UC SANTA BARBARA

THE Current

February 16, 2022
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‘A Hopeful Monster’

When Charles Darwin first codified the theory of evolution by means of natural selection, he thought of it as a gradual process. “We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages,” he wrote in his seminal work, “On the Origin of Species.”

But Darwin didn’t have the full picture. “Evolution doesn’t necessarily take all these small changes like Darwin proposed,” said Scott Hodges, a professor in UC Santa Barbara’s Department of Ecology, Evolution, and Marine Biology.

Hodges, doctoral student Zachary Cabin and their colleagues just have identified a case of a sudden evolutionary change. In the journal Current Biology, the scientists describe a population of columbines that have lost their petals, including the characteristic nectar spurs. A drastic change caused by a mutation in a single gene. The finding adds weight to the idea that adaptation can occur in large jumps, rather than merely plodding along over extended timespans.

Ever since the theory of evolution was put forward, biologists have debated whether it always occurs in small, gradual steps over long timespans or sometimes as an equilibrium punctuated by abrupt changes. Often, large morphological changes appear within short geologic timescales where intermediate forms may not have fossilized. The question then remains whether many small changes occurred in a short period of time, or perhaps whether single large-scale mutation might be responsible. So, researchers really have to catch the development in action if they hope to build a case that sudden changes can drive evolution.

Enter the Colorado blue columbine. In one population, a mutation has caused many of the plants to lose their petals with the iconic nectar spurs. While not an uncommon occurrence in columbines, spurlessness seems to have stuck around in this area: About a quarter of the plants lack the distinctive feature.

A single gene

The team plumbed the plant's genome to find the source of the unusual morphology. They considered a gene, *APETALA3-3*, known to affect spur development. They found that this single gene controlled the entire development of the flower's spurs and nectaries.

"The gene is either on or off, so it's about as simple of a change you can get," said lead author Zachary Cabin. "But that simple difference causes a radical change in morphology."



A single broken gene causes mutant plants to develop flowers with no petals or nectar spurs.

Photo Credit: ZACHARY CABIN

If these flowers were preserved in the fossil record, scientist could well sort them into two wholly different genera. And there would also be a puzzling gap: no intermediate form documenting a transition from one morphology to the other.

“This finding shows that evolution can occur in a big jump if the right kind of gene is involved,” Hodges said. *APETALA3-3* tells the developing organ to become a petal. “When it’s broken, those instructions aren’t there anymore, and that causes it to develop into a completely different organ, a sepal,” he explained.

APETALA3-3 is a type of homeotic gene, one that specifies the development of an entire organ. A mutation in one of these genes can have a drastic effect on an organism’s morphology. For instance, one homeotic mutation causes a fly to develop legs where it should have antennae. “Most of the mutations of this nature are going to be like that, just awful,” Hodges continued. “The animal won’t have any chance of surviving. Biologist Richard Goldschmidt called them ‘hopeless monsters.’”

But once in a very long while, one of these radical changes might provide a beneficial trait in a particular environment, creating a “hopeful monster.” And a hopeful monster would show that evolution can proceed in single, large jumps, supporting the punctuated equilibrium hypothesis.

“We did not have a good example of a hopeful monster due to a single genetic change,” said Hodges, “until now.” Researchers have to catch these abrupt changes as they’re happening, otherwise they disappear into an organism’s genome. For example, other relatives of columbines have lost their petals and nectaries in the past, but it’s now impossible to tell if these events occurred in one fell swoop. The fact that it is actively happening in the Colorado blue columbine enabled the team to confirm their status as a hopeful monster.

“There’s definitely some luck involved with us being around at the right time to capture this,” Cabin said.

Surprising selection

Catching the change in action offers another benefit as well: the opportunity to study the genetics and selective pressures at work.

The team discovered five versions, or alleles, of *APETALA3-3*, only one of which codes for a petal with a functional nectar spur. The other four were broken, as Hodges put it. They also determined that spurlessness is a recessive trait. The flower will develop normally as long as the plant has one copy of the functional allele. But any two of the mutant alleles together will prevent this. “You can mix and match them,” Cabin explained.



About a quarter of Colorado blue columbines in this area display the recessive trait of spurlesness, more than can be attributed to mere chance.

Photo Credit: SCOTT HODGES

Across all species of columbines it’s possible to find rare individuals that develop flowers without nectar spurs. But with a quarter of the Colorado population missing the feature, Cabin and Hodges knew this was more than a chance occurrence. “To get that many of this mutant type really suggests that there’s selection favoring it somehow,” Hodges said, which he finds odd, since the spur produces nectar that attracts the plant’s pollinators.

Hodges is deeply familiar with columbines, and all of his previous research suggests that nectar spurs are important to the group. Even slight changes to the structure have driven speciation and diversification in the genus. “So, how the heck can you lose your spurs and still be favored?” he asked.

Attracting pollinators is only one factor contributing to reproductive success. It turned out the mutant plants actually produced more seeds than their counterparts, much to the team’s surprise. They began combing through their observations, searching for an explanation.

“The first time we really realized the pattern was at the airport on the way home,” Cabin recalled. He was reading off data as Hodges entered it into the computer. “Scott could see the pattern developing, because he had all the data in front of him, and was getting more and more excited.”



A caterpillar chows down on a wild-type columbine.

Photo Credit: SCOTT HODGES

The team had recorded herbivory from caterpillars, aphids and deer on the different morphs. Damage from caterpillars and aphids can hamper seed production, Cabin explained, while deer can devastate an entire plant. And as the data built up, a clear trend emerged: Deer and aphids preferred flowers with nectar spurs.

Shifts in floral morphology are usually driven by pollinators, but spurlessness seems to be driven by herbivory. “Natural selection can come from very surprising

sources," Hodges said. "It's not always what you'd expect it to be."

Timing it right

Now that they've identified their hopeful monster, Cabin and Hodges plan to investigate the DNA around *APETALA3-3* to build a timeline of when the mutations may have occurred. When the gene first mutated, only one of the plant's chromosomes was affected. That means that every descendant with that mutation would have the same genetic code around *APETALA3-3* for many generations, Hodges explained.

However, chromosomes do swap alleles occasionally in a process called recombination. By tracking the amount of recombination that has accumulated around the different versions of *APETALA3-3*, the scientists can estimate how long ago each mutation occurred. More variation requires more time to accumulate. And the closer this variation is to *APETALA3-3* itself, the more recombination events there have been since a mutation first appeared.

The researchers also want to track how spurlessness is spreading through the population. The different morphs do interbreed, but genetic evidence suggests that there's less mating between the two groups. The Colorado blue columbine may be diverging into separate species, especially since the two types seem to rely on different pollinators. "That splitting process would be slow," Cabin said, "but there is evidence that it could be on its way."

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