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Evolution's Wedges

Finding the genes that drive one species into two

By Daniel Strain
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ENLARGE

A gene known as eda helps determine how much armor a three-spined stickleback has (bony plates stained red at midsections). Armor changes, in turn, may split one species into two.
R.D.H. Barrett et al/Science 2008

Look to Texas to see evolution's true colors. There, speckling the state's green fields, you'll find the annual phlox, a flower also known as "Texas pride." Its petals, a light purple elsewhere, are bright scarlet in the southeast near Austin. This color change isn't a whim: It's the annual phlox's response to the presence of a close cousin, the pointed phlox. Native to East Texas, the pointed phlox also has purplish flowers.

Just two genes orchestrate the annual phlox's shift from purple to red flowers in the fields where it meets its cousin. But this color change has a big impact. Like prudish governesses, the genes keep the annual species from mating with the pointed relative, because butterfly pollinators rarely swap pollen between red and purple flowers. Such governesses are an example of what many biologists call speciation genes: genes that impede mating between related organisms, potentially keeping two nascent species apart or splitting one species into two.

Though biologists have known that studying such genes could help reveal how species come to be, only recently have individual candidates been uncovered. New techniques in genetic sequencing have made the search for these evolutionary wedges much easier, says Patrik Nosil, an evolutionary biologist at the University of Colorado at Boulder.

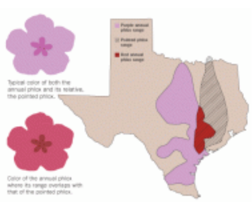
"Evolutionary biology is in a mini — I don't want to use 'revolution' because I'm not sure if what we'll find will be any different from what we already knew," Nosil says. "There's a lot of excitement and change right now because we're able to generate much more data."

While high school biology courses may emphasize the role of geographic barriers — big mountains and wide rivers — in driving would-be species apart, some scientists are more interested in the genetic story behind such divisions. During any one evolutionary split, several, or maybe even hundreds, of genes can contribute a tiny push.

Researchers are now focusing in on a handful of promising speciation heavyweights, with more expected over the next few years. While the phlox color genes act directly to keep the annual and pointed versions distinct, most newly found candidate speciation genes have arisen as by-products of evolutionary pressures not related to mating at all. Genetic tweaks inspired by environmental shifts, for example, may be cleaving apart species as diverse as stickleback fish and monkeyflowers. And a newly identified fruit fly gene demonstrates that competition among genes themselves, not just environmental changes, can drive one species into two.

The search for speciation genes isn't just an evolutionary scavenger hunt. Discovering such genes brings scientists closer to solving a biological mystery, says Nosil: "How easy is it to create a new species?"

Governesses



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SWITCH TO SCARLET

View larger image | In areas where the annual phlox's range overlaps with that of a close relative, the phlox's color switches from light purple to scarlet. This shift — driven by two yet-to-be-identified genes — appears to prevent interbreeding with the pointed phlox relative (also a light purple color).

Map: geoatlas/graphi-ogre, graphic: Janel Kiley

on duty

As is the case with the phloxes, appearance doesn't always distinguish one species from another. Deciding what makes a species distinct from its evolutionary neighbors can get fuzzy, and there are about as many different definitions as there are biological disciplines. An old and often cited explanation comes down to sex. In true Romeo-and-Juliet style, members of separate species don't mate, at least not successfully.

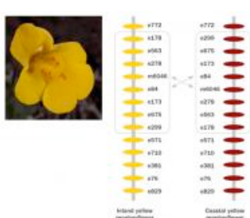
When the annual and pointed phlox do manage to interbreed, their hybrid children rarely produce mature seeds. Because of this reproductive dead end, individuals extra wary of interbreeding should flourish over others that are less discriminatory. “If a new mutant stops them from hybridizing, that’s favored,” says Robin Hopkins, an evolutionary biologist at Duke University.

Previous work showed that the purple-to-red change slows mating between the two species by up to two-thirds. Hopkins and Duke’s Mark Rausher discovered that several enzymes are behind that shift. Breeding and genetic experiments revealed that those enzymes are produced under the watch of two genes. The researchers identified the enzyme culprits in January in *Nature* but still have to locate the specific genes.

Wherever they are, the two genes don’t seem to make the phlox smell sweeter or better catch the eye of passing butterflies. The yet-to-be-identified governess genes do one and only one thing, Hopkins says: stop sex between the two species. As far as speciation genes go, few examples put their stamp so directly on mating.

Most new species are, instead, accidental monsters. The genes that give rise to these creatures come about through mundane evolution — such as improvements to cellular machinery or antipredator defenses — that impacts mating only through twists of fate. Successful reproduction is a very important thing for organisms, so why evolution would tolerate two populations of would-be parents that can’t interbreed has been hotly debated among biologists.

“Every single piece of machinery that is necessary to keep you fertile and alive already exists,” says evolutionary geneticist Nitin Phadnis of the Fred Hutchinson Cancer Research Center in Seattle. “So the big question is why something functioning perfectly well changes through evolutionary time.”



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FLOWER FLIP

Some of the differences between two populations of yellow monkey-flower are driven by genes that sit on an area of a chromosome that has been flipped (below). Such flips, called inversions, may help keep the two populations different.

Wsiegmund/Wikimedia Commons; D.B. Lowry and J.H. Willis/PLOS

The speciation flood

For Dolph Schluter, the answer begins with a flood. Around 10,000 to 20,000 years ago, receding glaciers doused the Pacific Northwest with meltwater, forming a spiderweb of new streams and lakes. Animals rushed in to take advantage of these new habitats. Most important, from the point of view of Schluter and other evolutionary biologists, was the appearance of a silver fish, usually no longer than a credit card, called the three-spined stickleback (*Gasterosteus aculeatus*).

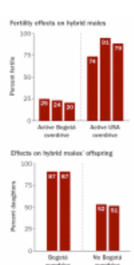
Though not separate species, the sticklebacks living in streams today and those still living in the ocean are two very different beasts with varied behaviors and appearances. In the lab, marine and freshwater fish can knock boots and, hence, the populations can exchange genetic information. But in nature, the two groups may have trouble mating.

If a stickleback from a stream wanders back into the big ocean, it will very much be a fish out of water. If this unlucky immigrant can't dodge attacks by predatory fish or compete for food with the locals, then it may die before getting the chance to breed with a native. So, even if its newly acquired traits don't touch mating directly, they could prevent sex indirectly. Over time, a lack of mixing between the populations might allow more differences to build up, making it so that the fish couldn't mate even if they got the chance.

As long as genes for stream living slow interbreeding, "then the genes for speciation and the genes for adaptation are one and the same," says Schluter, of the University of British Columbia in Vancouver.

One promising candidate for an adaptation-turned-speciation gene is called ectodysplasin or *eda*. It's one of a handful of genes that give rise to the stickleback's extravagant armor. Ocean fish are covered in an array of plates and spines, looking something like swimming knights. Stream fish, which have a different *eda* version, are much smoother.

"Most freshwater populations are low-plated, and in every one of those low-plated populations that have been investigated so far, *eda* is partly or largely responsible," Schluter says.



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The success of the smooth gene variant seems to stem, in part, from the edge it gives stream fish against a new breed of predator. Young fish with less armor were more likely to survive to adulthood in artificial ponds stocked with insect diners, Kerry Marchinko, a colleague of Schluter's, reported in 2009 in *Evolution*. Sticklebacks with less protection seem to grow faster, quickly becoming too big for stream-dwelling bugs to catch.

But discovering whether *eda* alone could affect survival enough to slow interbreeding and drive the creation of a new species would require further, expensive experiments, Schluter says. Without that data, *eda*'s status as a speciation gene remains as slippery as a freshwater stickleback.

Not too far from the stickleback's cozy streams, a little yellow flower illustrates how changes that go beyond individual genes can ensure that two populations on the verge of speciation remain different.

Like sticklebacks in separate locales, populations of yellow monkeyflowers (*Mimulus guttatus*) living along the Pacific Coast are physically different from members of the same species dwelling east into central California and Oregon. At the most basic level, coastal monkeyflowers are robust and live for multiple years, whereas inland monkeyflowers are spindly and live for just one.

About 20 to 30 percent of the differences between the two populations arise from genes sitting within a single region of one chromosome, evolutionary geneticists John Willis of Duke and David Lowry, now at the University of Texas at Austin, reported in 2010 in *PLoS Biology*. But this region isn't an ordinary genetic plot of land: It's what's called an inversion. At some point in the past, this chromosome chunk did a flip in one of the two populations, landing with the side that used to be up pointing down.

"One orientation of inversion is better in places that have year-round soil moisture and the other form is better in places that dry out during summertime," Lowry says.

Inversions, like the spines of ocean sticklebacks, are good armor. Chromosomal flips keep the genes inside from getting traded to different chromosomes when organisms mate — important security since, like a good sports team, some combinations of players work best together. In the monkeyflower, for instance, genes that aid survival in inland soils probably pair well with genes underlying the live-fast-die-young lifestyle.

Inversions may function as evolutionary closers. Inland genes stay inside inland plants and coastal genes in coastal plants, so future progeny will be more likely to resemble one population or the other but not resemble a mix.

Lowry thinks more data may reveal that similar flips are big players in the splitting of a range of plant and animal species: "We're entering an era where we're going to see more inversions, and their importance is going to be clear."

Though it's not yet known whether monkeyflowers and stickleback species will fully split, in both cases differences have to do with the habitats the species call home. But not every speciation event starts in the wild. Some begin in an environment of a completely different nature.

Selfish evolution

"Genes in the genome are chasing moving targets in the environment," says Daven Presgraves, an evolutionary geneticist at the University of Rochester in New York. "The other part of the environment that is starting to emerge is, it could be other genes in the genome." In other words, it's a jungle out there, but it's an equally scary jungle in there, too — in the cell, that is.

This internal warfare remained largely hidden from scientists until the 1980s, when theorists began to wonder whether individual genes could be as selfish as individual organisms. Since animals usually carry two copies of most chromosomes, the average maternal or paternal version of each gene gets passed down to only half of a creature's progeny. Selfish genes, on the other hand, are downright Machiavellian, maneuvering themselves into as many offspring as possible. "These sort of cheaters place themselves far more than 50 percent in the next generation and, therefore, get a huge evolutionary advantage," Phadnis says.

In a cheating genetic world, individual genes continually try to outcompete one another, much like predator and prey, by exploiting helpful mutations. Recently, researchers showed that genetic selfishness could actually disrupt breeding and possibly spur speciation.

A few years ago, Phadnis, then a graduate student at the University of Rochester, and his adviser Allen Orr identified what may be the best characterized selfish speciation gene candidate. The gene, which the team dubbed "overdrive," sits on the X chromosome in two populations of the fruit fly *Drosophila pseudoobscura.*

At first overdrive looks harmless enough. When two fruit flies from North or Central America, the "USA group," mate, the offspring come out normal. Same for mating among fruit flies in Colombia, the "Bogotá group."

When Bogotá females breed with USA males in the lab, though, their sons are almost entirely sterile, the team reported in *Science* in 2009. Genetic engineering experiments revealed that the culprit behind this sterility was the version of overdrive in the Bogotá group. Lucky for the offspring of Bogotá-only matings, these South American fruit flies have evolved one or more genes that switch overdrive off. Hybrids, however, get a mix of genes that can't always quash overdrive, allowing the gene to run wild.

This sterility-causing overdrive didn't rise to prominence in the South American flies because it gives them an edge in their environment. Instead, the gene version likely spread because it's a dirty cheater.

Phadnis and his colleagues first got a whiff of overdrive's selfish nature from a rare observation. Sometimes, hybrids that would typically be sterile do manage to reproduce. But when they do, they sire mostly daughters. With a little lab testing, the team confirmed that, when unchained, the Bogotá overdrive appears to ensure its spot in the next generation by somehow forcing through the X chromosome it sits on. In fact, the genes that turn overdrive off probably evolved to stop its cheating ways.

Overdrive isn't the only such nefarious gene. Yun Tao and his colleagues at Emory University in Atlanta, for instance, are narrowing in on a similar daughter-biased gene that causes sterility when the close cousins *Drosophila simulans* and *Drosophila mauritiana* interbreed. The researchers haven't homed in on the exact cheater yet, but they are vetting a candidate for the off switch, a gene they are calling "too much yin."

These discoveries entail an entirely new outlook on evolution, Presgraves says. "Now, we're in this world where we're not looking around the globe so much anymore. You're looking at genomes," he says. "And what you're finding is this dizzying diversity of selfish things."

In the end, tugs from both inside and out may give rise to complementary sets of speciation genes, Schluter says. "Once we have them all before us, we'll understand the whole picture much better." While patterns will probably emerge, each organism may follow its own path to speciation — so answers to how easy it is to create a species could be as diverse as the planet's living communities themselves.

Still, Tao thinks he could learn a lot by following one path to a brand-new kind of animal. He would start by engineering a cheater gene such as overdrive into an unsuspecting species of fruit fly, the iconic *Drosophila melanogaster,* perhaps. As the fly's genome struggled to combat the daughter-biased gene, it would evolve. In essence, Tao would then get the opportunity to watch speciation and the varied genetic changes that accompany it unfold before his eyes.

"Can we drive the species to a new species within a couple of years?" Tao asks. "That would be a wonderful experiment."

SUGGESTED READING :

P. Nosil and D. Schluter. The genes underlying the process of speciation. Trends in Ecology & Evolution, April 2011.