HOW A WILD PIG MAY UPROOT THE TREE OF LIFE

GREG CRITSER

Who knows of every tryst in the depths of the wood? Who can number the illegitimate pleasures shared by creatures of separate species?

— Buffon, 1770

IN 1994, paleontologist Stephen Jay Gould — arguably the most celebrated postwar thinker in his field — attended a conference on evolution. It was a familiar arena for Gould. Since the early 1970s, he'd been articulating and, alternately, defending his seminal work on what he termed "punctuated equilibrium." Gould had succeeded in convincing many scientists, especially other paleontologists, that the fossil record simply did not support the scientific consensus about evolution — the belief that the process by which a new type of organism typically arises is a slow accumulation of minor changes over time. The fossils don't show that, Gould said, because there are no "transitional forms." That is, from looking at fossils, it seems that organisms come into being abruptly, via "punctuation." And thereafter, the typical fossil organism does not gradually change, he said, it simply exists in the same form until it becomes extinct. He dubbed this lack of change "equilibrium" or "stasis."

Many of his fellows saw this as a kind of scientific creationism. The mere use of the term "transitional forms" was a red flag in conversations about evolution and creationism.

Punctuated equilibrium troubled many biologists because it neutered natural selection. If the typical fossil form changed in no way whatsoever, it certainly wasn't going to change under the influence of natural selection.

But punctuated equilibrium was an observation about fossils *over time*. Gould said little about how such a process might actually work. It is a question that has stuck in the craw of establishment scholars; try as they might, they have yet to entirely reckon his work — his observed fact — with their own ideas of how evolution occurs.

The situation might be called intellectual stasis.

Still, rogue ideas sometimes break through. During coffee at that 1994 conference, Gould bumped into a tousle-haired genetics graduate student named Eugene McCarthy. McCarthy told Gould he agreed with his basic observations, but he wanted to talk about mechanisms that might account for them. "I remember asking him, you know, well, how does it work, what is the mechanism?" McCarthy says. "He looked at me and said, 'I don't know. I am just presenting a known fact, an observed fact. Someone else will have to find out how it works.""

McCarthy had long pondered a hypothetical answer to that question, what he called "stabilization processes." Under that heading he lumped a variety of well-known genetic mechanisms (many of which involve hybridization) that rapidly produce new stable forms of life. For example, polyploidization, a process that creates offspring that have one or more extra sets of chromosomes than their parents do. The change takes a single generation and can alter many traits that remain stable in subsequent generations. As McCarthy saw it, such mechanisms could account for Gould's punctuation and stasis.

In the theory McCarthy constructed on the basis of these processes, "natural selection" is not the same thing that Darwin described. In the traditional view of evolution, there is competition among individuals in which those who leave more offspring pass on more of their genes, and thus prevail. In McCarthy's world, natural selection involves competition not between individuals but between "forms." In other words, some stable forms of life persist longer than others and give rise to more offspring forms. As a result, their traits spread to more progeny forms than do those forms of life that have fewer offspring.

This formulation of natural selection in terms of forms means that different forms of life can be successful in different ways, because under stabilization theory it makes no difference whether *individuals* compete or cooperate. You can have successful forms in which individuals compete, like sharks, or you can have successful forms in which individuals cooperate, like bees. Thus, where mainstream biologists see evolution as "red in tooth and claw," McCarthy sees it as a process where unselfishness and cooperation can often make evolutionary sense. Things mate that shouldn't mate. Forms thrive until they're spent, and then they're *gone*. McCarthy's is an ancient realm of free love, partying in happy stasis until the extinction police arrive.

McCarthy is an expert on bird hybrids, having written an exhaustive reference work on the subject for Oxford University Press. He has been working for years on a similar book about mammalian hybrids and has investigated the possible hybrid origins of human beings. He has even proposed exactly what kind of beastly lovers might long ago have mated to produce *Homo sapiens*: a primate resembling a bonobo and an ancestor of the ordinary pig.

As one might expect, discussing McCarthy's pig-primate hypothesis in the scrum of modern media can be awkward. In the summer of 2013, when reporters first discovered his website and began writing about the idea, some rated him as irresponsible, uninformed, naive, and even just this side of mad. Jimmy Kimmel had his predictable fun with it all — a mocked-up video clip of a McCarthy-like figure lecturing on the subject and using a stuffed toy pig and chimpanzee to demonstrate how the two would "do it."

McCarthy was dismayed, but not really surprised, by some of the vicious personal attacks from certain fellow scientists. "I thought that *challenge* was the whole purpose of proposing a new theory, a new hypothesis," he says. But the blowback hasn't really fazed him: "Everywhere I look now, I see pig. And if you listen to me too much, it will happen to you too."

McCarthy's home turf is the city of Athens, Georgia — green on the banks of the Oconee River. It is a place that conjures two American idylls. One, the New Athens, looks pretty 21st century: suburbs, foodies, mixologists, tattooed and indecently clad coeds (on a hot day), the University of Georgia and its

huge genetics department and a place down the hill that serves "some awesome tacos!" Three years ago some 4,000 denizens of this New Athens wrote in Charles Darwin for a congressional race.

Closer in, and underneath everything, percolates the Old Athens: unapologetically expansive front lawns, cigarettes, statues to fallen Confederates, beer joints that serve just beer, an easygoing daily newspaper to read on an easygoing afternoon. In the same congressional race, the citizens of Old Athens reelected Tea Party-favorite Paul Broun, famed for his flaming antiscience vitriol: "All that stuff I was taught about evolution and embryology and the big bang theory, all that is lies straight from the pit of hell."

McCarthy has spent most of his life studying those "lies." He earned his PhD in evolutionary genetics in 2003 from the University of Georgia, but his thinking about evolution began some 20 years before, when he was running a small construction company in Athens. In fact, as he tells it, he'd first read Darwin when he was 15, at his bibliophile grandmother's knee.

McCarthy came back to Darwin in his 20s. Reading Chapter 8 of On the Origin of Species — "On Hybridism" — changed everything:

It gave a lot of examples of fertile hybrids — and that struck me. Until then I was under the belief that all hybrids were sterile, like the mule. But Darwin was really saying fertility was not an on-or-off proposition. The hybrids produced from one type of cross can be much more fertile or viable than those from another.

McCarthy pauses, then gives in to a bit of understandable intellectual afterburn: "I can guess that either most scientists have read that and dismissed it, or they haven't really read Darwin at all."

McCarthy kept reading and thinking about hybrids. If hybrids from some crosses were fertile, couldn't new forms of life be produced in that way? If so, what about *Homo sapiens*? Ever since grammar school, when he first read about the discovery of Lascaux Cave, McCarthy had been interested in the question of human origins. Now, Darwin's chapter put that subject in a different light. Could we be hybrids? If so, who were our parents?

McCarthy learned about a method biologists commonly use to identify putative hybrids of unknown origin. So he decided to apply it to humans. Investigators first look for an organism that shares many traits with the suspected hybrid, and then pose it as one probable parent. (In the case of humans that would be the chimpanzee.) They then make a list of all the traits in the proposed hybrid that don't appear in that first parent. The animal with the greatest number of those traits would be the likely second parent.

"I wanted to find that other parent, to know what happened long ago out there in the forest," McCarthy says. He was looking for one of Buffon's hypothetical trysts, but a special one, the long lost dalliance that, among all the "illegitimate pleasures shared by creatures of separate species," led to the production of the human race.

McCarthy searched the literature to find all the traits that distinguished humans from chimps and bonobos. In the end he was able to find about 100, most of which experts said distinguished us not only from apes but also from all other primates. These traits, he discovered, are consistently found in pigs. Among the most compelling is the human kidney, which is of a type ("multipyramidal with a beanshaped cortex") that occurs in no other known animal except the pig. Other traits we share with pigs — our bare skin, our thick layer of subcutaneous fat, the aberrant design of our skin's circulatory system

are not found in other primates, including our light-colored eyes and our protrusive rubbery nose.
Many of our piglike features, then, are externally visible. As McCarthy puts it, "Through my eyes,

humans are pretty much just chimps in a pig skin."

But still — and McCarthy readily admits this — we have many more traits in common with chimpanzees than we do with pigs. So how does he reconcile this fact with the idea that we're pig-chimp hybrids? By assuming that we are the products of *repeated backcrossing* to chimpanzee.

Backcrossing falls under the heading of the various mechanisms that McCarthy dubs stabilization processes. It rapidly — in terms of geological time, instantaneously — produces a new type of organism (Gould's punctuation) with descendants that are stable in subsequent generations (Gould's stasis).

What is backcrossing? When you cross two parents and get a hybrid, that hybrid — if it's fertile — can mate either with another hybrid or with individuals of either of the two parental types. For example, a liger is produced when a tiger mates with a lion. The liger can be mated back ("backcrossed") to, say, a lion. Genetically, the resulting backcross hybrid would be only 1/4 tiger. If that backcross hybrid then backcrossed again to a lion, the result would be a hybrid that was only 1/8 tiger, and so forth. In such a scenario, one would soon only expect a few tiger traits to remain within an overall lion background.

In the same way, McCarthy says, with an initial cross between a pig and a chimp-like animal, with several generations of backcrossing to chimp, you could end up with a backcross hybrid that is mostly chimpanzee but with a significant percentage of piglike traits. Such are humans, he suspects.

The tryst that would permit this crossover of traits, McCarthy says, would likely require a pig father and a chimp mother. There are various facts that point to this conclusion, but mainly it's the fact that mammalian and avian hybrids produced in an initial cross are generally much more likely to backcross to the mother's "side of the family."

As McCarthy tells it, one moment brought the whole thesis together. It happened one day while he was reading a book about swine anatomy in the stacks of the science library at the University of Georgia. He came across a picture of pig vocal cords. Apes, he already knew, do not have cords. (They have a ridge made of cartilage.) The book in front of him showed that not only do pigs have vocal cords, but also that they have them in the *same form as humans*. "When I saw that, a chill ran up my spine," he says. "It was a watershed event for me. From then on, it was hard for me not to see pig shining through the chimp in human beings."

The idea that new types of organisms arise abruptly and then remain the same thereafter — then known as saltation — reigned before Darwin. Saltation let the era's freethinkers get away with heresy; it was a way to make divine origins politically compatible with the era's new scientific speculation about human origins. God starts things, God ends things. Yet even after Darwin's later intellectual triumphs, saltation remained a vivid scientific argument — one to which even the great 20th-century geneticist T. H. Morgan hewed before his work with mutating fruit fly genes sent him back to Darwin and natural selection.

But later on in the 20th century, evolutionary thinking grew increasingly monochromatic. In the 1930s, what became known as the Modern Synthesis congealed into a powerful scientific narrative. Among its central tenets was the concept of reproductive isolation: that new species can only be formed and maintained if they create a *barrier* to hybridization. Introducing the notion of successful fertile hybrids — the kind McCarthy proposes — into that theory is to throw a bomb into the establishment formula. It was not at all, McCarthy says, a welcome idea.

Modern Synthesis eventually became the standard against which all other theories of human

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evolution competed. In the 1940s, such thinkers as Julian Huxley — the grandson of Thomas Huxley, one of Darwin's greatest defenders — and Theodosius Dobzhansky — the brilliant Ukrainian fruit fly geneticist — rendered the Synthesis into an even more compelling, if inflexible, doctrine. Social anxieties figured heavily, in McCarthy's view. Periodic waves of creationism — and the need to respond to it — forged what he sees as a kind of religion of its own, science's default rejoinder to the nuts.

Inside the academy, the Synthesis forged a prickly and closed discipline. Important careers were built on it, true, but there were also epic lost opportunities. The Nobel Laureate Barbara McClintock, who in the 1940s discovered the so-called jumping genes — transposons — now familiar to any college biology major, was ostracized for so long that, as she later noted, "I just stopped publishing in 1953." (She began again in the 1980s.) Though his punctuated equilibrium was widely embraced by his fellow paleontologists, Gould drew fire from geneticists, who continued to hew to the Synthesis. And proponents of epigenetics — the study of heritable trait changes *not* brought about by changes in DNA — were long marginalized despite growing evidence, because their claims didn't fit with accepted theory — for example their suggestions that acquired traits can be inherited. Now epigenetics is a driving force in mainstream genetics, and an ATM for NIH funding.

The Modern Synthesis ran particularly deep in the burgeoning genetics department of the University of Georgia. One of McCarthy's advisors, Wyatt Anderson, a National Academy member, came right out of the Dobzhansky lab. McCarthy spent a few years in Anderson's lab during the early'90s, a period during which Anderson served as dean of the University of Georgia's College of Arts and Sciences.

"Wyatt was very conservative in his approach to science," says McCarthy. As such, he seemed to have little interest in hybridization. "But he respected me as a scholar, which I think is the reason he generously offered me a place in his lab, despite his apprehensive attitude toward my work."

The fact that McCarthy wasn't directly working on Anderson's projects meant that he had to earn his keep teaching biology and genetics, and as the departmental computer consultant. (He'd been an undergraduate math major.) Because he helped them with numbers, most people in the department put up with McCarthy's off-the-grid ideas about hybrids.

There were so many questions to be answered! How common was hybridization in a natural setting? How many crosses produced fertile hybrids? How many different kinds of stabilization processes were there? It began to look as if genetics *could* explain Gould's observed fact.

For centuries it has been widely believed, even by many scientists, that hybridization between animals occurs only in captivity — zoo animals penned together and forced to mate, birds trapped in a cage without access to a mate of their own kind. But the idea that hybrids needed humans to help the process along did not square with McCarthy's encyclopedic knowledge of bird hybrids — he'd documented more than 4,000 different types of crosses, about half occurring in a natural setting. And they were overwhelmingly fertile: for every avian cross that produced sterile hybrids, he'd found seven where the hybrids had managed to have offspring. He began researching a new list — compiling the thousands of available reports about hybrid mammals. And, as it turned out, fecund hybrids seemed to be about as common among mammals as they had been among birds. "I kind of saw myself as a journalist — I simply wanted to report as many detailed cases as I could find, and then let the reader decide."

McCarthy's pig-chimp thesis pushes hybridization one problematic step further. After all, he's not

proposing a mating between two closely related species; he's talking about matings between two very distinct types of organisms. Conventional wisdom has long held that such distant crosses are impossible. "That's the most important issue for Gene's pig-chimp thing," says David Geiser, who was a graduate student in the genetics department at UGA with McCarthy. "The distance between the pig and the chimp is huge."

But "distance" may not be the impregnable barrier it's said to be. Two of the most commonly cited barriers of this type are the differences in the parents' chromosome counts and the lengths of their gestation periods. According to the 20th century's foremost authority on mammalian hybrids, Annie P. Gray, there is "no close correlation [...] between the chromosome count or the duration of gestation and the ability of species to hybridize."

After all, what does distance really mean? McCarthy points out that it is well established that chickens and turkeys can hybridize. And yet, most people would agree that they are very "distinct" types of animals.

"After looking at so many different crosses," he says,

the evidence on hybridization taken as a whole suggests there is some sort of unrecognized mechanism that allows a small percentage of hybrids from some of these distant crosses to develop and mature. The result is the production of occasional very rare hybrids that are very weird.

On his website, McCarthy quotes reports about a wide variety of bizarre hybrids, including dog \times cow, chicken \times duck, and even rabbit \times pigeon. When asked whether he took such reports seriously, he replies,

I neither believe them nor disbelieve them. I simply report that they exist and quote them. In fact, I don't think belief has any place in science. Belief is the stuff of religion. Within a scientific context, I make every effort never to believe *anything* that I don't absolutely have to believe.

There are animals that give even mainstream biologists pause. The platypus, Ornithorhynchus anatinus, has the bill of a duck, but the rest of its body, except for its webbed feet, is like a beaver's. It spends most of its time in the water and is one of the very few egg-laying mammals. When 18th-century explorers sent home a sketch and a pelt of the beast, many regarded it as an elaborate hoax by some bonkers taxidermist. Even after researchers documented its existence, no one could quite agree what it was: Mammal? Bird? Reptile? Modern genomics vexed the subject even more. The platypus has 10 sex chromosomes — some like those of mammals, some like those birds. In 2008, *Nature* published a draft of the animal's genome, revealing the presence of two genes that previously were observed only in birds, amphibians, and fish — but not in mammals.

Such findings do not — or should not — go entirely against expectation, McCarthy wrote me in one of his precise yet playful emails. "After all, it's not as if a mammal spermatozoon that suddenly found itself in the cloaca of a bird would clasp its blushing cheeks and cry, 'Oh my ears and whiskers! I should *not* be here! *Whatever* shall I do?"

McCarthy's ideas made him a target, and it was not just an intellectual debate. "It was a source of

mocking in the department — and often by not the most well-read people," says Geiser, now a professor of plant pathology at Penn State. "It was personal. Gene was hurt."

It did not help that McCarthy, despite his gentle demeanor — he doesn't use the "f-word" — could also breathe fire on the subject of careerism. "He was the so-called 'kook," says Susanne Warrenfeltz, a friend who was in the department at the time and who is now a research scientist at UGA. "He was always talking about pure science versus career science." In the realm of today's professionalized science, it did not endear.

The real problem was his sidelining of Darwin. "One thing evolutionists really, *really* want to believe in is Darwin," says Warrenfeltz. "They are so glad that they beat out God as the creator! So when Gene started talking about hybrids — even as the data grew — they did not want to hear it. It bothered them."

In 2006, McCarthy left the department, he says, "because I was tired of working for weenie PIs [principal investigators]." Like so many who get *pushed* out of a career, he wrote a novel — *The Department* — in which he let the bile flow, with recognizable portrayals of the tyrannical and immoral "weenies" he had to endure.

McCarthy didn't leave university life before gaining some converts. While at UGA, he spent several years in the lab of genetics professor John McDonald, now associate dean for biology at Georgia Tech. McDonald was sympathetic if not to the pig-chimp thesis itself then to his bigger ideas. He eventually gave McCarthy a research position. "He was a great researcher, and very enterprising with new ideas that you could actually test," says McDonald of McCarthy. "And you can imagine how that rubbed some people. Gene is simply insisting that the role of traditional speciation in human evolution be tested. He liked to push the limits. I like that. Others really don't.

"And I have to admit it, the more he talked about the pig-chimp thesis, the harder it was for me to look in the mirror and not see pig."

Growing up in Augusta, Georgia, a river town on the South Carolina border, McCarthy spent many of his childhood evenings talking with his invalid grandmother. A longtime participant in the Great Books Foundation discussion groups, she had him sit and read aloud to her many of her favorites, things a teenager would otherwise be unlikely to encounter, including Plutarch, Locke, most of Shakespeare — and Darwin.

As he got older, he rebelled. There was discord at home, according to his friend and UGA colleague Stuart Katz: "His father kicked him out of the house." McCarthy, who was 16 at the time, left high school and took off hitchhiking across the US, doing manual labor, often camping out, and even spending some nights under bridges.

But something happened out there in the forest. When McCarthy came back from his adventures, he was — as all parents of rebel children hope they become — "motivated." He had discovered something — strength, perhaps some toughness. Now 20, he headed back to school, got his BS in math and a Phi Beta Kappa key, and eventually entered graduate school. He came across as resourceful, independent. The independence came with an edge. "If he thinks you are not telling the truth," says Katz, "he's pretty much done with you." Not exactly a trait for professional success. McCarthy and his ideas were largely ignored.

But what the old world of science and scientific publishing cannot countenance, the new world of electronic media and scientific entrepreneurism can — and does. In 2008, he says, after Oxford

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backpedaled on their offer to publish a tome presenting his alternative theory of evolution (it was under contract for nearly a year), McCarthy decided to publish it on his website, *Macroevolution.net*, rather than go through another protracted submission process. He got buy-in from advertisers and, according to McCarthy, many supporters.

These days he's spending a lot of time using a new computer program that he created to look for traces of pig genes in the human genome. He calls it BoomStick, after the nickname for a sawed-off shotgun. It takes at random millions of short pieces of the pig genome (the "pellets" of the shotgun blast) and finds their matches, if any, in the target human genome. The result is a picture of each chromosome in the target genome showing where pig matches concentrate. The algorithm is computationally intensive; things are going very slowly, especially since McCarthy doesn't have access to adequate computer facilities. "We've got a long way to go," he says.

The human genome is so vast. And who knows exactly what we're looking for? The problem with backcrossing is that it so dilutes the genetic contribution from the non-backcross parent — which in this case would be that from the pig — that it becomes hard to recognize. So it's like looking for what may or may not be a needle in 400 haystacks.

Today, McCarthy's most influential supporter is John Avise, also a former UGA professor. Now a professor at UC Irvine, Avise is one of the world's leading thinkers on evolutionary genetics, which he's explored through his work on fish, birds, mollusks, rodents, turtles, and a number of other organisms.

Avise is interested in McCarthy's network model of evolution, which pictures evolutionary descent not as a tree of life but as a web — with all of the various types of organisms that stabilization processes produce interconnected by hybridization. Citing McCarthy in his recent book, *In the Light of Evolution*, Avise notes:

If the network model [...] proves to be more nearly correct for many taxonomic groups, then the challenges for [...] evolutionary biology will be entirely different (McCarthy, 2008). First, phylogeneticists would have to admit that their dream of reconstructing a branched tree of life had been merely a pipedream [...]. Traditional concepts of species, phylogeny, ancestry, and classification, as well as the significance of reproductive isolation, would all have to be reevaluated.

Biologists would have to embrace the notion that biological processes falling somewhat outside the standard neo-Darwinian paradigm [...] could play major and previously underappreciated roles in evolution. They would have to reevaluate the origins of genetic variation.

"I see Gene as potentially an outstanding scientific entrepreneur," Avise says. "He's got the tools he's dogged, independent, and a very good writer.

"He just hasn't sold himself." A