



The Origin of Species

Speciation: from Darwin to Mayr and back again

Diethard Tautz, Director at the Max Planck Institute for Evolutionary Biology in Plön (Germany), writes about the current status of scientific knowledge on how existing species split into new ones.

“THE ORIGIN OF SPECIES” was printed in large bold letters on the title page of the 1859 edition of Darwin’s book *On the Origin of Species by Means of Natural Selection*. I suspect that even then it was the publishers who chose the layout of title pages and not the author. It would be interesting to know whether Darwin had indeed approved this accentuation, since his book is a magnificent introduction to the mechanism of natural selection, but contains relatively little about the origin of species. At the time, Darwin did not even have a workable definition of ‘species’, so how could he have written on speciation? Darwin’s (and Wallace’s) great achievement was realising that the blind force of natural selection can produce the adaptations that are the hallmarks of different species. But how existing species split into new ones was not directly addressed by them.

This may sound like nit-picking, but it touches upon a serious problem. How can one discuss the general mechanisms under-

lying a process (*speciation*) when one does not have a definition for its outcome (*species*)? There has of course been no lack of attempts to find such a definition. Many eminent biologists have tried it. In fact, almost every student of biology will have tried it, or will do so sooner or later. And everyone will fail – like his or her predecessors – but will have learned a lot about biology in the process. It is simply impossible to combine all aspects of species into a single concept – especially when dealing with organisms as diverse as palaeontological species, asexually reproducing species or bacteria. Thus, when discussing mechanisms of speciation, one tends to reduce this to the “normal” sexually reproducing taxa and to the so-called biological species concept. In 1895 Wallace gave the following version of this concept, “A species is a group of living organisms, separated from all other such groups by a set of distinctive characters, having relations to the environment not identical with those of any other group of organisms, and having the power of continuously reproduc-

ing its like”. In 1942, a shorter version, with important omissions including the ecological references, was popularized by the late Ernst Mayr, “Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups”.

This shifted focus to reproductive isolation, rather than environmental adaptation, is for a good reason. The theory of population genetics was developed in the 1930s, based on the principles of Mendelian genetics. One of the non-intuitive, and in fact surprising, outcomes of this theory is that only a small amount of gene flow is sufficient to homogenize allele frequencies within a gene pool. Mayr’s species concept essentially defines a gene pool, and population genetics seemed to imply that only very powerful forces could disrupt it. To the biologists at the time, this strongly suggested that only geographic separation could cause such disruption. This was the origin of the allopatric paradigm of speciation. It was most forcefully advocated by Theodo-

sus Dobzhansky and Ernst Mayr, who integrated this paradigm into their “synthetic theory of evolution”. It is still the paradigm most prominently presented in almost every textbook. Although it may be a little too early to conclude a historical analysis of recent decades, it may well be that, one day, this period of uncompromising dogma will be seen as the Dark Ages of speciation research. The allopatric paradigm was based on a few facts, a lot of faith, and on paradigmatic despots ruling the field. And we haven’t yet reached the speciation Enlightenment. Anyone who tries to publish alternative speciation scenarios will, sooner or later, be confronted by medieval referees. Personally, I have a good collection of dismissive comments from such colleagues.

So what is the problem with the allopatric paradigm? In its textbook version (this one taken from Wikipedia), it would read like this, “Allopatric speciation is the phenomenon whereby biological populations are physically isolated by an extrinsic barrier and evolve intrinsic (genetic) reproductive isolation, such that if the barrier breaks down, individuals of the populations can no longer interbreed.” This is really nothing other than saying that speciation is a double accident of nature. The first accident occurs when populations are split by extrinsic forces, and the second occurs when the accumulation of mutations leads to genetic incompatibility. Neither of these accidents was formulated into a quantifiable scientific theory by their fathers. So the allopatric paradigm is not a theory, but merely the verbalization of an *ad hoc* concept. And it does not, for example, explain why beetles and other insects are among the most speciose taxa, even though they can fly across almost any “extrinsic barrier”.

Of course, there is no doubt that allopatric speciation can occur in principle. But modern evolutionary biology demands quantitative models. These have emerged in the past decade and are open to testing. They cover the full spectrum from fully allopatric to fully sympatric scenarios and in-

voke quantifiable parameters such as mutation rates, selection coefficients, and migration rates; some are set within an explicit ecological theory. Several of them abandon the prejudice that organisms mate when they meet and instead put mate choice at the centre of the model. Most importantly, adaptations and natural selection play a central role in these alternative speciation models, coming full circle back to Darwin.

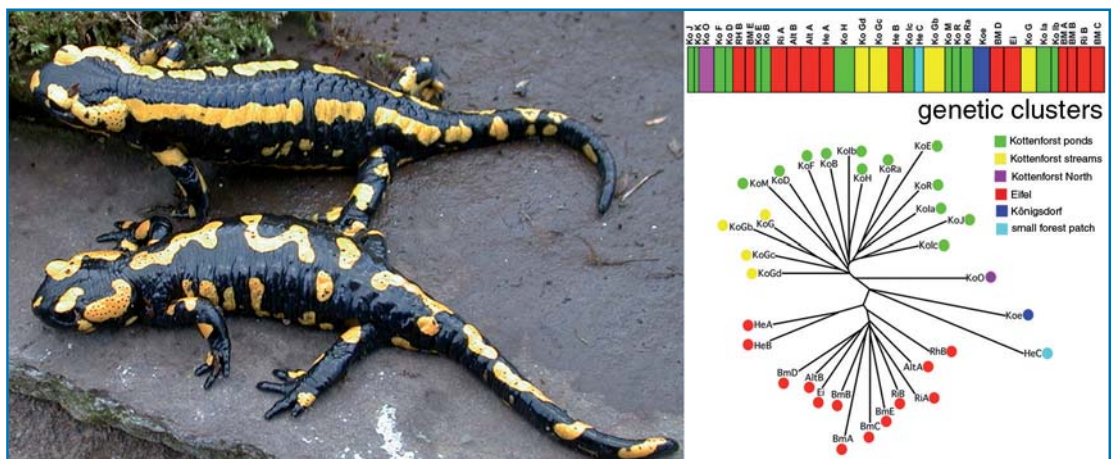
Sympatric speciation models

The biggest conceptual challenge of past decades was to develop models of fully sympatric speciation that help us understand how the homogenizing force of even a small amount of gene flow may be overcome. Again, there is an interesting history to such attempts. One of them was developed by John Maynard Smith in the 1960’s, but this was rather special and half-hearted and he self-confessedly did this, “...just to tease Ernst Mayr...”. A famous quip from these days was, “Sympatric speciation ideas are like the measles – everyone gets it and we all get over it!”. Since we know today that it is actually not very difficult to develop more realistic models of sympatric spe-

ciation, one may conclude that their relative lack earlier on resulted from the active (and well-documented – see the writings of Guy Bush) suppression of such ideas by the ruling despots.

There are currently two complementary types of sympatric speciation models. One is based on the principles of mate choice and sexual selection – themes already discussed by Darwin. The idea is simple: when mate choice is based on a specific external character (such as colour, odour, behaviour etc.) it should be possible for the combined evolution of the character and the preference for this character quickly to split a gene pool. For example, if there is a polymorphism for red and green spots in males, it would seem possible that females evolve a differential preference for either red or green spots. As long as the offspring of such assortative matings has a higher probability of jointly inheriting the preference and the character (genetic linkage), a gradual split of the gene pool will ensue. The weak part of this model is that some form of genetic linkage is required and that it does not explain differential adaptations to the environment.

The second general class of models fall under the heading “ecological speciation”. They assume that differential adaptations to the environment are the starting point and that this goes along with the development of mate-choice characters and preferences. A particularly interesting member of this mod-



One species or two?

Modern speciation research focuses on cases that are not yet clear-cut, since these offer the opportunity to study the process of species splitting. The picture above shows two types of fire salamanders in West Germany. They differ in their colouration patterns, but this is unimportant since these patterns can change during an individual’s lifetime. It is therefore necessary to use refined genetic tests and comparisons of multiple populations to identify a speciation process (figure on the right – modified from Steinfartz *et al.*, *Mol. Ecol.* 16, 4550).

ciation, one may conclude that their relative lack earlier on resulted from the active (and well-documented – see the writings of Guy Bush) suppression of such ideas by the ruling despots.

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el family is the “adaptive speciation” model. It adds another conceptual aspect, namely that of intraspecific competition.

Intraspecific competition can be compared to the gold-rush phenomenon. When the first gold was found in California in 1848, it made the first diggers rich.

But many others followed, and soon there were so many that the last thing one wanted to be was a digger in the gold fields. Instead, it became more attractive to diversify and to run a grocery store or a saloon, even though this did not promise the big bonanzas that the diggers hoped for. This initial diversification worked, until there were plenty of grocery stores and saloons as well. Thus, a continuous adaptation was required for finding individual niches, until a complex economy emerged. This is how one can envisage the evolutionary process as well. When a new resource opens up in the environment, a population will quickly adapt to make best use of it. However, those individuals that are adapted best will flourish, and will therefore also be the most abundant, competing most fiercely with each other. Thus, individuals who focus on less lucrative, but also less overcrowded, resources can have an advantage. However, in contrast to the gold-rush situation, such resource changes do not happen within the lifetime of an individual; they can only come about via natural selection over several generations. So to enable their offspring to make effective use of a new resource over time, individuals will have to find mating partners with the same differ-



Somebody who *didn't* write about speciation.

ential adaptations. Thus, assortative mating has to evolve alongside ecological adaptation. Explicit modelling of such a scenario by Michael Doebeli and Ulf Dieckmann has shown that this mechanism can indeed

work and that it can even lead to allopatric distributions of the respective populations.

Models of adaptive speciation are, conceptually, the exact opposite of the allopatric paradigm. Adaptive speciation can only work under sufficiently sympatric conditions, since intraspecific competition requires ecological contact. Its driving force is natural selection and not geological accident, and it predicts a tight association of speciation with differential niche use. Accordingly, models of adaptive speciation describe the speciation process as a direct and active consequence of natural selection. Darwin and Wallace would have loved them.

Experimental approaches

It is one thing to develop relatively complex models, but another to show that they have a sufficiently close connection with observable natural systems. Indeed, the experimentalists are lagging behind in this field, although promising avenues of research are emerging.

One of them is to find more cases of sympatric speciation in natural settings and to assess which of the conceptual models applies best. Because of the prevailing par-

Further reading

Books

- ▶ Schluter, D (2000): *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford, UK
- ▶ Coyne JA, Orr HA (2004): *Speciation*. Sunderland (Massachusetts): Sinauer Associates
- ▶ Dieckmann U, Doebeli M, Metz H, Tautz D (2004): *Adaptive Speciation*. Cambridge University Press

Speciation models

- ▶ Gavrilets S, Li H, Vose MD (1998): Rapid parapatric speciation on holey adaptive landscapes. *Proceedings of the Royal Society B*, 265, 1483-1489.
- ▶ Kondrashov AS & Shpak M (1998): On the origin of species by means of assortative mating. *Proceedings of the Royal Society B*, 265, 2273-2278.
- ▶ Dieckmann U, Doebeli M (1999): On the origin of species by sympatric speciation. *Nature*, 400, 354-357
- ▶ Doebeli M, Dieckmann U (2003): Speciation along environmental gradients. *Nature*, 421, 259-264.

Experimental approaches

- ▶ Schliwen UK, Tautz D, Pääbo S (1994): Sympatric speciation suggested by monophyly of crater lake cichlids. *Nature*, 368, 629-632.
- ▶ Bush GL (1998): The conceptual radicalization of an evolutionary biologist. In *Endless Forms: Species and Speciation*, eds. Howard D & Berlocher S, pp. 425-438. Oxford, UK: Oxford University Press

- ▶ Schliwen U, Rassmann K, Markmann M, Markert J, Kocher T, Tautz D. (2001): Genetic and ecological divergence of a monophyletic cichlid species pair under fully sympatric conditions in Lake Ejagham, Cameroon. *Mol. Ecol.* 10, 1471-1488.
- ▶ Barluenga M, Stölting KN, Salzburger W, Muschick M, Meyer A (2006): Sympatric speciation in Nicaraguan crater lake cichlid fish. *Nature* 439, 719-723
- ▶ Steinfartz S, Weitere M, Tautz D (2007): Tracing the first step to speciation: ecological and genetic differentiation of a salamander population in a small forest. *Mol. Ecol.* 16, 4550-4561.
- ▶ Thorpe RS, Surget-Groba Y, Johansson H (2008): The relative importance of ecology and geographic isolation for speciation in anoles. *Philos Trans R Soc Lond B* 363, 3071-3081.

Speciation genes

- ▶ Ting CT, Tsaour SC, Wu ML, Wu CI (1998): A rapidly evolving homeobox at the site of a hybrid sterility gene. *Science*, 282, 1501-1504.
- ▶ Presgraves DC, Balagopal L, Abmayr SM, Orr HA (2003): Adaptive evolution drives divergence of a hybrid inviability gene between two species of *Drosophila*. *Nature*, 423, 715-719.
- ▶ Bombliès K, Lempe J, Epple P, Warthmann N, Lanz C, Dangl JL, Weigel D (2007): Autoimmune response as a mechanism for a Dobzhansky-Muller-type incompatibility syndrome in plants. *PLoS Biol.* 5, e236. (note that this is an example of a manuscript where the authors had to remove the word "speciation" from the entire text, due to quarrels with their referees)
- ▶ Mihola O, Trachtulec Z, Vlcek C, Schimmenti JC, Forejt J (2008): A Mouse Speciation Gene Encodes a Meiotic Histone H3 Methyltransferase. *Science* Vol. 323: 373 - 375

adigm of allopatric speciation, carrying out such an assessment objectively has been difficult. As long as it was claimed that a sympatric model should only be invoked after all possible, and even abstruse, scenarios of an allopatric history had been excluded, it was tricky to make much progress. The “allopatric ghost of the past” has overshadowed many such studies. How inadequate this is becomes clear when one reverses the points of view: an allopatric model should be invoked only after all possible sympatric scenarios of the past have been ruled out. Take this as a paradigm and you would have difficulties finding convincing cases of allopatric speciation! In fact, one of the rare explicit tests of allopatric speciation for Anolis lizards in the Antilles by Roger Thorpe and colleagues has failed to provide such evidence.

Luckily, there are some cases where even Ernst Mayr conceded that sympatric speciation has occurred. Among them are radiations of cichlids in small crater lakes, a field pioneered by Uli Schliewen. All three of the lakes that have been studied in ecological detail suggest that the splitting of their species was associated with niche diversification and assortative mating. In other words, they are in line with models of ecological speciation.

Most sympatric speciation models make another important conjecture, namely that the splitting process can be fast, within hundreds or thousands of generations. From an experimentalist's point of view, this means that one can look at ecological situations that have formed very recently and assess whether such a splitting process is ongoing. Sebastian Steinfartz has studied such a situation in a forested area near Bonn in Germany, where fire salamanders have started to use small ponds for their larval growth phase, rather than the small streams which are their normal larval habitat (the adults live on the forest floor). He showed that this new behaviour has a genetic basis, that there is assortative mating between different ecological types and that the split between the types has only recently occurred in the forest (see Figure). Situations like this are ideal for studying the genetic and behavioural basis of a speciation process right at its starting point.

A second interesting avenue for contemporary speciation research is the attempt to identify “speciation genes”. Here one maps and identifies genes that cause partial or full hybrid sterility in interspecific crosses. Of course this requires some genetic tricks, since sterile individuals do not lend them-

selves easily to breeding studies. Yet, this approach was successfully applied to *Drosophila*, mouse, and *Arabidopsis*, yielding highly interesting insights. For example, one gene identified in *Drosophila* is a protein of the nuclear pore. This was initially very surprising, since one would not have expected such a basic cellular factor to play a role in a decidedly organismic process like speciation. But there is now a very good theory. The nuclear pore complex is one of the defence barriers against viruses that need to replicate in the nucleus. Because viruses evolve quickly, one would expect defence barriers also to evolve quickly. And since the nuclear pore complex is built out of several interacting proteins, they have to coevolve. As a consequence, they become incompatible when combined from different gene pools. So strictly speaking, this is an incompatibility locus that has built up over time as a response to natural selection. In principle, this is in line with the allopatric scenario with a selection component. But such incompatibility loci would build up equally well after populations have split under sympatric conditions. Thus, these genes are not necessarily directly involved in the initial splitting of the species, and the term “speciation genes” is a slight misnomer for them. To find genes that are directly involved in the splitting process itself will require more work and new approaches.

Where to?

An enormous amount of evidence on speciation patterns and processes has been collected since Darwin's time. This research provides excellent support for Darwinism's central tenet, the power of natural selection in creating adaptations. Still, we are far from understanding the dynamic and molecular basis of the speciation process *per se*. But after a long time of conceptual stagnancy, we are now coming into a phase that encourages plural thought about speciation, together with new theoretical and experimental approaches. The time will surely come when a book can capitalize the words THE ORIGIN OF SPECIES for the right reasons.



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