

The Early “Evolution” of “Punctuated Equilibria”

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Schermerhorn Hall on the Columbia University campus was the scene of a number of important scientific developments in the twentieth century. For one thing, early on in the century, it had housed the famous “fly room” in the lab space of the Zoology Department on the ninth floor—where Thomas Hunt Morgan, his colleagues, and students essentially invented the modern science of genetics. There, they mapped the bands on the giant chromosomes of the salivary glands of fruit flies—showing that genes occur in specific places on chromosomes. And, for a while at least, those labs were home to Theodosius Dobzhansky, a Russian expatriate, and arguably the most important evolutionary biologist of the twentieth century. Columbia University Press published Dobzhansky’s book *Genetics and the Origin of Species* in 1937.

The lower floors of Schermerhorn Hall housed the Geology Department. Indeed, over the main door was etched the Biblical injunction “Speak to the Earth and It Shall Teach Thee.” And speak to it the Columbia geologists did—and the Earth spoke back, revealing some of its most profound secrets. I was there as an undergraduate, and then graduate, student in the 1960s—just when Marshall Kay and his fellow geologists were involved in developing the early stages of Plate Tectonics Theory. They were beginning to see that the earth’s

crust was not stable: the continents and ocean basins change over time. The Earth, too, evolves.

Riding the Schermerhorn Hall elevator 1 day from the subterranean geological depths up to the zoology aerie on the ninth floor, a fellow graduate student in paleontology asked me what the book was that I was holding. It was *Systematics and the Origin of Species*—a Dover reprint edition of a book by Ernst Mayr, first published by Columbia University Press in 1942. Mayr, too, was associated with the Columbia Zoology Department—but his main affiliation was with the American Museum of Natural History, where he was a Curator in the Department of Ornithology.

Mayr was a champion of the concept of geographic speciation—or, as he more formally called it, *allopatric* speciation. The core idea is that a period of geographic isolation is a virtual necessity if new species are to arise. Populations of ancestral species become separated—isolated—from the rest of the species; if evolutionary change occurs (whether through natural selection or genetic drift) to the point where interbreeding is no longer possible between the population and the rest of the established species (i.e., should they come back into contact), then “speciation” has occurred. In this view, geography is essential to the origin of new species—and thus to the evolutionary process as a whole.

Although Darwin as a young thinker was well aware of the importance of geography and isolation in evolution, he chose to minimize its significance when he finally published his *On the Origin of Species By Means of Natural Selection* in 1859. There, he wrote “Though I do not doubt that isolation is of considerable importance in the production of new species, on the whole I am inclined to believe that largeness of area is of more importance, more

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especially in the production of species, which will prove capable of enduring for a long period, and of spreading widely.” Darwin, evidently, was intent upon developing a theory that applied to the most cases: although it was simple for him to see the importance of isolation in producing the different species he saw on different islands in an archipelago (the Galapagos, of course, being the prime example), he had a harder time seeing how isolation actually could occur on continents—which hold far more species than do island chains.

Although a handful of evolutionarily minded biologists over the intervening years also insisted on the importance of geographic isolation in evolution, it was not until Dobzhansky and Mayr resurrected and expanded on the idea in the 1930s and 1940s that allopatric speciation became a hot topic—and eventually the conventional view of how new species arise. It remains so today—although just how important a role speciation plays in the evolutionary process is, nowadays, a matter of some dispute.

That elevator ride from geology up to zoology, connecting the two different intellectual worlds, symbolizes the first, most general, answer to the question: What, *exactly*, is “punctuated equilibria?” For I, a graduate student in paleontology, fascinated by biological evolution (although I was registered in the geology department), was in the early stages of the process of connecting geology—specifically my trilobite fossils—with zoology in a novel way: I was beginning to see that the notion of geographic speciation could be applied directly to patterns I was seeing

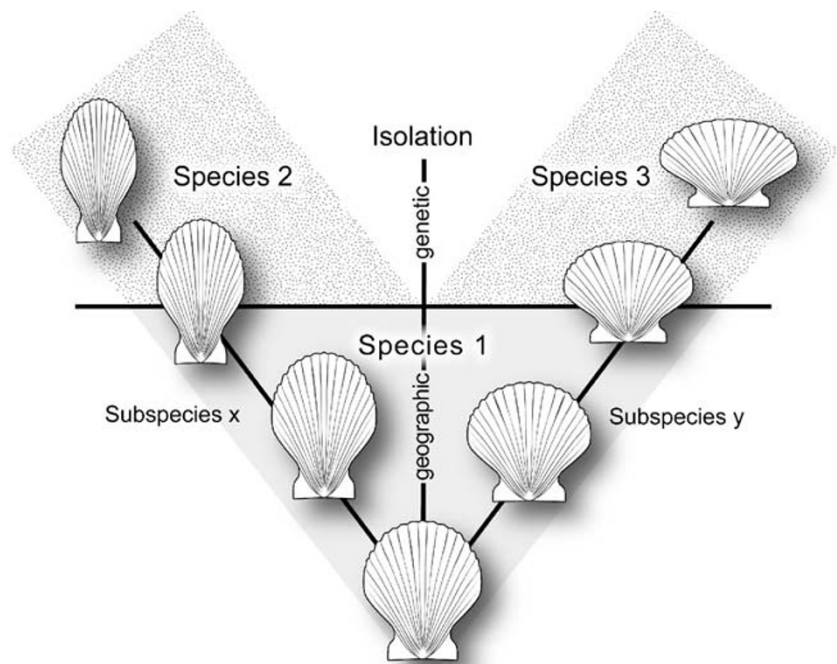
in my trilobites—helping to resolve a puzzle I had stumbled upon in the course of my doctoral research.

The puzzle? My trilobites didn’t seem to be evolving—at least in the slow, steady sort of way that I had been taught to expect to find as I chased my specimens up rock faces and over hundreds of thousands—even millions—of years of time (Fig. 1). This was actually more than a simple puzzle; it was a source of real alarm—as I knew that *positive* results were expected of fledgling scientists. And I was simply not seeing the patterns that everyone predicted should be there. I was beginning to think that the idea of allopatric speciation might provide part of the solution to my problem.

A few years earlier, as I was entering my junior year at Columbia College, seven or eight new graduate students showed up to study paleontology and related fields in the geology department. Two were absolutely crucial to my budding evolutionary and paleontological career. One was Harold B. Rollins, who was to teach me virtually everything I know about how to find, collect, clean up, and study fossils. Bud loved the field and lab—and was also eager to discuss all the theoretical concepts we encountered—ecology and paleoecology, as well as evolution.

The other new graduate student was Stephen Jay Gould. Now *there* was a stimulating thinker. Steve showed me that it was important to start publishing scientific papers right away. He thought it was absurd to think that discussions of theoretical matters should be in the hands of older, more mature scientists when really, if anything, it should be the province of the young, coming to their subjects with fresh

Fig. 1 The standard view of evolutionary change. Using successions of fossil scallops as an example, the diagram shows the division of an ancestral species into separate lineages that are then further transformed gradually into descendant species. This drawing, an oversimplification of Darwin’s own views, was nonetheless the prevailing image of what evolution through time “looks like”—the image I learned in my early training as a paleontologist (Steve Thurston, American Museum of Natural History—“AMNH”)



minds and new insights. Why wait until you are 60?, he used to ask. And of course, he was right.

In those days, all of us geology graduate students had offices in the bowels of Schermerhorn Hall—where we would study every night and, like as not, retire to the local bar for conversation and refreshment before getting up and doing it all over again the next day. However, after the course load was finished and we turned full-time to our doctoral research programs, most of us went to our *other* office, 40 blocks south at the American Museum of Natural History. Although Mayr had already left for Harvard, followed by the third of the great trio of twentieth-century evolutionary biologists—the paleontologist George Gaylord Simpson—the American Museum curatorial staff was still outstanding. Many of them, like paleontologists Bobb Schaeffer, Norman D. Newell, and Roger Batten, were also part-time Columbia faculty members (as I was also to become when I started on staff at the American Museum in 1969). They were important mentors not just to me but to Gould, Rollins, and the other graduate students as well.

I had started out working with Roger Batten on fossil snails, publishing my first paper on an evolutionary problem in 1968. However, I switched to trilobites—extinct arthropods with a complex anatomy whose often well-preserved fossils I felt sure would reveal lots of evolutionary change through time. It was Bud Rollins who introduced me to the trilobite *Phacops rana* (“rana” because its bulging eyes make its head look very frog-like—Fig. 2). He took me up to his old boyhood stomping grounds in the Chenango Valley in upstate New York, near Colgate University (his alma mater)—and there we combed the quarries, roadside ditches, and road and stream outcrops, collecting Middle Devonian fossils—including my new target, *P. rana*—to our hearts’ content.

I was hooked on *Phacops* and was determined to chase as many specimens of *P. rana* and related species wherever they could be found—and through as much of their 6- to 8-

million-year history as possible. In the summers of 1966 and 1967, my wife, Michelle, and my teenaged brother Rick took turns riding with me as we got to know the eastern and midwestern parts of the USA and Canada as few people ever do. Those days, gas was \$0.25/gallon, hamburgers also a quarter—and some fleabag motels cost as little as \$4.00 a night!

Sedimentary rocks, usually teeming with fossils, of the same age as those around Hamilton, NY (the “Middle Devonian,” which began roughly 380 mya), crop out in a band that begins a little west of Albany, NY—stretching as far as the shores of Lake Erie just south of Buffalo—and then popping out again in southwestern Ontario. Present also on both sides of Michigan’s Lower Peninsula, these same fossils can also be found in northwestern Ohio (the justly famous “Silica Shale”) and in eastern Iowa. Most of the localities in the Midwest are in limestone quarries—where rocks are blasted and the fossil-laden rubble hauled off to crushers to be turned into cement—unless rescued first by eager paleontologists.

Middle Devonian rocks also run from the Catskills and Poconos in New York and Pennsylvania southwestward down through the folded Appalachian Mountains of southern Pennsylvania, West Virginia, and Virginia. Most of the Middle Devonian sediments of the Appalachian regions are (just like in the Hamilton region in central New York) shales and sandstones—the hardened remnants of ancient, very muddy bottoms. These sediments were deposited in seaways just west of land that had been thrust up when what is now Europe, Africa, and North America came together as the proto-Atlantic Ocean closed up: as soon as dry land is raised above sea-level, the process of erosion begins immediately—and muds and sands begin to accumulate right away.

Further west, far away from the mountains in the east, the seas were shallow and clear. North America 380 mya lay astride the equator—and, as is usually the case, these ancient tropical seas teemed with life. Most invertebrates—mollusks (clams, snails, ammonite cephalopods), corals, bryozoans, brachiopods, trilobites, even some sponges—have skeletons composed in large part of calcium carbonate (the minerals apatite and calcite)—which are the main constituents of limestone. Most of the lime of those limey sea bottoms came from the broken-up shells of dead invertebrates. Intermingled with those sediments were the whole shells—often gorgeous, often perfectly preserved—of the specimens we were after.

Why were there ancient seas over the middle of the North American continent? Simple: there were no sufficiently large polar icecaps trapping enough water in frozen form to keep the continents from being flooded. In fact, for most of the time over the past half-billion years, the world’s continents have been flooded to some degree by shallow seaways. Think of the dire warnings of the coming effects of global warming—where all the predictions are for extensive

Fig. 2 The “frog trilobite” *Phacops rana*



coastal flooding—first stages of the seas lapping back over our high and dry landscapes as the polar caps ominously begin to melt more rapidly than was first anticipated.

So here I had almost ideal conditions to perform my evolutionary “experiment.” What changes would I find in *Phacops*? Would there be geographic variation—between populations living in the muddy nearshore environments and those that lived in cleaner waters in places like modern-day Ohio and Michigan? And would species appear to keep changing so much that the ones living millions of years after the beginning of the lineage would be almost unrecognizably different from their ancestors?

What does evolution through millions of years actually look like? For although evolution had been an accepted scientific principle at least since Darwin had published the *Origin of Species* in 1859, and although some nineteenth-century paleontologists had made a stab at studying evolution in the remains of fossils they had collected in such places as the Cretaceous chalk cliffs of Dover (not all that far from Darwin’s home Down House), few modern studies had been done—especially with the idea in mind that geographic variation within species is an essential component of the evolutionary process: the lesson learned from Dobzhansky and Mayr writing just a generation before mine.

The only way to find out: get out there and get your hands dirty, visiting as many outcrops and sampling as widely in time and space as possible—and supplementing our own collections with specimens already in collections in museums such as the American Museum of Natural History, the National Museum of Natural History (of the Smithsonian Institution in Washington; Natural History was at that time called the United States National Museum); the Field Museum in Chicago, the Museum of Paleontology of the University of Michigan—and several others. I began to amass hundreds, then thousands, of specimens.

I remember hanging around a laundromat in Alpena, MI, waiting for the clothes to dry. I absent-mindedly pulled out an especially beautiful, complete, rolled-up specimen I had found earlier in the day—and thought, with a sinking heart, that I could not tell it apart from all the other *Phacops* we’d been collecting on the trip—and the trips before! Discouraging—but even then, I realized that it would take detailed cleaning and then examination and measurement of many specimens under the microscope during long winter days and nights back in my office/lab at the American Museum before I was likely to be able to see the differences between these trilobites living in different times and places—before, in other words, I would be able to tell them apart and see what evolutionary changes had occurred over time and space.

However, even then, things were not immediately obvious to me. I measured the lengths and widths of the heads and tails of *Phacops*—including many small anatomical details that were so well preserved in these fossils. The specimens from

each sample recorded a range size—as trilobites, like crabs and shrimp, grow by shedding their exoskeletons, taking on water to expand quickly, then laying down another rigid external skeleton. However, all the plots I made showed that these trilobites grew simply—a single straight line would smoothly connect all the growth stages in any sample. Even worse, all the samples seemed to have the identical statistical line describing their size and shape as they grew.

Then the dam broke: once again, inspiration came from someone else, this time the published papers of paleontologist Euan N.K. Clarkson, who was working on the eyes of some closely related trilobites in Great Britain. Phacopid trilobites, in general, have a special kind of compound eye, where each lens is actually covered by its own translucent layer (“cornea”)—unlike the eyes of crabs and insects, in which the much smaller (and usually more numerous) lenses are crowded together and covered by a single corneal membrane. Clarkson described the hexagonal, honeycombed look of a typical phacopid trilobite eye—pointing out that the lenses are arranged in a series of vertical columns (“dorsoventral files,” to be technical about it).

Why not give it a shot?, I thought. Nearly all my specimens had at least one eye still on the head—and usually just a little scraping with a dental tool was enough to let me see the lenses well enough to count them up. Here is the sort of thing I found (Fig. 3):

345 565 676 565 454 321—starting from the front of the eye, I saw three lenses, then four in the next column, etc. On my data sheets, I would write such a string of numbers down—and then count up the columns—18 in this case—and also the total number of lenses (82 in this example)—writing eventually: 345 565 676 565 454 321 (18, 82).

The smallest specimens in any sample would have, of course, smaller eyes—starting out with, maybe, 14 columns of lenses, then 15, then 16, then 17 and sometimes eventually 18, as I looked at progressively larger specimens in the growth series. But pretty quickly, before the trilobites

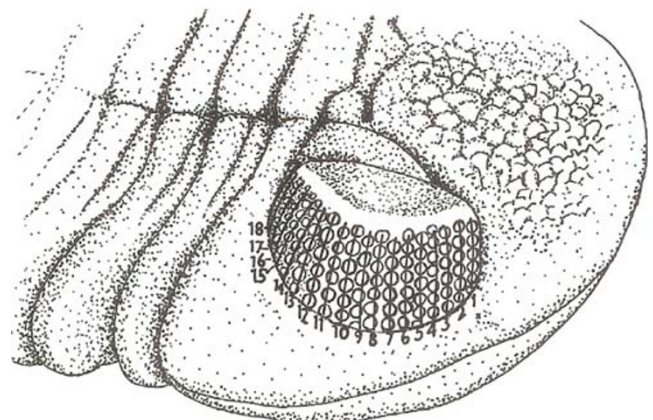


Fig. 3 Sketch of the right eye of a *Phacops* specimen with 18 columns (“dorsoventral files”) of lenses

grew very large at all, they would settle on a final, “adult” number of lenses—stabilizing, no matter how larger they would later grow, at a number: sometimes it was 18, sometimes it was 17 (usually), and at other times, it was 15.

It may not sound like much, but finally here was an anatomical feature that seemed to show some differences between my samples. So I did the next logical thing: I made a series of maps showing time slices through the 6- to 8-million-year period I was sampling. The maps (Fig. 4) showed the location of my samples—and more critically, just where the lands and seas were at any one particular time. For the seas were more extensive at some times—and much more restricted in others. There was a pattern of shifting seaways, changing environments, all in a geographic setting. And some evolutionary change to work with! At last!

The oldest samples all seemed to have 18 columns of lenses—just like the slightly older species, now found in Germany and northern Africa, that were probably the ancestors. However, almost immediately, a new form with only 17 columns appeared in the eastern part of the range. Indeed, I had a sample from a quarry in New York State which seemed to show that some specimens had 18 columns, others only 17—and one specimen where the first column was reduced to a single lens. I interpreted this sample as showing variation in file numbers, probably recording a transition between the ancestral 18 and descendant 17 columns of lenses. The New York quarry was at the edge of the entire range of these trilobites—so it looked to me like allopatric speciation had occurred.

The 18-column species remained alive and well, living in the clear coralline seas of what is now the American Midwest, while their offshoot, with 17 columns, persisted unchanged on the muddier sea floors in New York and down through what are now the Appalachian Mountains. After a few million years, the seas largely withdrew from the continental interior (Fig. 4)—evidently driving the ancestral 18-column species extinct. When the seas were restored to the midregion of the continent, the 17-column descendant migrated in with the rest of the fauna.

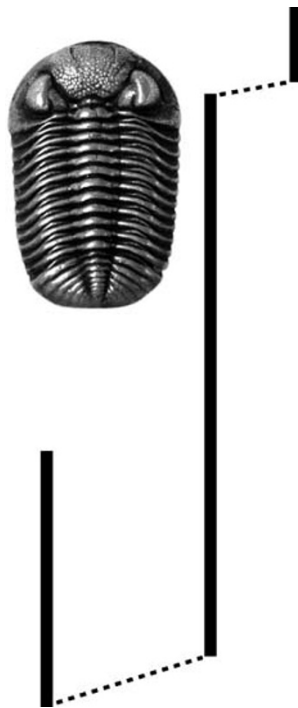
The fossil record in Michigan and Ohio, then, shows the 17-column species occurring directly above the 18-column species—giving the false appearance of sudden, saltational evolution. In reality, the descendant 17-column species had evolved allopatrically at least 2 million years earlier—and had simply migrated to the Midwest after the 18-column species had been driven to extinction through habitat loss. Later, the 17-column species gave rise to a descendant 15-column species—also interpretable through allopatric speciation in changing environments.

However, the stability these species showed as they lasted long periods of time was just as fascinating as the patterns suggesting that allopatric speciation had been at work when evolutionary change did occur. Nothing—no



Fig. 4 Sequence of maps showing the shifting distributions of seaways and exposed land areas through Middle Devonian times in North America (Armistead Booker, Seminars on Science, AMNH)

Fig. 5 The evolution of *Phacops* seen as long periods of evolutionary stability (“stasis”)—“punctuated” by episodes of rapid evolutionary change during speciation events (Steve Thurston, AMNH)



part of my trilobites—seemed to show any prolonged, slow, steady gradual change—the main pattern of evolutionary change that tradition dictated would be the main evolutionary signal I would detect with all this sampling. Once the eyes had changed, they remained stable—as did every other part of the anatomy of these trilobites that was preserved. Once evolution had occurred—through a rapid burst of change in speciation—things seemed to slow down to an evolutionary crawl—for millions of years.

This stability—now known as “stasis”—was what always made “punctuated equilibria” seem so anti-Darwinian to many biologists—paleontologists, zoologists and botanists alike. Darwin’s everlasting message was that

evolutionary change is on the whole steady, gradual, and progressive. Given the passage of enough time, evolutionary change of this sort would be virtually inevitable.

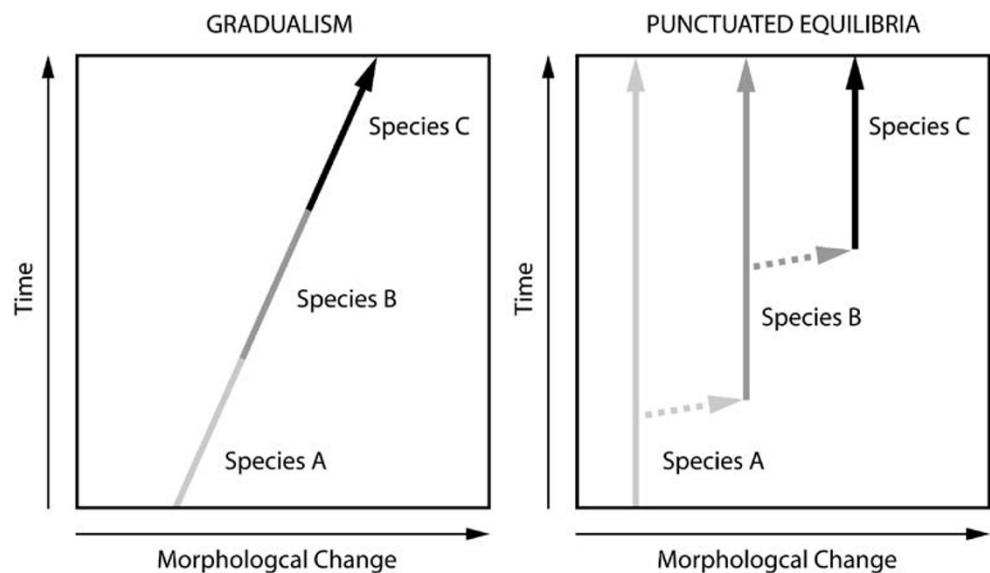
Back then, I had no clear idea how or why species could remain so amazingly stable over hundreds of thousands—even millions—of years. It was my job as a fledgling paleontologist simply to point out that it was so. Not just my *Phacops* fossils, but virtually every other species preserved in the rocks alongside them, tend to remain amazingly stable through thick and thin for truly prodigious periods of time—millions of years, orders of magnitude longer than the brief spans of time, measured in thousands of years, for evolutionary change to occur. (I will devote a future “Editor’s Corner” to what we think we know causes such unexpectedly long periods of evolutionary stability—“stasis”).

I found out that paleontologists back in the nineteenth century were aware of this phenomenon of stasis. But, after 1859, no one much liked to discuss it—as Darwin had virtually assured the world that such could not be. If the fossil record did not readily show patterns of gradual, progressive evolutionary change—well, then, there must be something wrong with the record. Too much information missing—not enough fossils preserved to reveal the details of the change that was expected to be there.

It was up to me simply to demonstrate that this stability was in fact true of my *Phacops* lineages. I then showed that evolutionary change (from the 18-column ancestral form—which had appeared to have entered North America when the continents collided at the beginning of my Middle Devonian chunk of time) seemed to happen in geographically restricted areas of the trilobites’ range (based on some lucky samples I had collected which seemed to document the variation that was part of the transition).

And evolution, when it occurred, seemed to be rapid—especially when compared with the vastly longer periods

Fig. 6 The “Darwinian” view of the gradual evolution of species (*left*) compared with the new, “punctuated equilibria” concept of stasis and speciation (Steve Thurston, AMNH; Armistead Booker, Seminars on Science, AMNH)



(millions of years) when nothing much at all seemed to be happening in an evolutionary sense. I estimated that these periods of adaptive change through natural-selection change took something between 5,000 and 50,000 years—a mere blink of an eye geologically speaking—but comfortably long enough according to most population geneticists concerned with evolutionary rates. It all seemed to fit in beautifully with what I had read in Dobzhansky and Mayr about the process of geographic speciation (Fig. 5).

That was it: my idea, based on all that hard work in the field and lab—is that evolution is not the slow, steady transformation of anatomical bits and pieces that it was traditionally considered to be. Rather, nothing much happens for truly long periods of time. When evolution occurs, it does so rapidly, in geographically isolated populations. This is the core set of ideas of what soon came to be called “punctuated equilibria.”

My dissertation passed and I got my Ph. D.—a major relief. I wrote the results up for the journal *Evolution*—giving it the ponderous title *The Allopatric Model and Phylogeny in Paleozoic Trilobites*, published to little attention in 1971.

I had given the manuscript of that *Evolution* paper to Steve Gould to read and criticize before I dared submit it. A few months later, when the paper was in press, Steve asked me to join him in contributing a paper on speciation to a book project *Models in Paleobiology*, organized by Thomas J.M. Schopf. Steve had wanted some of the other topics—but they had already been assigned to other authors. Steve said he could not think of anything else to say about speciation that I had not already said in my paper.

Steve had a knack for names: he suggested we refer to the stability that seems so typical of the histories of nearly all species that have ever lived as “stasis.” And he thought a good name for my idea of stasis-plus-rapid evolution in geographic isolation would be “punctuated equilibria” (Fig. 6).

The name stuck, of course. The paper attracted a wave of attention—much of it negative, as we were accused of turning against Darwin and of promoting a form of “saltationism”—discredited ideas of evolution proceeding in sudden “jumps” (“saltus” is the Latin word for “jump”) through some unknown genetic mechanism or other.

However, all we were doing was resurrecting a pattern that Darwin, as a young man, knew about (Darwin wrote in

one of his notebooks in 1838 that “My very theory requires each form to have lasted for its time: but we ought in some bed if very thick to find some change in upper & lower layers—good objection to my theory”). He was well aware of stasis in those days—and it became, as Steve later said, one of “paleontology’s trade secrets”—so counter to what the heart of evolutionary theory had had to say about what evolution really should look like if sampled through time.

That is the beginning of punctuated equilibria—and to this day, the core of the idea. We each added an extra theoretical dimension to my original 1971 paper when the longer version *Punctuated Equilibria: An Alternative to Phyletic Gradualism* (Eldredge and Gould, 1972) came out a year later. These first two papers—plus a follow-up review paper *Punctuated equilibria: the tempo and mode of evolution reconsidered* (Gould and Eldredge, 1977) are posted on, and can be downloaded from, my website <http://www.nileseldredge.com>.

However, that, as I say, was only the beginning. Punctuated equilibria opened up a whole new way of thinking about evolution: What causes stasis? How can evolutionary trends occur if species remain so stable for millions of years? Is it true that most evolutionary change is actually tied up with relatively brief and infrequent episodes of speciation? And is it true that extinction of many species within regional ecosystems (not to mention truly global mass extinctions) is actually the trigger for waves of speciation events—meaning that most speciation (thus perhaps most evolution) takes place in coordinated events in geological time? Does the molecular evidence agree with the morphological evidence we have in our fossils?

These and other issues have kept me, Steve, and many of our colleagues busy for the past 35 years. It only gets more exciting as time goes by—quite an elevator ride these past 40 years! I will look at some of these other issues—such as the causes of stasis and the nature and importance of evolutionary “turnovers”—coming out of punctuated equilibria in future “Editor’s Corners.”

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