

Speciation in the fossil record

Michael J. Benton and Paul N. Pearson

It is easy to claim that the fossil record says nothing about speciation because the biological species concept (which relies on interbreeding) cannot be applied to it and genetic studies cannot be carried out on it. However, fossilized organisms are often preserved in sufficient abundance for populations of intergrading morphs to be recognized, which, by analogy with modern populations, are probably biological species. Moreover, the fossil record is our only reliable documentation of the sequence of past events over long time intervals: the processes of speciation are generally too slow to be observed directly, and permanent reproductive isolation can only be verified with hindsight. Recent work has shown that some parts of the fossil record are astonishingly complete and well documented, and patterns of lineage splitting can be examined in detail. Marine plankton appear to show gradual speciation, with subsequent morphological differentiation of lineages taking up to 500 000 years to occur. Marine invertebrates and vertebrates more commonly show punctuated patterns, with periods of rapid speciation followed by long-term stasis of species lineages.

The confidence of palaeontologists in their attempts to discern patterns and processes of SPECIATION (see Glossary) has fluctuated over the years. Darwin¹ hoped for great improvements in our knowledge of fossil LINEAGES, especially through the Tertiary period, 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 our thinking about the palaeontological contribution to our understanding of evolution. However, in the early 20th century, Darwin's dream of complete phylogenies had been virtually forgotten in the face of debates about the new field of genetics.

Later attempts to emphasize the role of palaeontology² in the Modern Synthesis focused more on higher levels of evolution than on speciation, and most palaeontologists and biologists continued to ignore the fossil record in their debates about species and speciation. This approach changed in the early 1970s with the publication of a model of speciation by PUNCTUATED EQUILIBRIA^{3,4}. There followed a search for well-documented examples of speciation in the fossil record, although in retrospect most of the published examples showed little evidence. Before examining some data, however, it is important to consider the terminology and concepts.

Biological and morphological species concepts

The BIOLOGICAL SPECIES CONCEPT⁵ (see Hey⁶, this issue) and its variants cannot be applied directly to the fossil record, but population-based thinking does lie behind palaeontological studies. Palaeontologists have adopted the related MORPHOLOGICAL SPECIES CONCEPT, in which species are discerned by phenotypic

differences. Similarly to systematists of modern taxa, palaeontologists became enthusiasts for population-based thinking in the mid-20th century: large collections of fossils were obtained and every possible measurement made. Species were distinguished by distance measures between the centroids of multivariate clusters of points⁷. This approach is common today, and there are statistical tools that indicate population limits and distances between populations, even when specimens are rare⁸.

Palaeontologists assume that their concept of morphologically defined species is in line with the biological species concept. In particular, speciation is usually accepted as being marked by the onset of permanent REPRODUCTIVE ISOLATION in the descendants of populations that once interbred. It is also assumed that, although morphological differentiation need not form part of this model, populations will nonetheless diverge genetically and this will be reflected rapidly enough in the divergence of phenotypes that the point of splitting and detectable morphological differentiation effectively coincide. This might be true given that the finest geological timescales are generally in the order of hundreds or thousands of years. Unfortunately, although there are cases where annual and seasonal cycles can be detected, for example in long sequences of lake sediments, studies of evolution in these sequences do not generally show speciation⁹.

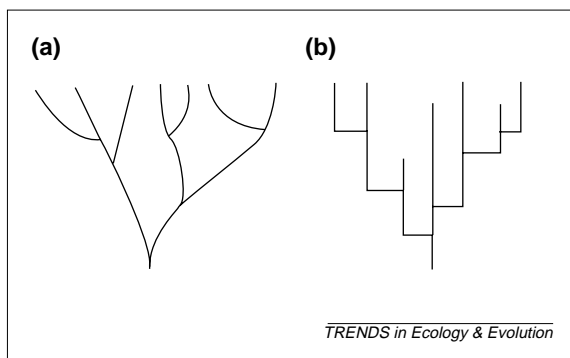
The assumption that morphologically recognized species in the fossil record correspond to biological species is an essential underpinning of palaeontological studies of speciation. Genetic and morphological differentiation need not coincide, but there is extensive evidence for such a coincidence at the temporal and spatial scales used in studies of fossils^{10–12}. Indeed, this equivalence is accepted by systematists of extant organisms, who rarely carry out experimental interbreeding tests to solve a TAXONOMIC problem of species definition.

In fact, most species-level systematics of metazoans and macroplants, whether of extinct or extant forms, are still carried out using the morphological species concept. Species are defined and distinguished on the basis of variations in morphology. It is reasonable to claim that the methods of palaeontological and modern species documentation are similar, and fossils need not be regarded as wholly divorced from studies of modern life. In practice, a good-quality fossil taxon can offer as much skeletal data as does an extant one.

The 'biological' view of species lineages adopted by most systematists fits well with the concepts of

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Fig. 1. Contrasting expectations of species-level evolution, the classic phyletic gradualism model (a), and the punctuated equilibrium model (b). Degree of morphological change is indicated on the x axis, time is indicated on the y axis.



modern phylogenetic systematics (CLADISTICS). However, it conflicts fundamentally with the 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, it should constitute a different species; but by the definitions usually adopted, that can only be admitted if a cladogenetic event has occurred¹³.

The punctuated equilibrium revolution

Palaeontologists received a considerable boost in the 1970s with the publication of the theory of evolution by punctuated equilibria^{3,4}, an idea that could only be tested using the fossil record, and which attracted many evolutionists and geneticists. The 'PHYLETIC GRADUALISM' viewpoint assumes that evolving lineages change at variable rates (Fig. 1a), but more or less continuously (anagenesis). Speciation was often seen as a by-product of this process of change: sometimes lineages become so different from their starting points that they evolve into a new species (the CHRONOSPECIES concept). Speciation by splitting (CLADOGENESIS) could also happen, but the process is no slower or faster than normal rates of lineage evolution.

The opposing viewpoint, evolution by punctuated equilibria (Fig. 1b), is different in both pattern and process. Rapid morphological change at cladogenesis, rather than anagenesis, is the most important process. The normal state of a lineage is STASIS, and from time to time, speciation takes place, although such events are rapid and revolutionary. The punctuated equilibrium model makes two claims, that rates of change along a lineage are punctuated, and that rapid change is correlated with speciation events. The second claim is the more controversial, but its supporters regard it as the defining element of the punctuated equilibria model.

The punctuated equilibria model was based on two well-established observations from fossils and from the present day. The first was that palaeontologists had known about stasis for years, but not articulated this knowledge. In fact, even in the very best of fossil records, it is rare to see long episodes of gradual change. If anything, fossils tend to remain similar in

appearance through many metres of sediment (i.e. thousands or millions of years), and then change rapidly. The second insight was that, if most speciation happened according to the allopatric model⁵, it would appear as a rapid event in the fossil record (see Turelli *et al.*¹⁴, this issue). The detail of the gradual divergence of two isolated populations would not be seen. This would be particularly true of peripheral isolates, that is, small, isolated, marginal populations that might be expected to evolve most rapidly.

The key novelty of the model of punctuated equilibria is stasis. Stasis played no part in the geographic speciation model, indeed, most evolutionists expect that anagenetic evolution is important. However, the concept of widespread stasis essentially denies the existence of any kind of lineage evolution.

The punctuated equilibria versus phyletic gradualism debate of the 1970s and 1980s was huge fun for all concerned, not least because the protagonists kept shifting ground and revising their claims. The first phase was based on the ideas just described, taken from the original papers^{3,4}. From 1975 onwards, several supporters of punctuated equilibria extended the model to espouse the new idea of SPECIES SELECTION, a higher-order process in which species were sorted and, in some models, could even undergo selection of 'emergent' higher-order characters. Species selection could, in theory, occur independently of and even in opposition to, natural selection at the level of the organism¹⁵. This led to the idea of an 'expansion' of evolutionary theory to many hierarchical levels^{16,17}, with hints of an apparent rejection of aspects of the neodarwinian view. Such extreme positions were abandoned fairly rapidly by most enthusiasts, and palaeobiologists continued in their staunch adherence to natural selection during the later 1980s and 1990s. Species selection is generally considered to be theoretically possible, but represents only a weak force and is unlikely to result in significant adaptations of the type that occur in the natural selection of individuals¹⁸. However, the notion of stasis stuck: too much fossil evidence pointed to its importance, and it is entirely consistent with quantitative genetics¹⁹.

The ubiquity of stasis

The emphasis on the evolutionary importance of cladogenesis over anagenesis^{3,4} might be the most significant contribution of palaeobiology to the question of species and speciation. If lineages are not evolving in a sustained direction (gradualism), but fluctuate with no significant change (stasis) 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 case studies of segments of the fossil record have been published in an attempt to determine

Box 1. Stasis in Pliocene molluscs

The prevalence of stasis has been shown^a in detailed studies of lacustrine gastropods and bivalves from Lake Turkana (Kenya) through the past 4 million years (My) (Fig. 1; Reproduced, with permission, from Ref. a). The studies were especially strong in terms of the quality of dating and the sample sizes used. 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 radiometrically dated to provide accurate time fixes, showing that the sequence of sediments studied ranged in

age from 1.3 to 4.5 My ago. The succession is 300 m thick and represents roughly continuous deposition, so it is possible to interpolate finer-scale dating throughout.

Hundreds of thousands of specimens of some 19 species of gastropods and bivalves were collected and measured through this time interval. Based on multivariate analyses, lineages were followed up through the sequence and evidence for variation from the mean within each lineage was sought. Stasis was the normal state of affairs, but rapid morphological shifts took place three times, two of which correspond to substantial lake-level rises. This was interpreted^a as evidence for punctuated speciation events and that rapid

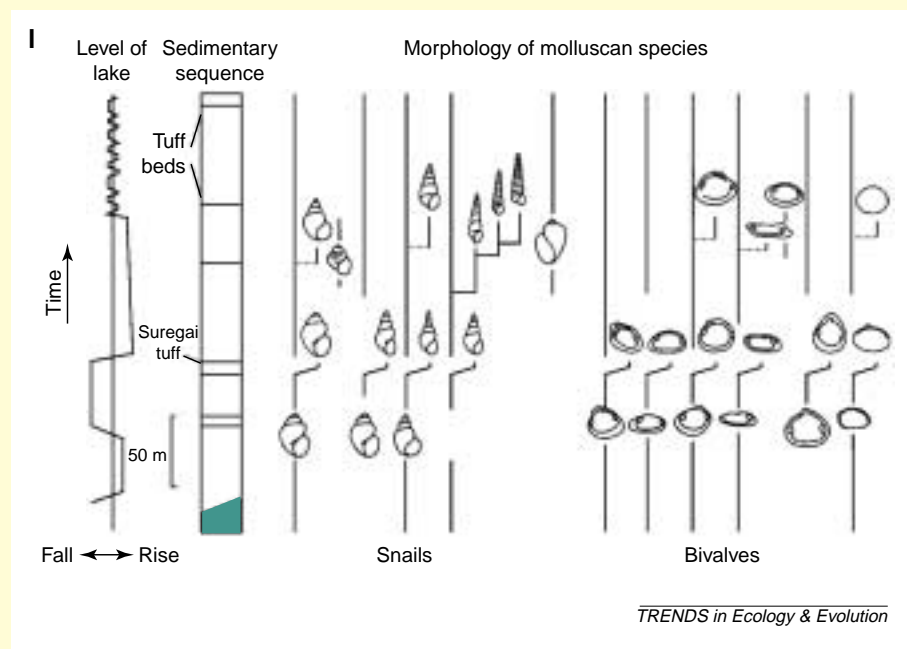
environmental changes had caused major evolutionary change. The new species were apparently short lived, because the parental stock had survived in neighbouring unstressed lakes, and returned to colonize Lake Turkana after the lake-level changes had taken place.

However, these conclusions were controversial. Critics^b 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, it was suggested that the studies had failed to detect any speciation events. Certainly, such ecophenotypic effects can occur 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, or therefore evolution, has occurred.

Despite this debate, the Lake Turkana studies did demonstrate the ubiquity of stasis. Here were 19 mollusc lineages persisting through 4 My of fluctuating and stressful conditions, without detectable phenotypic change.

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whether evolution proceeds 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 the possibility of migrations of taxa in and out of the study area. It soon became clear that what was a gradual anagenetic pattern to one person was an obviously stepped, punctational pattern to another^{20–23}. Larger-scale studies from the 1980s and 1990s sometimes involved tens of thousands of assessed specimens, very fine-scale stratigraphies and subtle attempts to determine the nature of the species involved (Box 1). Even in these massive exercises in data documentation, the objection could be raised that apparent speciation events might sometimes be simply ECOPHENOTYPIC rather than the

result of evolutionary change²⁴. It is difficult to distinguish ecophenotypic changes from true evolutionary change in morphological species. Clearly, palaeontological studies are most convincing if they involve both living and extinct forms.

An analysis of the results of 58 studies on speciation patterns in the fossil record, published between 1972 and 1995, demonstrates the widespread occurrence of stasis in the fossil record²⁵. Organisms ranged from radiolaria and foraminifera to ammonites and mammals, and stratigraphic ages ranged from the Cambrian to the Neogene, with the majority concentrating in the Neogene, the past 25 million years (My) of the history of the earth. Of the 58 studies, 41 (71%) showed stasis, associated either with anagenesis (15 cases; 37%) or with punctuated

Box 2. Gradual speciation in the diatom *Rhizosolenia*

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 accumulate on the sea floor, 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. The relative depths within each core provide a chronology, and this can be tied to an absolute age scale using magnetic field reversals in the sediment. This technique was used to study several million years of evolution of *Rhizosolenia*^{a,b}, which encompasses a well-marked speciation event (Fig. 1).

The valves of *Rhizosolenia* are conical in shape, terminating in an apical process that is rooted in an annular structure known as the hyaline area (Fig. 1). The valves are usually broken at their distal ends, but it was possible to measure three distinct BIOMETRIC (see Glossary) variables: the length of the apical process, the height of the hyaline area, and the width of the valve at an arbitrary 8 μm 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 several populations in eight different cores, spanning 2 million years (My) and about 60° of longitude. Measurements from a

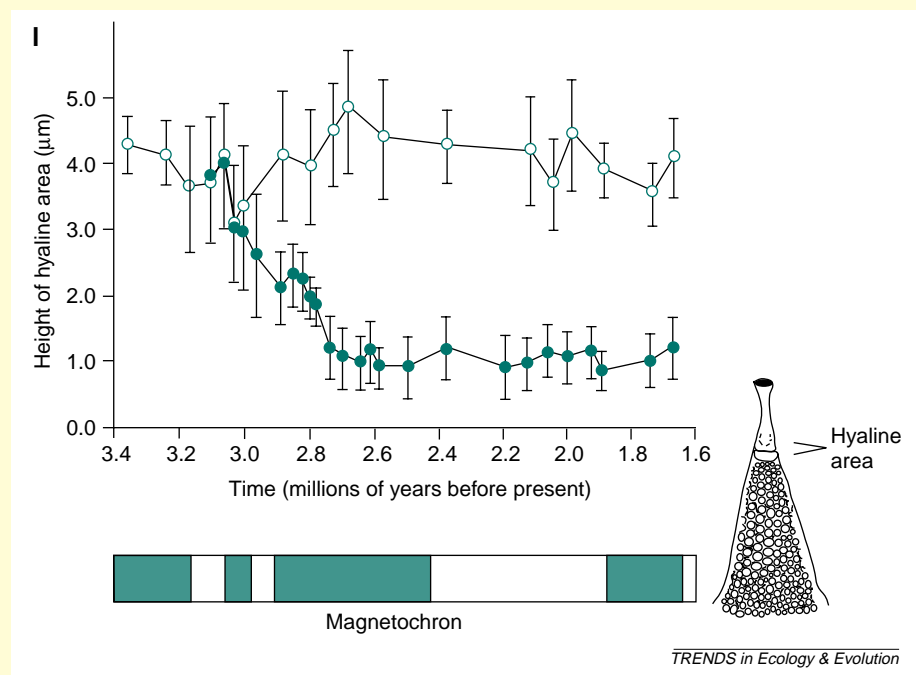
single site are shown (Fig. 1): all others yield the same pattern of lineage splitting. In this case, the other characters begin to diverge about 3.1 My ago (Mya), before the evident split in the height of the hyaline area shown here.

Planktonic diatoms generally reproduce asexually but, like many predominantly asexual organisms, they occasionally produce sexual offspring, perhaps to counteract the build up 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 3.1 Mya. Before 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, and in all cases the parental species, *R. bergonii* (open circles), continues essentially unchanged, and the daughter species, *R. praebergonii* (closed circles), diverges. This descendant species later invaded the Indian Ocean where it appears abruptly in the sediment record^b.

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patterns (26 cases; 63%). It therefore seems clear that stasis is common and had not been predicted from modern genetic studies.

Thus, there is evidence that lineage evolution is punctuated, with sharply varying rates of evolution, from zero (stasis) to high (PUNCTUATION). Do these phases of rapid evolution correspond to speciation events, the second claim originally made^{3,4}? Studying speciation in the fossil record is difficult for two reasons: first, much information is lost in gaps in the rock record; and, second, it might be expected that many species are short lived and can never be found as fossils. Their absence from the fossil record could distort the picture seen by palaeontologists. So what does the fossil record say about speciation?

Fossil evidence of speciation

In the analysis previously described²⁵, only 16 of the studies surveyed 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 the mode of speciation depends on the organisms in question.

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 have accumulated continuously over vast periods of time. Studies on the diatom *Rhizosolenia* probably provide the most detailed recent work on speciation in planktonic organisms (Box 2).

In this case, speciation is evidently sympatric, because the same splitting event is seen in most of the sedimentary cores taken from around the equatorial belt of the Pacific. There is no evidence of an invasion of one species into this area 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, for more than 500 000 years after the morphological distinction first becomes visible. Third, one of the new biological species evolved more rapidly than did the other, becoming gradually smaller and evolving a markedly diminished hyaline area (the zone behind the apex), whereas the other retained a morphology more similar to that of the ancestral species. Finally, the two species must have evolved slightly different environmental tolerances, because although their geographical ranges overlap throughout the period studied, one of the two daughter species was entirely absent in one of the cores examined.

Other detailed studies of speciation in marine microfossils support some of these points. An early study on radiolaria²⁶ and a more recent study on the planktonic foraminifer *Globorotalia*²⁷ 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 morphology. In some instances, it is possible to provide independent tests of hypotheses such as depth or habitat differentiation during the speciation of planktonic microfossils by studying the isotopic composition of their shells²⁸.

Marine invertebrates from the continental shelf
SYMPATRIC SPECIATION and gradual evolution are probably much rarer among shallow water marine invertebrates and continental vertebrates, where there are potentially many more physical barriers to interbreeding. In the open ocean, such barriers are rare, and speciation processes among planktonic microorganisms might be rather different from those among larger organisms living in diverse and constantly changing habitats.

Studies of lineage evolution among marine invertebrates from shallow waters suggest more punctuational patterns of speciation. The range of organisms and the timespans involved have been

reviewed recently²⁵. Such studies are much harder than those of deep-sea microfossils because continental shelf sediments accumulate sporadically, and this makes it harder to acquire information with a high sampling precision. Nonetheless, immensely detailed studies have been carried out, for example, on various genera of bryozoans through the past 10 My in Caribbean sediments, and these suggest punctuational patterns of speciation (Box 3). The same is true for virtually all other studies on fossil marine invertebrates in which speciation has been recorded^{25,29}.

Terrestrial vertebrates

The problems that have been identified in the completeness of the fossil record of marine invertebrates are even more substantial for the fossil record of terrestrial vertebrates. Sediments are deposited sporadically in rivers and as soils, and there are generally long intervals between the deposition of adjacent beds of rock. Sediments in lakes can be continuous, and sequences can record annual varves, but the whole history of a single lake might be short in geological terms. 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 between samples. At high taxonomic and stratigraphic scales (e.g. genera or families per 5 My time unit), the continental fossil record is no worse than the marine fossil record³⁰ and there is no evidence for a reduction in its quality as it goes back in time³¹. However, such common assumptions are clearly both true at the taxonomic and stratigraphic scales necessary to study speciation in action.

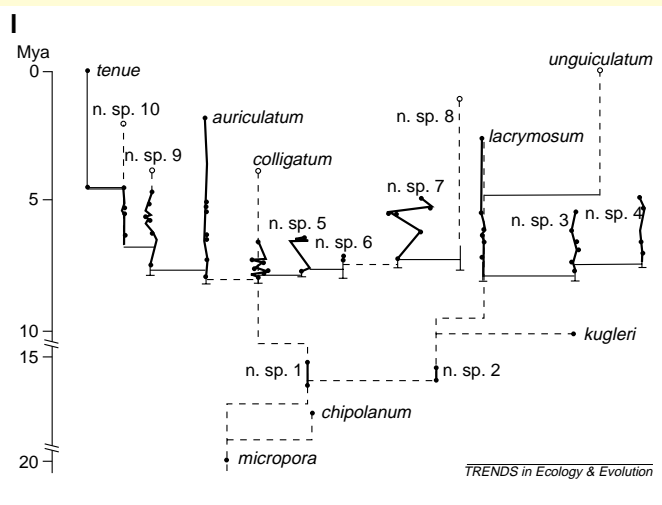
Such considerations should not, however, lead one to despair of good evidence for speciation among vertebrates. Extensive work documenting patterns of evolution of Paleogene mammals^{32,33}, especially those from the Eocene (55–34 My ago) of North America, has followed some lineages bed-by-bed through great thicknesses of rock. It has been argued that the evidence supports anagenetic patterns and gradualistic speciation, although the results have been criticized^{20,21} for being founded on incomplete timescales, without adequate control for possible migrations in and out of the basins that have been sampled.

The most recent parts of the fossil record, particularly those of the past 5 My, 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 of their 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 might be the norm. With respect

Box 3. Punctuational speciation in the bryozoan *Metrarabdotos*

Metrarabdotos is an ascophoran cheilostome bryozoan that is represented today in the Caribbean by three species. Coastal rocks off the Dominican Republic and elsewhere in the Caribbean document the past 10 million years (My) of sedimentation in shallow seas, and they yield abundant fossils of this bryozoan. The fossils show that *Metrarabdotos* radiated dramatically from 8 to 4 Mya, splitting into some 12 species, most of which had died out by the Quaternary (Fig. 1). A variety of protocols for distinguishing species within *Metrarabdotos* have been established^{a-c}, taking into account the genetics and the amount of morphological differentiation of related extant species, and then extending comparable statistical tests of morphological differentiation to the fossil forms (highly significant correlations were found between the genetic and morphometric differences among the modern forms). Based on 46 morphometric characters, a mechanism for distinguishing lineages among the fossils was established.

Lineage splitting in *Metrarabdotos* seems to have been rapid and punctuational in character. Speciation was especially rapid from 8 to 7 Mya, with nine new species appearing in that time. There is some question about sampling quality, because sampling is poor in the preceding interval, and so some of these new species might have appeared earlier. However, the interval from 8 to 4 Mya, represented largely by information from the Dominican Republic, has been intensely sampled (DSI, Dominican Sampling Interval). Thus although there are questions over the origins of the nine basal species within this interval, the origins of the remainder (*tenuis*, n. sp. 10, and



n. sp. 8) are more confidently documented as being punctuational.

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to morphological evolution, the prevalent theme is a complex mosaic pattern with different features evolving at very different rates in different species, and morphological evolution is not necessarily related to speciation^{34,35}.

Evolutionary patterns and processes

Speciation is a consequence of reproductive isolation and thus 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 such as 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 also occurs rarely, might be long term and gradual. At the other extreme are organisms such as freshwater fish that live in spatially structured and often transient environments. Here, speciation might be so common that every lake and river has its own reproductively isolated population of a particular type of fish, but these populations might neither be very distinctive nor last very long. In between might lie the majority of invertebrate and vertebrate groups, generally exhibiting stasis, but occasionally speciating in a punctuated manner following a major environmental perturbation.

The plurality of evolutionary modes (gradualism without stasis, gradualism plus stasis, and punctuation plus stasis) might be real. Sheldon³⁶ proposed that gradualism might characterize taxa that live in stable environments, and which change in line with slow environmental changes, whereas stasis might be a feature of taxa in unstable environments, which can vary rapidly and dramatically, but in which the organisms do not evolve in line with every environmental fluctuation.

Palaeontological data contribute through the historical record they present. Field studies of modern 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 so on. Historical evidence might sometimes be brought into play, for example, the date of the artificial introduction of a new species on to an island, or the timing of the final retreat of ice sheets from Canada or northern Europe. But, at best, these approaches rely entirely on the reconstruction of an historical process from the patterns observed today. They can offer timescales of only a few hundred years, and speciation probably takes much longer than that.

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High-resolution radiometric dating is now beginning to offer the possibility of observing speciation in action, particularly in the Neogene. With time measurement precision down to thousands of years, or even hundreds in some cases, palaeontologists will be able to follow the behaviour of lineages in detail. Lacustrine sediments, with their annual varves, offer even more exciting prospects.

When one considers the way in which archaeological records can blend insensibly into palaeontological ones, 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 certain lineages have speciated in the past.

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