On the Many Origins of Species

Researchers thought it took mighty barriers like mountains to make new species. Now they are learning that the process can rest on something as slight as a taste for a new fruit

The making of a new species is one of evolution's most heralded feats, and scientific understanding of the process has itself been evolving at a rapid pace. Many advances were showcased this spring at a conference, "Endless Forms: Species and Speciation," held 19 to 23 May in Asilomar, California; some are presented in this Special News Report. New species that form without the benefit of geographic isolation are the topic of our first story, accompanied by a piece exploring a mysterious case of biogeographic species-making. Our second story details the many mechanisms, from third-party intervention to slight changes in a sperm surface protein, that add new plants and creatures to the planet.

Guy Bush's scientific debut was not an auspicious one. In 1966, Bush was a newly minted Ph.D. biologist from Harvard University, nervously presenting his first paper at a scientific meeting. He had reason to be anxious. His data pointed to a controversial finding—that a new species of fruit fly was forming in trees right beside its parent population, a process called sympatric speciation. The conventional view was that such things don't happen: New species form only after two populations are separated by a physical barrier. And after moments of dead silence from the audience, the famed geneticist Theodosius Dobzhansky spoke: "That's very interesting, but I don't believe it. Sympatric speciation is like the measles. Everybody gets it, but they all get over it."

Today, 30 years later, Bush is still infected. Now a professor at Michigan State University, he quips: "I've had this rash that's never gone away." And it has turned out to be catching. By applying new biochemical and molecular tools to their fruit fly, the apple maggot *Rhagoletis pomonella*, Bush and his students have convinced a lot of scientists that the choice of a new host plant can separate populations just as a mountain or a river can. "I'm delighted to say that I think they've developed a convincing case," says Douglas Futuyma, an evolutionary biologist at the State University of New York, Stony Brook. Evolutionary ecologist Dolph Schluter of the University of British Columbia, who has spent years arguing with Bush, now sees signs of sympatry even among the stickleback fish he studies. "I felt a bit like the president of the flat-Earth society when shown the first photograph of a round Earth from space," he says.

The case for sympatry is now so strong, says John Endler, an evolutionary biologist at the University of California, Santa Barbara, that the debate is less over whether sympatric speciation can take place than over how

Amazonian Diversity: A River Doesn't Run Through It

For explorers of the Amazon River basin, no feature stands out more than the winding, intricate river systems. Biologists, too, have been impressed by the Amazon and its tributaries, viewing them as barriers that created a great diversity of plants and animals. As rivers changed courses, they would have cut populations into two, creating new groups that followed separate evolutionary paths. But rivers may not run throughout Amazonian diversity. Instead, the engine behind much animal speciation may be ancient ridges now lying buried and nearly invisible.

Hidden barriers. Now nearly invisible, ridges *(purple)* segmented the Amazonian basin millions of years ago and may have divided the spiny tree rat into different species.

James L. Patton, an evolutionary biologist at the University of California, Berkeley, reported at the speciation meeting that he has found a surprising correlation between the 3-million-year-old history of one hidden ridge and genetic differences among the small mammals he studies. Richard Harrison, an evolutionary biologist at Cornell University, notes that the work offers an unusually clear view of this process, known as allopatric speciation, in which the geographic barriers responsible for it are often difficult to pinpoint. "Patton's is a classical and elegant example," he says. "It's giving us a window on an evolutionary event we had no idea of."

Patton and his Brazilian colleagues from the Instituto Nacional de Pesquisas da Amazonia originally set out to verify the river hypothesis, which hasn't been seriously challenged since it originated with Alfred Russell Wallace, the noted 19th century evolutionist. Wallace had observed that the geographic ranges of the basin's many primate species coincided with boundaries set by its rivers: the Amazon, Negro, and Madeira. The idea is especially appealing as an explanation for the region's diversity, notes Patton, for these rivers are not only among the largest in the world but the most dynamic. "It's easy to imagine that they would influence speciation," says Patton, because they are prone to flooding and changing course, severing a single population.

Patton and his team collected gene samples from 52 species of mammals, including tamarins, rodents, and marsupials, from both banks of the 1000-kilometer Río Juruá, a tributary of the Amazon in western Brazil. The researchers examined the anioften and under what conditions. The noted Harvard biologist Ernst Mayr, the most influential skeptic of the notion, now says sympatry could be real but is an "unimportant" process in nature, responsible for only a small number of new species when compared to the geographic process, known as allopatry (see box). But others such as Bush argue that sympatry could have helped create the diverse array of plant-feeding insects and freshwater fish that exists today.

Proposals without proof

Although most biologists have only recently changed their minds about sympatric speciation, Charles Darwin thought it was possible back in the 1850s, and said so in a manuscript for his book *Natural Selection* (published after his death). "I do not doubt that over the world far more species have been produced in continuous than in isolated areas," he wrote. But he did not spell out the details.

Others stepped in to try to solve the mystery. One was Benjamin Walsh, a minister and avid insect collector who eventually became state entomologist for Illinois. Walsh was the first to be inspired by the apple maggot *Rhagoletis*, a native American species whose natural host is the hawthorn tree. A local newspaper recorded that by 1862, some of the flies had lighted on apple trees in an orchard in the Hudson River valley of New York and acquired a taste for the fruit, which had been introduced from Europe, ignoring the small, red fruit of the hawthorn. Walsh proposed in 1864 that when the two groups of fruit flies had started eating and laying their eggs on different host plants, the sister populations effectively isolated themselves from each other enough to become separate species—a process that eventually became known as sympatry (from the Greek *sun* for together and *patra* for fatherland).


G. BUSH AND J. JENKINS

A little difference. Related hawthorn maggots *(left)* and apple maggots *(right)* live side by side, but fruit and mating preferences keep the two populations separate.

It was a provocative proposal, but one without proof. There was no firm evidence that the two groups of fruit flies were separate species: They looked and acted alike, and could well have been interbreeding. And there was no mechanism to explain how adapting to different plants would prevent the two populations from interbreeding. So the notion of sympatry rattled around until 1947. In that year, Mayr took it on and showed that none of the cases for sympatry proposed by Darwin or others was supported by evidence. Meanwhile, the argument for allopatry as the main mode of speciation was getting stronger. Case after case—ranging from Darwin's finches in the Galápagos Islands to beetles in North Africa—showed that new species formed when two populations were cut off from one another by the sea, a mountain range, or other physical barrier. By the early 1960s, influential scientists such as Mayr thought sympatry was an unimportant process. "One would think that it should no longer be necessary to devote much time to this topic …" he wrote

mals' mitochondrial DNA (mtDNA) to identify genetically distinct groups. Because mtDNA is inherited only from the mother, is not scrambled by sexual recombination, and appears to mutate at a regular rate, differences in the mtDNA of two related groups can also serve as a "molecular clock" to date their separation.

For the tamarins, Wallace's river theory appears to have been on target. At the Juruá's mouth and widest points, where the barriers to interbreeding should be greatest, there are two distinct subspecies of saddle-back tamarins. At the Juruá's narrow headwaters, however, the two interbreed. "It's exactly what the riverine barrier predicts," says Patton.

But the rodents and marsupials presented a surprise. Instead of diverging across the river, as do the tamarins at the river mouth, these smaller animals were separated genetically into upriver and downriver lineages. "Eleven of the 17 species we sampled show this kind of divergence," says Patton. And while current taxonomy lumps upriver and downriver groups into single species, Patton says the genetic differences between these populations are so strong—some of their mtDNA differs by 13%—that they indeed may be separate species, although morphologically the animals cannot be told apart.

What is really striking, he says, is that all 11 are separated at almost the same geographical point on the river, although there is nothing remarkable about the spot—no bend, no hill, no valley. "When I saw that repeated pattern, I thought, 'Wow! What is going on here?' " Patton recalls. Because the pattern applied to species with a wide range of lifestyles—from treetop specialists such as the spiny tree rat to ground-dwellers such as the spiny mouse—Patton was certain that some exterior force was at play. "When various species have the same pattern of geographic distribution, it's unlikely that it's due to their biology," he says.

Only recently has Patton come up with a possible explanation. While acknowledging that the geological history of the Amazon basin is poorly understood, Patton has uncovered some tantalizing correlations between geologic events and the evolutionary history of the small mammals. Today, the Amazon basin appears to be a relatively flat landscape. But according to a study of its tectonic history (*Science*, 4 December 1987, p. 1398), the basin is actually composed of several subbasins, separated by ancient ridges or arches that were formed when the Andes were uplifted 2 million to 5 million years ago. "One of these," called the Iquitos arch, "cuts perpendicularly across the middle section of the Juruá," says Patton—precisely at the point where the small mammals apparently break into distinctive genetic groups. It matches up in time as well as geography: The mtDNA analysis suggests that the species diverged between 1 million and 3 million years ago.

Patton speculates that the uplift of the arch separated the small mammal populations about 3 million years ago. Those divided populations began accumulating distinctive genetic changes. Later, as the Andes began to erode, the Amazonian subbasins filled in, forming today's vast, flat basin. No longer divided, the mammals have come into contact again, although Patton is not sure if they are interbreeding: "That question will have to wait for nuclear DNA data."

There are similar ancient—and hidden—arches throughout the Amazon basin. Have they influenced the speciation of the small mammals in these regions? If so, says Patton, "they ought to have affected every other organism as well." To answer that question, Patton's team is heading back to the field this summer, to collect the small mammals along another tributary of the Amazon, on both sides of another hidden arch. –**Virginia Morell**