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Filling the Cup of Alteration

Uniformitarianism then and now.

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William Shakespeare (1564–1616) was a remarkable man. Combing through his work, one can find almost every conceivable bit of wisdom, good idea, or point of view. But until stumbling across the quote in Box 1, I hadn't realized that Shakespeare, at the turn of the seventeenth century, in addition to being a poet and playwright, was also a modern geologist. Though without a university education, he somehow understood a key aspect of geology. Those lines in ***Henry IV*** were spoken as a geological metaphor for the winds of political change. But metaphors develop from widely understood notions.

Box 1: William Shakespeare, Geologist

O God! that one might read the book of fate,
And see the revolution of the times
Make mountains level, and the continent,
Weary of solid firmness, melt itself
Into the sea; and other times to see
The beachy girdle of the ocean
Too wide for Neptune's hips; how chances mock,
And changes fill the cup of alteration
With divers liquors!

2 Henry IV, III,i: 44–52, 1600

Despite Shakespeare's clear priority by more than a century, historians of science stubbornly credit the founding of modern geology to James Hutton (1726–1797)[1] and the new baby—Charles Lyell (1797–1875), born in the year of Hutton's death, to whom the geological baton was transferred.[2] The major conceptual insight that accounted at a single stroke for much that was observed in geology is the idea known as *uniformitarianism* (Fig. 1), though the term itself was not coined until 1840, by William Whewell.[3] The idea of uniformitarianism, that the basic processes of Nature were the same in the past as they are today, was largely motivated by the observation that geological changes generally are very slow, a corollary that became known as *gradualism*. Its importance was that after long periods of time these slow, continually acting processes can accumulate large change.

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As far as proper priority goes, Hutton, like all educated people, must have read Shakespeare, so it might make a juicy, if typically fictional tabloid story to accuse him of cribbing his ideas from the Bard. In any case, the way ideas are sometimes just "in the air" and picked up independently by creative contemporaries is illustrated by the story of a young American named James D. Dana (Fig. 2). Dana was America's leading geologist of the nineteenth century. In 1838, just two years after Darwin's *Beagle* voyage had returned to England, Dana set forth on a voyage of global exploration designed to put an American foot in the door of what had been European domination of maritime exploration, the grand tradition that included James Cook (1729–1778), Darwin, and many others. The objectives of the U.S. Exploring Expedition of 1838–1842 were to determine whether there was an Antarctic continent and to chart the volcanic island chains in the Pacific that had proven so dangerous to American whalers and traders.[3,4]

Lyell had speculated about the process that formed the many Pacific arcs of islands ringed by coral atolls, with active volcanoes at one end and no island inside the atoll at the other end. Essentially, Lyell thought that rising and subsiding volcanoes of different ages were responsible. Dana developed an almost opposite, but still gradualistic hypothesis, according to which the islands were built serially along the chain by undersea volcanoes, the cones of which eventually emerged from the surface and were colonized around their edges by coral. Dana noted the linear change in age of several Pacific island chains and, in 1873,[5] published his idea that the first island was oldest, that it had been raised and then eroded back beneath the sea, while later islands in the chain were younger or just building, as spots on the ocean floor move over a volcanic source, forming a kind of geosyncline (Fig. 2).[6] Many of Darwin's earliest publications were on geology, and he had addressed this problem independently, earlier than

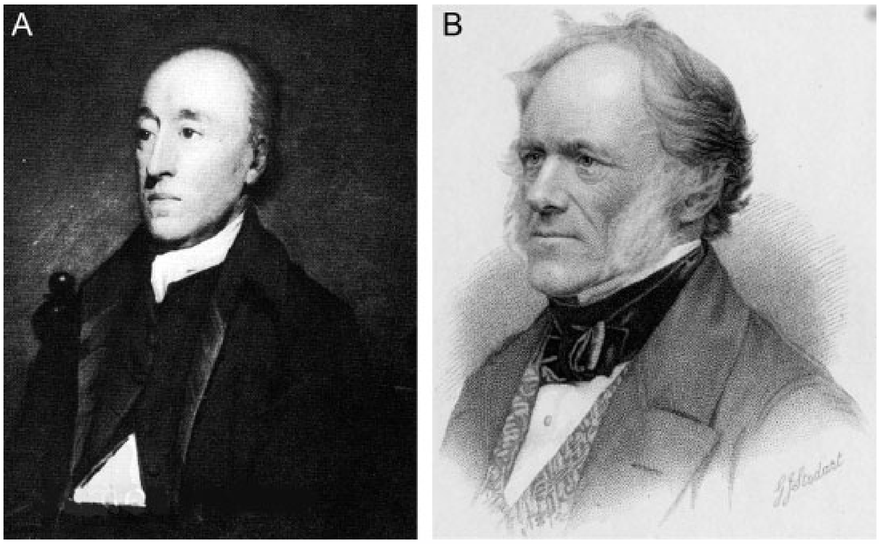

Figure 1. Readers of the book of fate. A. James Hutton (by Sir Henry Raeborn, in Scottish Nat. Port. Gallery). B. Charles Lyell (engraved by G. J. Stodart from a photograph from pages.britishlibrary.net).

Dana, and had basically arrived at the same explanation. Dana was nonplussed when he later read Darwin's account. But if uniformitarian gradualism was in the air, Darwin took a deeper breath of it and moved the idea a major step forward, from the processes of inanimate Nature to life itself.

DARWIN HAD HIS REASONS

Darwin is credited with applying Lyell's notion to biology, but actually the idea had long been wafting around.[7] Alfred Wallace was making geological observations of his own in Indonesia when he sniffed out the same extension to biology as did Darwin. But you might be surprised to learn that back in 1809 the idea was at the heart of Jean Baptiste de Lamarck's (1744–1829) evolutionary theory of the inheritance of acquired characteristics. Lamarck wrote that "With regard to living bodies, it is no longer possible to doubt that nature has done everything little by little and successively" and "Throughout the changes which nature is incessantly producing in every part without exception, she still remains always the same in her totality and her laws. . ."[8]

A scantly remembered British physician, Joseph Adams (1756–1818), also wrote, in 1814: "By these means a race is gradually reared with constitutions best calculated for the climate: a law which, I suspect, has been too much overlooked, in our inquires after the causes of the more marked varieties in the human species."[9] Because Adams' book was about the evolution of heredity disease, historians of biology seem to have missed the fact that he is one of those who clearly anticipated the core ideas of evolution.

Like the steady drip, drip, drip that slowly but ineluctably erodes Shakespeare's mountain one micron at a time, incremental biological forces can also produce major changes over long time periods.[10] Uniformitarian gradualism provided a consistent rather than an *ad hoc* interpretation of life that did not require the special pleadings that various catastrophist views, including multiple creationism and periodic cataclysmic extinctions suggested. The power of extrapolating from directly observable, if slow, *processes* of change across the eons of geologic time justified the theory of speciation by gradual natural selection.

We can observe short-term change directly and play with it experimentally. In that sense, every process invoked by evolutionary theory can be tested in one way or another by observation or in model systems The race for success that Darwin and other naturalists observed in the wild typically seemed to involve small differences among competitors. Darwin relied heavily on his knowledge of agricultural and recreational breeding of plants and animals, where it was clear that you could use differential reproduction to select gradually for woollier wool, hoggier hogs, or poutier pigeons. However, no matter how persuasive these kinds of data are, experimental work cannot directly make observations over countless thousands of years. And of course the particular thorn in Darwin's side was not just the need to account for changing variation, but to explain the origin of distinct species by means other than instantaneous creation.

It is one of many ironies that agricultural breeding does not produce species either. But if we're willing to make the uniformitarian assumption that there were no forces operating in the past that are not still operating today, we can convince ourselves that the evolutionary intuition we reach by extrapolating across deep time from observations on the here and now is actually correct. This was the striking conceptual key to the legerdemain by which Darwin explained how something you couldn't see because it was too slow was responsible for everything you could see about biological diversity. Darwin's rapture is reflected in the quote in Box 2.

Another irony is that Darwinism today still has to fight rear-guard action against creationistic world views. A centerpiece of that resistance movement is that since you can't observe species forming in Nature, uniformitarianism doesn't help; hence, evolution can't be true. How that false syllogism is taken to *imply* creationism is puzzling, since the purported creation events are also tucked safely and unobservably away in the prehistoric past.

The persistence of this resistance to evolution is interesting but derives no support from science. From the early twentieth century, the uniformitarian gradualism assumption is how Darwin's world view became formalized by the mathematical theory of population genetics, which is the formal way to extrapolate the process to show how it could work. An important reason was the still-current concept of polygenic control of quantitative traits

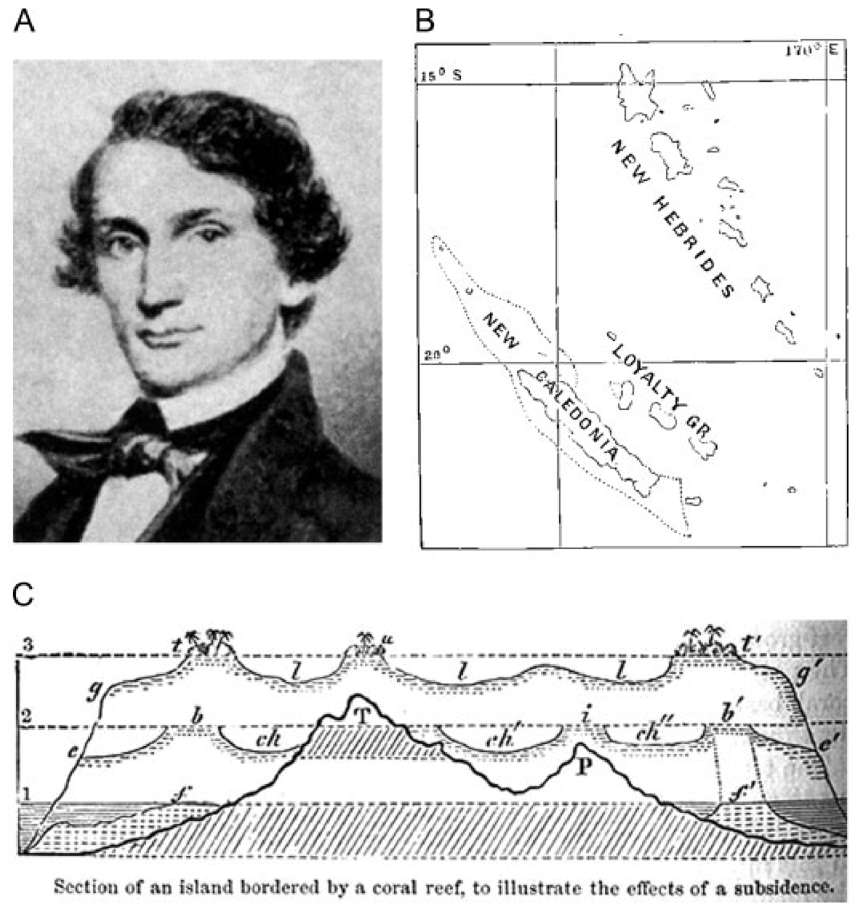

Figure 2. A. James Dwight Dana (1813–1895), from W. M. Davis, 1928, The Coral Reef Problem: American Geographical Society Special Publication 9, Fig. 1. B. The linear array of Pacific island chains. C. The process of volcanic island-coral reef formation. B and C from Dana's 1873 *Manual of Geology*.[5]

by countless individual genes varying in the ordinary Mendelian way but with individually infinitesimal effects. Population genetics theory couldn't demonstrate evolution directly, but provided a quantitative basis for testing it indirectly, for example by predicting the pattern of DNA sequence divergence among species that would be expected on the basis of observed morphological differences and the geological dating of fossils. The tests have added exceedingly powerful support to the idea.

Darwin's famous belief was that *natura non facit saltum*, as he put it—a creeping if not creepy view of Nature (not to be confused with the Bible's "every thing that creepeth upon the earth") that does not allow for discrete jumps, or saltations, in evolution. In *Descent of Man* (1871), Darwin clearly stated that he stressed gradualistic natural selection to show that there was a mechanism for the production of new, adapted species, a process that did not require divine intervention: Nature works by uniformitarian, Lyellian gradualism rather than by creationistic or catastrophistic discontinuities. In Darwin's world view, things do not just arise suddenly *de novo*. Leaps of Nature, unlike leaps of faith, were prohibited. The evolutionary teapot simmers along, slowly generating new species, but you'll never see it boil.

Once Darwinism was established as the formal theory of life, "saltation" became a flash-word to be rooted out and purged by the ever-vigilant Darwin Police. But any kind of Prohibition leads to speakeasies, and in this case they are the insurgents who occasionally appear with claims of having discovered some new violation of uniformitarianism. It's not new but, in some new clothes, biology seems to be getting jumpy again.

A WATCHED TEAPOT THAT SOMETIMES BOILS

Some of today's saltation rum-runners even seem to be coyly reviving Richard Goldschmidt's famous argument that occasional mutational "hopeful monsters" might account for major biological adaptive advances.[11] Goldschmidt was not as superficial as the ridicule leveled at him suggests.[12] Furthermore, modern genetic research has shown that uniformitarian gradualism isn't quite as absolute as classical Darwinian fundamentalism insists: Not all genetic effects are created equal and infinitesimal. However, when we look carefully at the inequality, we find no justification for theoretical atavisms.

Among events that opened the door first was the remarkable finding of the genetic basis of homeotic mutants in flies. Homeotic changes are changes in count or segment identity of meristic traits; that is, traits characterized by multiple similar units. Examples had long been known empirically. However, a couple of decades ago developmental genetic work in experimental fruit flies showed that changes in single genes, now known as *Hox* genes, could cause variation in the number of segments in structures controlled by those genes, like an extra set of wings or ectopic antennae. Homeotic changes in the number or regional identity of vertebrae have been experimentally induced by modifying these same (homologous) *Hox* genes in mice, resulting in lower cervical vertebrae with ribs or lumbar vertebrae morphologically like thoracic ones. Strikingly similar variation is routinely seen in modern collections of normal skeletons, including human skeletons. Many of these variants are harmless, but could be the fuel of adaptive evolution. Among numerous examples are variable numbers of nipples, cusps, or teeth—or differences in the number of neck vertebrae between geese and whales. They are discrete changes, but they aren't monsters, even if they have generated hopeful ideas for jump-seekers.

In 1972, Eldredge and Gould coined the phrase "punctuated equilibria" in

Box 2:

"I had brought with me the first volume of Lyell's "Principles of Geology," which I studied attentively; and the book was of the highest service to me in many ways. . . . [It] showed me clearly the wonderful superiority of Lyell's manner of treating geology, compared with that of any other author, whose works I had with me or ever afterwards read."

Life and letters of Charles Darwin, 1887 (his private autobiography)

reference to evidence from the fossil record that traits remained rather similar for long time periods, then manifest rapid change (see Eldredge and Gould[13] and Wikipedia[3].) I thank John Fleagle for pointing out to me that this claim originated by observations of meristic variation in fossil arthropods—trilobites. The evolutionary questions raised by such traits were noted much earlier by William Bateson, and largely in connection with vertebrate evolution.[14,15] From a modern point of view, we know that change in meristic traits is easily accounted for in a perfectly straightforward genetic way by the quantitative nature of the signaling and combinatorial gene expression processes that produce those traits.[16,17] These are not new evolutionary principles.

A second source of potentially discrete evolutionary change is gene duplication. Indeed, if we accept the rather modest proposal that genomes are part of life, they evolve *mainly* or even only through discrete events. When DNA is replicated, chemical mistakes occasionally occur in which whole segments can be copied more than once and transmitted to the next generation. This can produce two copies of a gene when, in the former generation, there was but one. The second copy is then free to vary and evolve new functions if it affects the organism in ways that its environment favors. If genomes are anything, they are the product of a history of duplication events. Even a mutation changing a single nucleotide is, of course, a discrete event that can have major effects.[18] Variation in vertebrate segmental structures like limbs, teeth, craniofacial features, and vertebrae are examples of traits that seem to arise some time after enabling gene duplication events.[19–21] This is true not just of the skeleton, but also the brain, as well as other soft-tissue and physiological systems; it is *generally* how evolution works. But while duplications are discrete events and, as far as we know, novel traits, they and their effects still have to evolve gradually, the old-fashioned way.

A third line of evidence that not all in life is infinitesimally uniform has become available with advances in gene-mapping technology. Scans of entire genomes can find variation in genes in families of humans or experimental animals or plants that is associated with variation in quantitative traits, like the various shape and size of components of the skull, jaws, and limbs. Most variation in such traits is due to genes having contributions that individually are so small that the genes can't be identified. These are the polygenes of classical gradualism. However, mapping studies also consistently find that a few genes have alleles, or sequence variants, that *do* have substantial individual effects on the trait. These genes are called Quantitative Trait Loci (QTL). Alleles at these loci show the sense in which not all genes are created equal.

The uneven distribution of the effects of alleles at different genes contributes to quantitative variation in a trait at any given time, and is consistent with the necessarily indirect evidence of what has happened over evolutionary time. There is still much to be learned and much debate about the genetic "architecture" of complex traits, but there is no doubt that variation with more than trivial effects routinely exists.[22–24] Alleles at QTL might be favored by selection and, when that happens, phenotypes might evolve relatively rapidly. QTL alleles have more than infinitesimal effects on the trait and arise as discrete mutational events, so that, almost by definition, they constitute "saltations." But while QTL show that not everything genetic is gradual, there are no monsters involved.

A fourth kind of evidence is being cited these days as well. Essentially, it has to do with ways that variation can build up (or sneak up?), accumulating unnoticed until an environmental stressor of some sort comes along. That stress can release the pent-up variation, leading to rapid, if not exactly saltational evolution. That would be a discontinuous phenomenon in the sense that the pent-up variation is suddenly released.

A well-studied example involves a class of genes called *chaperonins*. Genes code for strings of amino acids called polypeptides, but polypeptides are not by themselves mature, functioning proteins. They must first fold up on themselves in ways determined by their specific amino acid arrangement, then be further processed and modified. But a polypeptide is born into a cellular soup of chemicals that might harm it before it can mature, so the proteins coded by chaperonin genes bind to newly hatched polypeptides and help them gently fold into functional shape. A famous group of chaperonins are the genes that code for *heat shock proteins* or Hsps. Clearly, chaperonins have long been of fundamental importance because they are found in all branches of life. Hsps are activated to protect against the potentially degrading effect of unusual temperature changes in the environment, among other things. However, under various kinds of stress the chaperonins may fail and fall off of the polypeptides they have been hired by evolution to protect.

One would think that if protection falls away it's curtains for the cell. But that seems not necessarily to be so. Experiments have shown that Hsps cover for a considerable amount of variation in proteins that is never noticed until it is released by stress-induced failure of the Hsps.[25] This is a sudden burst of variation, but it must be screened by selection in the usual way if it is to serve as an adaptive mechanism in a new stressful environment.

The hidden protein variation is not designed in advance specifically for any particular stress. Some interpret this mechanism as a strategy to improve one's chances under unspecified stress, seeing it as a kind of "evolvability" system. Several other such mechanisms not involving chaperonins have also been suggested.[26–28] What these mechanisms seem to do is produce hopeful molecular monsters rather than morphological ones. A molecule is not an organized, complex new trait suddenly popping up. It is interesting, however, that many of the genes normally protected by chaperonins are related to the developmental pathways that would have to go awry to produce major morphological monsters.

A TEMPEST IN THE TEAPOT?

These are interesting findings that get press ink, but are they telling us more about hopeful monsters or hopeful scientists wanting monstrous insights that overthrow Darwin's basic ideas? The answer is that Darwin can rest easy. And the reason is a confusing of *product* with *process*.

It's true enough that homeotic and other segmental changes are discrete rather than continuous. However, they involve differences in the number of similar already-existing structures, and hence variation in the same well-established process, not a discontinuity of process nor a sudden new process, and hence no real departure from classical evolutionary ideas. Mutations in QTL are part of the normal, perfectly mainstream nature of mutation and genomic change. Given that mutations can strike any part of a gene, it is not any sort of surprise that their effects will not be uniformly small. The same is true of gene duplication. Likewise, the Hsp story is about the release of existing variation that must be screened by ordinary drift and selection, not monsters arising ready-made in times of stress. There is no violation of ordinary day-to-day biology.

If one wants to be a contrarian, given what we know about genes and genomes, we could argue that genetics has shown that discrete change—saltation—is the *only* way heritable change happens. In that sense, Darwin would have been totally wrong, but only as a rather minor technical-

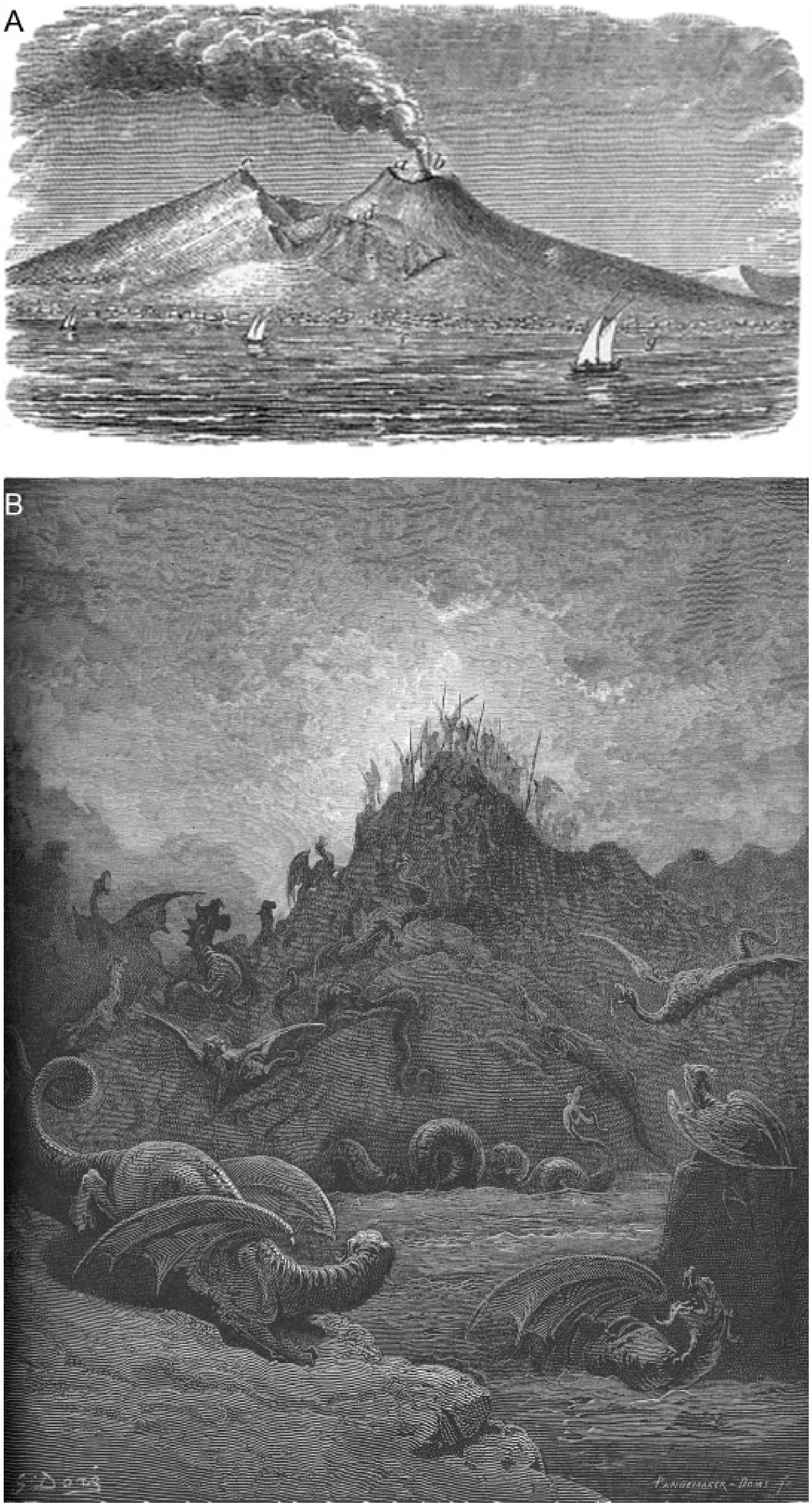

Figure 3. Hopeful monsters. A. Passage from Hell? (from Dana[5]). B. In the confines of Hell. From Gustave Doré illustrations from Milton's *Paradise Lost*, 1866.

ity, because most mutational change, even if discrete, is either devastating and we rarely see it, or has miniscule Darwin-like effects.

In the end, without any revolutionary thinking, we can see that Nature doesn't always just inch along with infinitesimal creep. Darwin would have no problem accommodating his views of Nature these new facts. Although gradualism was key to the views of evolutionary thinking in both geology and biology, growing out of the uniformitarian assumption, the key fact was not that everything had to be gradual, but that slow, gradual change was very difficult to observe directly. Nevertheless, such change was a major way in which large changes happened in Nature without catastrophic events. The key aspect of uniformitarianism is that the same *processes* have been taking place throughout the history of life. But uniformitarianism does not imply gradualism.

The real exceptions that would be needed to give Darwin's ghost the shakes would be entirely new *kinds* of traits arising instantly, ready-made, and properly wired into the rest of the body. We know of few, if any, such instances. Indeed, we know enough about the hierarchical nature of developmental genetics to know why that is so. Organized traits have to develop in proper developmental context with what's going on in the rest of the embryo. We know examples of what seem to be simple and hence, possibly rapid change of substantial sorts, such as related species of sea urchin or amphibian that do or don't undergo separate tadpole stages, or repeated evolution of blindness in cave fish that can be restored by interbreeding. But these changes arise as understandable switches in developmental processes, and some examples caught in the act are polymorphic within species. These events don't suddenly generate whole new traits.

Uniformitarianism is the belief that the cosmos is basically a universal, continuous, Newtonian (law-like) river of causation. In fact, the same belief is consistent with probabilistic causation, so long as its behavior is law-like as, for example, Mendelian segregation and genetic drift. Uniformitarianism provides a workable framework for research because it does not require *ad hoc* invocation of exceptions and special cases or creation events. No matter how jumpy Nature may occasionally turn out to be, none of the apparent exceptions to continuity or gradualism suspend the basic ways that Nature fills life's cup of alteration, as Shakespeare might put it. These exceptions reflect the ability of genetic change under some circumstances to produce new variations on existing themes. On the basis of present evidence, the hope of scientists to escape from obscurity in the shadows of Darwin seems to be as vain as the hope of monsters to escape from the shadows of Hell (Fig. 3). Nonetheless, the way uniformitarianism actually works from day to day need not be uniform, even if the *rules* of life work uniformly. And a sudden burst like Mount St. Helens doesn't change the rules of geology, either.

NOTES

I welcome comments on this column: kenweiss@psu.edu. I have a feedback and supplemental material page at http://www.anthro.psu.edu/weiss_lab/index.html. I thank Anne Buchanan, Jeff Kurland, and especially John Fleagle for critically reading this manuscript.

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