Mechanisms of Speciation

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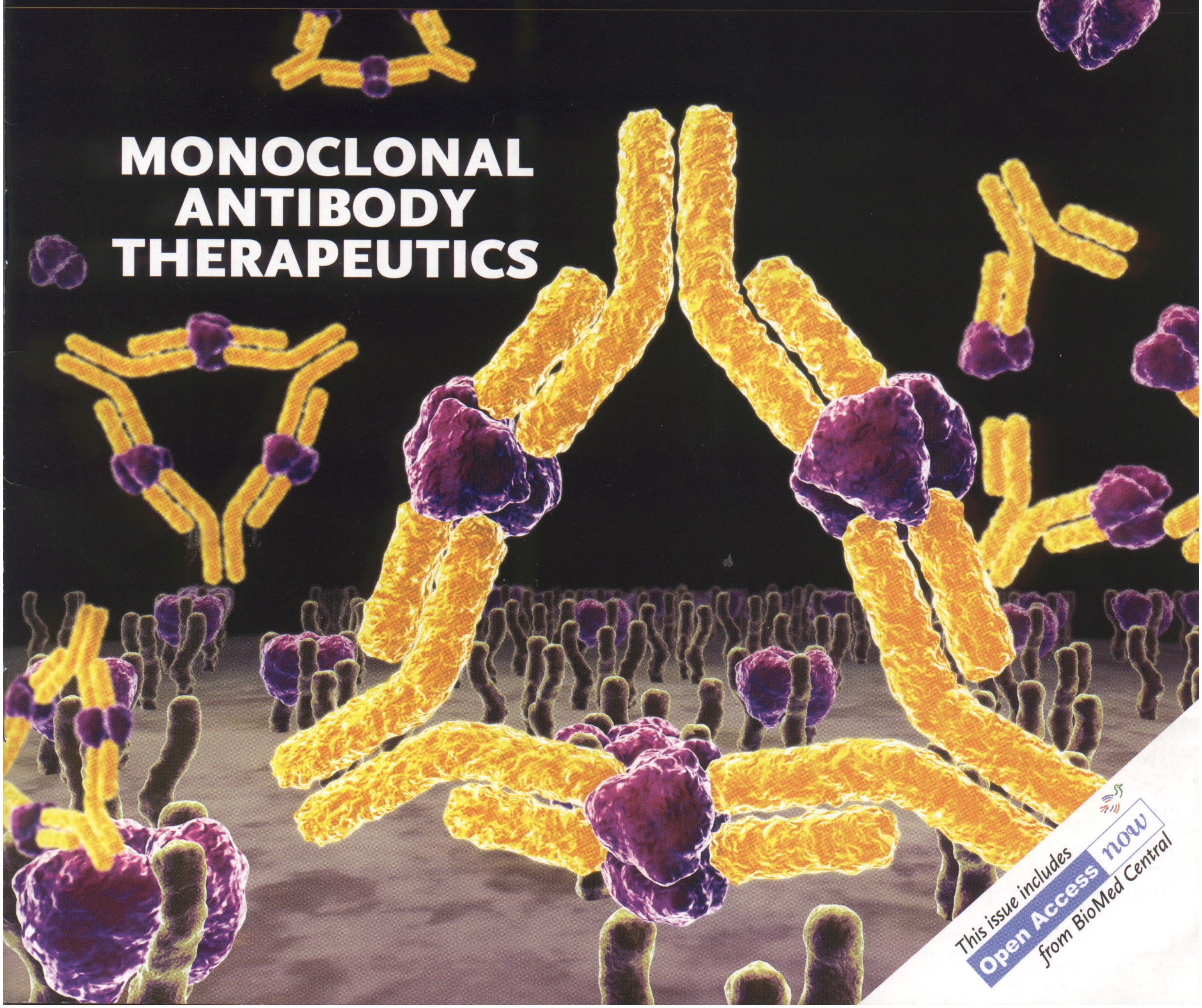


MONOCLONAL ANTIBODY THERAPEUTICS

MECHANISMS OF SPECIATION

New examples of sympatric speciation revive some nagging questions | **By Leslie Pray**

"A new species develops if a population which has become geographically isolated from its parental species acquires during this period of isolation characters which promote or guarantee reproductive isolation when the external barriers break down."

—Ernst Mayr, *Systematics and the Origin of Species*, 1942[1]

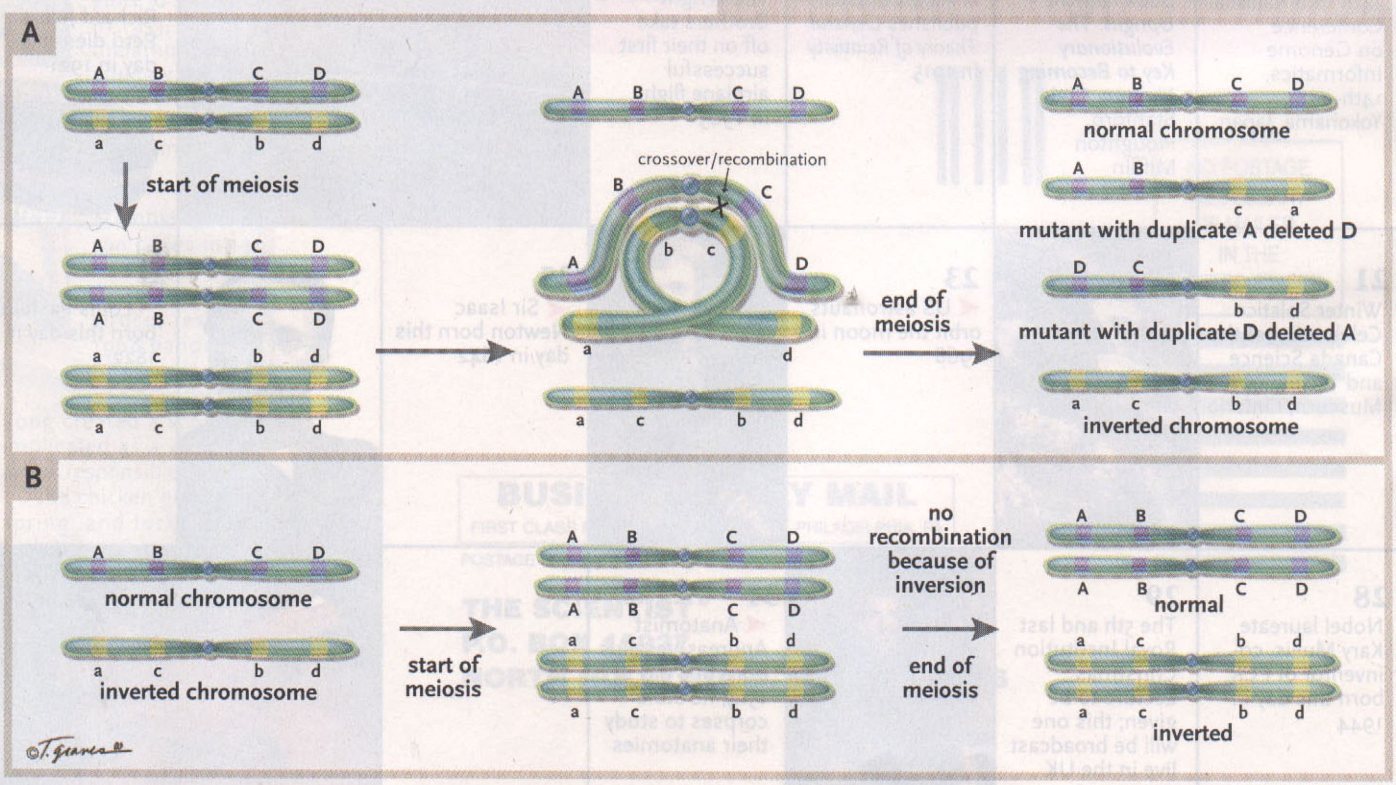
The duration of a cell cycle lasts anywhere from one hour to one day; *Drosophila melanogaster* lives for a couple of weeks. But the origin of a species, otherwise known as speciation, takes thousands, maybe millions of years, a fact that makes it extraordinarily difficult to study.

Consequently, the process of speciation has baffled biologists for nearly two centuries. Even Charles Darwin got it wrong. At least that's what evolutionary biologist Ernst Mayr argued in *Systematics and the Origin of Species* in 1942, and that's how Mayr still sees it today.

Darwin believed that speciation was the ultimate adaptational answer to competition among individuals for scarce resources. Not so, says Mayr, who has argued for decades that speciation is a nonadaptational byproduct of geographic isolation. Although Mayr credits 19th-century naturalists, including German explorer Leopold von Buch, for developing what has become known as the allopatric (or geographic) model of speciation, evolutionists did not fully embrace it until Mayr did so in his 1942 book. Since then, it has dominated speciation theory. "We've been laboring under Mayr's shadow," says evolutionary geneticist Jerry Coyne, University of Chicago.

But today, some evolutionists, including University College London's James Mallet, are calling for a back-to-Darwin approach to study speciation, arguing that growing evidence suggests that Darwinian natural selection may be more important than isolation after all, even in allopatric situations. Loren Rieseberg, an Indiana Uni-

THE NORMAL, THE INVERTED, AND THE RECOMBINED: *A conceptual diagram of pericentric inversion. (A) When the normal and inverted chromosome recombine, some chromosomal regions are eliminated and mutant recombinations will likely not be viable—the only gametes that will survive are the normal and the inverted. In (B), recombination does not take place because of the inversion. Eventually, in either scenario, the organisms with the ABCD combination will diverge so much from those with the acbd combination that they will become a separate species.*



versity professor and recipient of a 2003 MacArthur Genius Award, explains: "We are realizing that it is the strength of selection rather than the amount of gene flow that controls rates of speciation."

"That's just nonsense," says Mayr, who adamantly declares that Darwin confused his natural selection and speciation theories and that people are doing the same today. "Darwin's theory of speciation was wrong. He just didn't realize that he had to deal with populations. He left the population part out of it."

Although Darwin acknowledged the existence of allopatric speciation, he believed that most separations occur sympatrically, which happens without geographic isolation, while the incipient species are still in physical contact and able to interbreed. Although Mayr's 1942 classic has become known as the "bible of allopatric speciation," Mayr insists that he has never denied the possibility of the sympatric kind, contrary to what he claims are erroneous reports that he has. Rather, he simply pointed out at the time that no good cases of speciation occurred without geographic isolation. This, despite Darwin's insistence years earlier that speciation could and typically did happen even in the absence of barriers to gene flow, which is the movement and exchange of genes between interbreeding populations.

This is classic Mayr, says Stanford University's Steve Palumbi, who often lunched with the elderly biologist when Palumbi taught at Harvard University. "Ernst is a very opinionated sort of person, and he carries those opinions with him for decades. He remains quite seriously dedicated to his view of the world. Sympatric speciation—that is a very good example of Ernst's stubbornness. He will not agree to disagree."

Now, there are good examples of sympatric speciation, most notably the cichlids in East Africa, and much of the growing evidence in support of the back-to-Darwin approach comes from these newly acknowledged cases. Plus, recently improved theoretical models of speciation substantiate the plausibility of sympatry. The evidence has altered Mayr's views on sympatric speciation, although he still strongly believes that the allopatric method is the predominant mode and the only one to be found among the well-studied birds and mammals.

But, Mayr refuses to be convinced by one of the most famous examples of probable sympatric speciation, the apple maggot fly, *Rhagoletis pomonella*. When domestic apple trees were introduced into the northeastern United States some 150 years ago, a fly that had previously fed on wild hawthorn trees took up residency on the newcomers. One of Darwin's contemporaries, Benjamin Walsh, hypothesized that this adaptive host shift (from hawthorns to apple trees) might be a case of incipient sympatric speciation. In the early 1960s, as a professor at Harvard, Mayr challenged graduate students in his speciation class to prove Walsh wrong. Guy Bush accepted the challenge. "He made it his personal crusade to show that it was possible," says Bush's former graduate student Jeffrey Feder, now a professor at the University of Notre Dame. "At first he was as skeptical as Professor Mayr, but then he realized that if organisms mate in preferred habitats, as *Rhagoletis* does, sympatric speciation could occur." But Mayr was and remains unconvinced: "The question was, was this a different species? This is where Mr. Bush was never quite able to provide proof. If the process goes on, if it continues for thousands of years, then maybe. But right now, no."

CICHLIDS AND SYMPATRIC SPECIATION: MAYR'S VIEWS SHIFT

"The question to whether and to what extent sympatric speciation occurs among animals is one of the most controversial subjects in the field of speciation. Unfortunately, most of the discussions of this subject have been largely speculative, and, if one attempts to gather well-substantiated data, one is surprised to find how little concrete knowledge exists."[1]

Courtesy of The Harvard University Archives

ERNST MAYR *and some specimens, 1961, Harvard University*

In his 1942 book, Mayr went to some length to deny the role of sympatric speciation in the remarkable distribution of cichlids, a family of freshwater fish known for its large numbers of closely related species living together. So, it's perhaps somewhat ironic that today, Mayr cites cichlids as the strongest case for sympatric speciation. Lake Nabugabo in East Africa, for example, is a crater lake that is about a mile-and-a-half long and inhabited by six closely related cichlid species, all of whom could have descended from only a single, common, extant ancestor upstream. "No question about it, that it had to be sympatric speciation," he says. "I am now convinced and this is where I have changed my mind, that there are a lot of cases of sympatric speciation."

Importantly, though, even with the cichlids, there seems to be more at play than Darwinian competition for scarce resources. Axel Meyer, University of Konstanz, Germany, explains that in the past, biologists generally thought of speciation as a process occurring over the course of millions of generations. But Lake Nabugabo is an estimated 5,000 to 6,000 years old, and nearby Lake Victoria, with its several hundred cichlid species, all of which are believed to have originated in the lake, is estimated at 200,000 years old. At rates like that, says Meyer, something else must be happening besides the slow, gradual process of evolution by natural selection. The culprit, he believes, is mate choice, also known as sexual selection. Although Darwin wrote about sexual selection, it is not quite how he envisioned the sympatric speciation process.

Suppose a new mutation of a bright red body in males crops up in a population. Further suppose that certain females, for whatever reason, prefer to mate with the red males. Over time, the red males and the females who prefer them will breed only among themselves, their genetic makeup eventually altering to the point where they no longer breed with other species.

Meyer describes what he calls a eureka "Darwinian moment" while swimming in one of these cichlid-filled lakes. Amazed by the dramatic changes in the male fishes' vivid coloration that he saw as he swam from one part of the lake to another, Meyer realized that mate choice was probably the key to why so many different but closely related species can originate and live together in such a small area. Sexually selected traits, such as bright coloration, tend to evolve more quickly than other features, making them more likely candidates for a sympatric speciation mechanism.

A chromosomal rearrangement, or inversion, is another likely candidate. A chromosomal inversion is a physical alteration of a chunk of chromosome, which prevents genes in the inversion from undergoing normal meiotic recombination. The inverted genes effectively evolve in isolation, even as the remaining genome recombines. Eventually, although rather quickly compared to evolutionary rates in other parts of the genome, the isolated genes accrue enough change to drive speciation, even in nonallopatric situations. Rieseberg, who studies chromosomal speciation in sunflowers, says that the idea has been around for nearly a century, but only recently have models and evidence become strong enough to convince folks, including Arcadi Navarro, Universitat Pompeu Fabra, Spain, that chromosomal speciation may be widespread.

Navarro and University of Edinburgh geneticist Nick Barton recently demonstrated how chromosomal rearrangements may explain speciation processes that separated humans from their closest living relative, the chimpanzee.[2] The data, says Navarro, point to the likelihood that the human and chimp lineages diverged even in the presence of limited gene flow.

THE FOCUS IS ON MECHANISM

"Geographic isolation without the development of biological isolating factors cannot lead to species formation ... The question is: What are these biological barriers and how do they originate?"[1]

As University College London's Mallet explains, there is growing evidence that complete geographic isolation is not necessary for speciation to occur, as long as divergent selective pressures among the two (or more) populations in the process of becoming separate species are strong enough to outweigh the homogenizing effects of gene flow. Much of the evidence is molecular, as increasingly sophisticated molecular tools allow scientists to detect gene flow even between populations that appear to be completely separate.

Although, like Darwin, Mallet doesn't deny the occurrence of allopatric speciation, he says that focusing too much on geography "ignores the fact that two populations can also diverge when they are still in contact, if natural selection is strong enough."

Even Mayr agrees that natural selection, sexual selection in particular, is an integral component of sympatric speciation. He takes issue, though, when the argument for natural selection is extended to allopatry, as the Darwinian revivalists have done.

Although Mayr is the first to admit that Darwinian natural selection is most likely responsible for some, if not the most important, evolutionary changes that occur in an isolated population over time, he is adamant that allopatric speciation cannot be reduced to natural selection alone. "Natural selection and isolation are two different things. This would be correct even if the factor that changed things was not natural selection, but say, Lamarckian adaptation," says Mayr. (Lamarckian adaptation, now a refuted explanation for inheritance, states that an individual can inherit acquired characteristics.)


Courtesy of Ad Konings, Cichlid Press, El Paso

COLOR BY NATURE: Haplochromis nyererei *is one of the more than 500 endemic cichlid species found in Lake Victoria, East Africa.*

As University of Vermont geneticist Charles Goodnight explains, "Mayr placed primary importance on isolation. His allopatric model, and even his definition of speciation, is about barriers to gene flow. I suspect he felt that any number of forces could generate the differentiation needed for speciation once reproductive isolation was established. Thus, I think he wouldn't deny that, for example, disruptive selection could be the driving force behind divergence; however, he would argue that it was the allopatry that was the fundamental cause."

Semantic and philosophical issues aside, Goodnight points to other evolutionary mechanisms, besides natural selection, at play in allopatric speciation. Divergent selection could do the job, he says, but only under certain genetic circumstances. In particular, he cites the interaction between selection and drift (random, nonadaptive changes in gene frequency): "I think that this is the point that people miss. Drift alone is not enough since it, frankly, isn't a powerful enough force. Selection alone is not enough because uniform directional selection is not a diversifying force unless you have variation in local average effects. However, together, drift and selection become a powerful diversifying force."

The University of Chicago's Trevor Price says that the misguided focus on natural selection in the allopatric speciation process is just a phase, partially due to the relative ease of collecting the data necessary to support that view. Misguided or not, the neo-Darwinian banner represents a renewed focus on mechanism. Interactions between drift and selection, mate choice, and chromosomal rearrangements are the types of phenomena exciting the imaginations of speciation biologists today. Says geneticist Mohamed Noor of Louisiana State University: "There is less emphasis being placed on geography by itself now than there was even 10 years ago. You certainly shouldn't trivialize geography, but people are more interested in the mechanisms of speciation."

Nobody argues that Mayr's allopatric model is outdated. And some, like Chicago's Coyne, say, "In the end, Mayr is the one who is going to be left standing." ⊗

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