

PATTERNS AND RATES OF SPECIES EVOLUTION

Michael J. Benton

Department of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK

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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 (see Section *Patterns and Rates of Species Evolution*). 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.

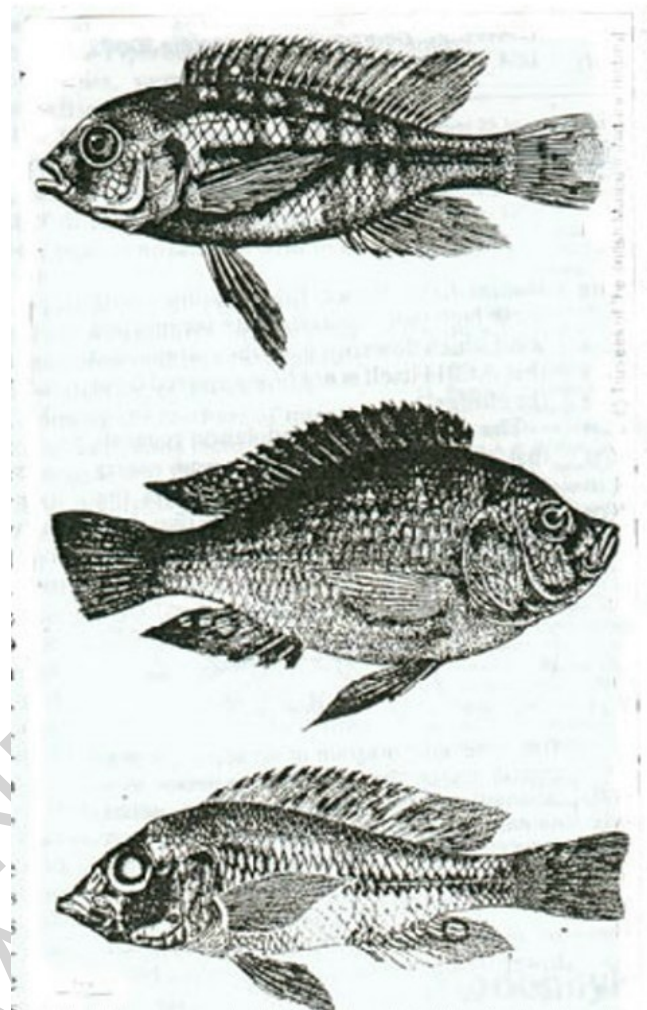


Figure 1. Three species of cichlid fishes from Lake Victoria, *Ptyochromis sauvagei* (top), *Lipochromis obesus* (middle), and *Astatotilapia piceatus* (bottom), showing the diversity of form. These species evolved from a single common ancestor within less than one million years. Based on several sources.

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.

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.

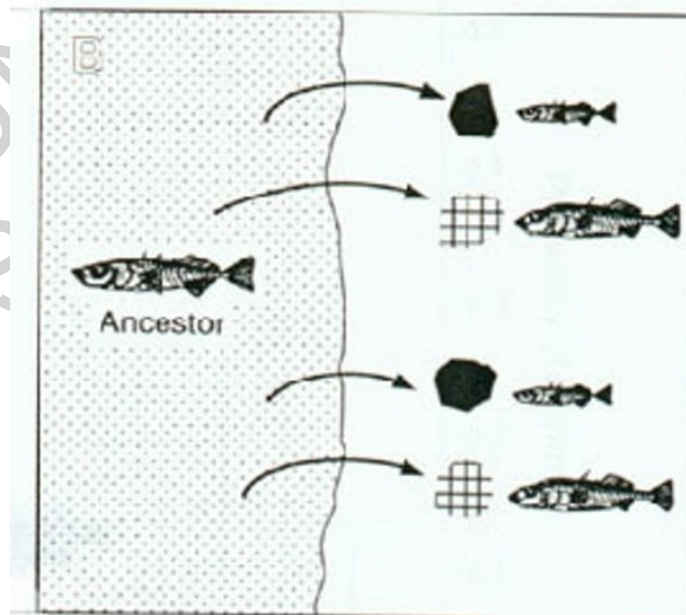


Figure 2. Model for parallel speciation of sticklebacks. The ancestral species (left)

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.

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).

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.

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Biographical Sketch

Michael Benton is Professor of Vertebrate Palaeontology at the University of Bristol. He has worked previously at the Queen's University of Belfast, and the University of Oxford. His major research interests are the history of diversity and macroevolution, based on evidence from the fossil record, as well as mass extinctions, and fossil reptiles.

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