepkoski 1984, Niklas et al. 1985, Benton 1985, and Labandeira & Sepkoski 1993.)

Recent plots of the diversification of families of marine, continental, and 'all' life (Fig. 9) founded on a new data base, The Fossil Record 2, published in 1993, confirm these varying models for diversification. The continental curve (Fig. 9B), dominated by tetrapods, insects, and land plants, is exponential. The marine curve (Fig. 9C) retains a Palaeozoic plateau level, and appears to show a slowing-down in diversification towards the Recent, which may indicate that marine diversity levels today are approaching an equilibrium level. The curve combining all marine and continental families (Fig. 9A) could be interpreted as a single poorly-fitting exponential curve, but the Palaeozoic plateau, reflecting the contribution of marine invertebrates (compare Fig. 9C), cannot be explained readily. The pattern could be explained equally well by a series of logistic curves, although the post-Palaeozoic portion is harder to fit than the Palaeozoic.

There may be fundamental differences between marine and continental life. Rates of taxonomic turnover in marine invertebrates declined through the Phanerozoic after the initial rapid Cambrian radiation, while vascular land plants show increasing rates of turnover through time. Terrestrial vertebrates show intermediate patterns. The suggested explanation is that adaptive space was filled early on in the sea, while land plants (and possibly vertebrates) have continued, and may still continue, to conquer new ecospace. The persistence of opportunities for expansion on land may reflect the later onset of diversification here than in the sea, and the fact that new groups of plants invaded unstable habitats and modified them.

5.4. Explanations for patterns of diversification

Logistic and exponential models for the diversification of life could be compared directly. However, there is a slight ambiguity in attempting that since the initial phase of a logistic curve is essentially exponential. The key distinction is between equilibrium and non-equilibrium (or expansion) models. The former

EOLSS - PATTERNS AND RATES OF SPECIES EVOLUTION

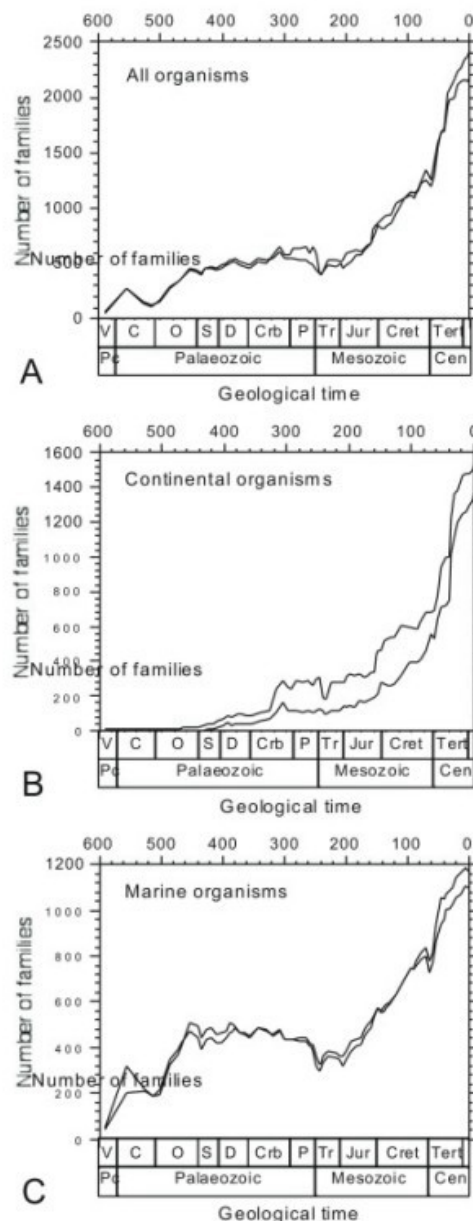


Fig. 9. Patterns of the diversification of life through time in terms of changes in numbers of families extant per stratigraphic stage, plotted for: A, all organisms; B, continental organisms; and C, marine organisms. In each graph, a maximum and minimum is shown, based on a combination of stratigraphic and habitat-preference information.

The minimum measure includes only families recorded as definitely present within each stratigraphic stage, or as definitely spanning that stage, and only families designated as restricted solely to the marine or continental realm. The maximum measure includes also all doubtful stratigraphic attributions of families, and all equivocal and shared habitat designations. The sum of minimum measures for continental and marine organisms is equal to the minimum measure for all taxa together.

imply the existence of global equilibria in diversity, while expansion models assume that there is no ceiling to the diversity of life, or at least that such a ceiling has yet to be reached.

Equilibrium models for the expansion of the diversity of life were based on an influential body of ecological theory. Logistic modelling of global-scale data on diversification assumes: (1) interactions among species within clades; (2) interactions between clades; and (3) global equilibrium levels. Many studies show that clades may radiate initially at exponential rates, but that the rate of diversification slows at a certain point as a result of diversity-dependent phenomena, such as competitive exclusion, increased species packing, and reduction of species ranges. This style of reasoning follows explicitly from classical experiments in competition where the increase of one population suppresses another that depends on the same limiting resource. An initial exponential increase of the successful population is followed by a plateau when the species begins to deplete the limiting resource (usually food); this corresponds to the local carrying capacity.

A key assumption of logistic modelling is that equilibrium levels exist, i.e. there are steady-state diversities at which speciation and extinction rates are balanced. In the case of global diversification patterns, limiting processes could affect both extinction and origination rates. Origination rates may be more diversity-dependent, however, because: (1) filling of niches could limit opportunities for new species to arise and become established; (2) additional species may intensify diffuse competition and create new directed competition, causing exclusion and thus possible extinction of some species; and (3) increased species packing may cause average local population sizes to be reduced, leaving some rarer species more prone to extinction by adverse environmental challenges.

There are three areas of concern with equilibrium models:

(1) There is no independent evidence for equilibria, i.e. for fixed carrying capacities on the Earth today. In evolutionary terms, equilibrium diversities imply that all available resources are in use and all ecospace is filled. If a new species originates, it must displace a pre-existing one. However, observations of cases where previously isolated floras and faunas come into contact suggest that species are just as likely to insinuate (i.e. enter new niches) and not cause extinction of other taxa.

(2) Multiple logistic models imply predictable outcomes of interactions between members of the different 'faunas', i.e. that members of one group will generally succeed where those of another will fail. Where major biotic replacements have been investigated, one group is more likely to disappear due to an extinction event than as a result of interactions.

(3) The diversification of the Modern fauna seems more prolonged and slower than predicted by a logistic model. The rising phase of the logistic curve has lasted for 250 million years, with some evidence of a slow-down towards the present. If there is no current plateau, then it would seem that in the second half of the Phanerozoic, the best-known part of the fossil record, the logistic rules have been forgotten.

The alternative to equilibrium is expansion. Are the aggregate patterns, or at least some of them (Figs. 8B, 9B), the result of unconstrained expansion? Certainly, some clades (such as insects, angiosperms, birds, and mammals) seem to continue radiating linearly or exponentially for many tens or hundreds of millions of years. Such ever-expanding patterns imply that these groups are highly successful and adaptable. The overall patterns of diversification (Fig. 9) incorporate the numerous constituent clades, some expanding, others diminishing, and yet others remaining at constant diversity at any particular time. From an expansionist viewpoint, there is no prediction of how the individual clades affect each other. New global diversity levels may be achieved by combinations of new adaptations, habitat changes, and extinction events. In the past 250 million years, the diversification of life has been dominated by the spectacular radiations of certain clades, both in the sea (decapods, gastropods, teleost fishes) and on land (insects, arachnids, angiosperms, birds, mammals). There is little evidence that these major clades have run out of steam, and nothing to indicate that they will not continue to expand into new ecospace.

Exponential increase could imply that diversification would last forever. Presumably there is a limit to the numbers of families, or other taxa, that can inhabit the Earth at any time: such a limit would be caused not least by the amount of standing room on the Ark. If a limit of living space were approached, ever-smaller organisms would presumably be favoured by selection. Equally, as has happened so many times during evolution, organisms would take unexpected measures to survive, for example, by occupying the air, burrowing into sediments and, in the case of some bacteria, living deep within the Earth's crust. With size reduction, the ultimate limit to the diversification of life might then become the availability of the chemical components of life, principally carbon.

Paleobiologists have debated, and continue to debate which model is correct. Perhaps all of life has diversified according to either an equilibrium or an expansion model. Or perhaps different sectors of life diversified in different ways. Evolution in the sea may have resulted in a greater level of stability, and patterns of increase may have generally been logistic, while life on land may have diversified exponentially since the first plants and arthropods crept cautiously out of the water. The implications of the equilibrium and expansion models are profoundly different, not merely for palaeobiologists, but for everyone concerned about the present and future state of global biodiversity.

6. Evolutionary patterns and processes

Speciation is a consequence of reproductive isolation, and hence the frequency of speciation in a group is likely to be related to the ease with which reproductive barriers appear. At one extreme there are organisms like planktonic protists that live in huge populations that seldom encounter barriers to dispersal, and which do not possess complex behaviours associated with reproduction. For these, genetic isolation of populations is a rare event, and speciation, which perhaps occurs rarely, may be long-term and gradual, lasting perhaps half a million years. At the other extreme are organisms that live in complex and often transient environments, like freshwater fishes. Here speciation may be so common that every lake and river has its own reproductively isolated population of a particular type of fish - but these populations may not be very distinctive nor last very long. In between may lie the majority of invertebrate and

vertebrate groups, generally exhibiting stasis, but from time to time speciating in a punctuational way as a result of a major perturbation in the environment.

The plurality of evolutionary modes (gradualism without stasis, gradualism plus stasis, punctuation plus stasis) may be real. Peter Sheldon proposed that gradualism may characterize taxa that live in stable environments, and which change in line with slow environmental changes, while stasis may be a feature of taxa in unstable environments, which can vary rapidly and dramatically, but which do not evolve in line with every environmental fluctuation.

The current research phase, in which field ecological studies are combined with palaeontological documentation of the fossil record offers hope for discerning patterns and rates of species evolution. Field studies of speciation in action depend on observations of essentially static situations from which the timing and processes are assumed. The evidence comes from distributions of closely related organisms on clusters of islands, hybrid zones, geographical barriers corresponding to species divisions, peripheral isolates, and the like. Sometimes historical evidence may be brought into play, for example the date of the artificial introduction of a new species on to an island. But, at best, these approaches rely entirely on the reconstruction of an historical process from the patterns observed today, and they can offer time scales of only a few hundred years, and speciation probably takes much longer than that.

High-resolution dating of palaeontological successions is now beginning to offer the possibility of observing speciation in action. With time precision down to thousands of years, or even hundreds in some cases, palaeontologists can follow the behaviour of lineages in detail. When one considers the way in which archaeological records can blend insensibly into palaeontological, in following lineages back through the Holocene and Pleistocene, there is clearly no need to erect an artificial barrier between biology and palaeontology. With care, biologists and palaeontologists can work together to reconstruct step-by-step how lineages have speciated in the past.

Global-scale studies of species diversity, both in the present and in the past, are still in their infancy. Current estimates of biodiversity range over several orders of magnitude. Looking into the past, it is still not clear how life diversified from one species, billions of years ago, to many millions of species today. The two current models, equilibrium and expansion, may apply in different life realms, or all of the diversification of life may have followed a damped expansion model.

Glossary

Allopatric speciation: Speciation by geographical splitting of a population, usually by the establishment of a physical barrier to gene flow.

Anagenesis: Evolution within a lineage, usually expressed by morphological change, but not necessarily associated with a splitting event.

Biological species concept: The definition of a species by reproductive isolation: a species consists of all those actually or potentially interbreeding populations which are reproductively isolated from other such groups.

Chronospecies: A species that is part of the continuum of a lineage documented in the fossil record, distinguished from the chronospecies below and above by the accumulation of sufficient morphological change over time.

Cladogenesis: The splitting of a species lineage into two species lineages.

Ecophenotypic change: Non-evolutionary change in the morphology of an organism, usually induced by environmental pressures.

Lineage: An evolving line, generally a species.

Morphological species concept: A species is defined by being sufficiently morphologically distinct from all others. The definition can include multivariate tests of the statistical distance between species centroids in relation to intraspecific variation about the centroids.

Morphospecies: A species defined solely on morphological criteria.

Phyletic gradualism: The classic palaeontological view that species evolve by gradual lineage evolution (anagenesis) and splitting (speciation) as a subsidiary process.

Punctuated equilibria: The view that speciation occurs relatively rapidly, and that virtually all evolution happens at speciation (cladogenesis), with long phases of stasis of lineages in between.

Punctuation: A rapid speciation event, forming part of the model of evolution by punctuated equilibria.

Speciation: The establishment of reproductive isolation between two or more previously interbreeding populations.

Species selection: The hypothetical process of sorting of species, with selection for survival of those that possess particular irreducible species-level characteristics (such as species size, species distribution, species duration).

Stasis: 'Standing still'; long episodes of apparently no morphological change in a species lineage.

Sympatric speciation: Division of a single species into two or more without prior geographic separation.

Bibliography

- Barlow, G. W. 2000. The cichlid fishes: Nature's grand experiment in evolution. Perseus. [The latest, and most detailed, review of the explosive speciation of cichlids in the African lakes.]
- Benton M. J. (1987) Progress and competition in macroevolution. *Biological Reviews* 62, 305-338. [This article discusses the relative roles of equilibrium and non-equilibrium models for the diversification of life.]
- Benton M. J. 1995. Diversification and extinction in the history of life. *Science* 268, 52-58. [This article presents information on the diversification of life through time.]
- Benton M. J. 1997. Models for the diversification of life. *Trends in Ecology and Evolution* 12, 490-495. [This article reviews the differences between logistic and exponential models, and their implications for the diversification of life.]
- Eldredge N. and Gould S. J. (1972) Punctuated equilibria: An alternative to phyletic gradualism, in *Models in Paleobiology* (Schopf, T. J. M., ed.), pp. 82-115, W. H. Freeman. [This article first presented the idea of punctuated equilibrium as a model for speciation.]
- Erwin D. H. and Anstey R. L. (1995) Speciation in the fossil record, in *New Approaches to Speciation in the Fossil Record* (Erwin, D. H. and Anstey, R. L., eds), pp. 11-28, Columbia. [This article reviews the evidence of 58 published studies on speciation in the fossil record.]
- Jackson J. B. C. and Cheetham A. H. (1999) Tempo and mode of speciation in the sea. *Trends in Ecology and Evolution* 14, 72-77. [This article reviews the authors classic work on bryozoan species evolution.]
- May R. M. (1990) How many species? *Philosophical Transactions of the Royal Society, Series B* 330, 292-304. [This article gives an overview of current estimates of global biodiversity.]
- Mayr E. (1942) *Systematics and the Origin of Species*, Columbia. [In this book, Mayr gave the first clear account of the allopatric model for speciation.]

- Rundle H. D., Nagel L., Boughman J. W., and Schluter D. (2000) Natural selection and parallel speciation in sympatric sticklebacks. *Science* 287, 306-308. [This article describes the sympatric speciation of sticklebacks as a result of natural selection on body form and habits.]
- Sepkoski J. J., Jr. (1984) A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology* 7, 36-53. [This article presents the multi-phase logistic (equilibrium) model for diversification of life in the sea.]
- Sepkoski J. J., Jr. 1996. Competition in macroevolution: the double wedge revisited. In: D. Jablonski, D. H. Erwin & J. H. Lipps (eds) *Evolutionary paleobiology*, pp. 211-255. University of Chicago Press, Chicago. [This article presents a full account of the equilibrium viewpoint on the diversification of life.]
- Sorhannus U., Fenster E. J., Burckle L. H. and Hoffman A. (1998) Cladogenetic and anagenetic changes in the morphology of *Rhizosolenia praebergonii* Mukhina. *Historical Biology* 13, 185-205. [This article presents evidence for long-term patterns of speciation in a marine protist.]
- Williamson P. G. (1981) Palaeontological documentation of speciation in Cenozoic molluscs from the Turkana Basin. *Nature*, 293, 437-443. [This article presents classic evidence for stasis in many lineages of molluscs.]

Biographical Sketch

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