The Worldviews of Stephen Jay Gould

An Overview of the Themes that Appear in Gould's Writings

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A total of 299 Stephen Jay Gould essays are captured in the ten collections that this effort summarizes, touching on a wide variety of subjects. Each can be read as a stand-alone piece – which, in fact, each one was at one time. One of the purposes of this overall project, however, is to allow the reader to pour through multiple essay summaries in a sitting. This allows one to grasp the range and cleverness of his views much more quickly, but it comes with a tradeoff: one can feel whipsawed across idea-space, especially if unfamiliar with his recurring themes. This section, therefore, is an attempt to provide – as concisely as possible – the relevant background one needs to feel "oriented" in Gould's world of essays. If Gould's essays are all over the map, think of this overview as "the map." We must begin with the nuances associated with the term "worldview" itself.

The Academic Nature of Worldviews

All established academic fields have reasonably well-defined communities – sometimes more than one – that hold a set of tenants in common. These "schools of thought" virtually *must* exist in a stable setting, and the orthodoxy that each one represents serves several important functions. One of these is simply that it establishes a common body of documentation that all members must be familiar with, even if they disagree with parts of it. This makes communication between members vastly easier, and allows coherent lines of attack on important problems. This does not necessarily mean that a particular school of thought is "correct." But correct or not, one of the unstated truths of this necessary human artifice is that a young academic who openly bucks the orthodoxy of his chosen academic field does so at some risk to his career. This may seem like a bad thing, and it certainly has the downside of suppressing, to one degree or another, useful dissent. However, since the vast majority of unorthodox ideas are simply wrong, the upside is that it deters speculation, reduces wasted time, and keeps the train on the track. The burden of proof, when one challenges orthodoxy, is and *must be* on the challenger. In principle, scientific schools of thought offer the challenger a chance at "victory" – specifically, the opportunity to replace the old orthodoxy with one at least partially shaped by the challenger – if he can "prove" his case with solid, convincing evidence gleaned from the external reality of nature. In practice, as Gould often notes in these essays, scientists are human too: they are highly reluctant to change their own hard-won worldviews, and are usually able to interpret supposedly "objective facts" in light of their own theories. Voices are often raised at scientific conferences, and published articles have been known to contain more than a trace of venom.

Gould, like many scientists, had an iconoclastic streak. He was a mainstream Darwinist in many ways, but challenged certain aspects of the orthodoxy. Some who disagreed with him argued that his dissents were inconsequential, and thus not worth the fuss that was being made over them. Others critics considered his views highly consequential, but just plain wrong. A significant fraction was convinced that his dissents were both important and probably correct. History is full of scientists who "guessed right" for essentially the wrong reasons – Gould documents several of these in his essays. History also contains hundreds of examples of cases in which brilliant people drew the wrong conclusions based on false data, or a misreading of that data. In those places where Gould differed from the orthodox views of evolutionary biology, was he right? The answers are beyond my expertise; I am an amateur in these fields, not a professional. This text will thus limit itself to an attempt to explain *what Gould's worldviews were*, based primarily but not exclusively on his own writings, and to show where they align with and differ from the orthodoxies of his professional community. His essays can be viewed with additional perspective when his overarching views are explicitly understood.

Pre-Darwinian Worldviews

To understand Gould's worldview, one must begin with Darwin's, and with those that existed before Darwin. Most cultures, including hunter-gatherer tribes that Westerners have come across in the past several centuries, have some sort of creation myth to explain the origin of their lineage and the world around them. These creation myths vary widely, but generally involve a specific event or a small number of events. As Gould points out in these essays, humans like a good "story" (with a beginning, middle, and end), and we greatly prefer origin stories to have a defining event rather than a gradual sequence of incremental steps. Most creation myths also incorporate an intelligent and self-aware creator or creators. In what we now call Western culture, our traditional creation myth has been captured as the story of Genesis in the Old Testament.

Our ancestors recognized that certain objects in nature behaved in more predictable ways than others. The motion of the heavenly bodies was both repetitive enough and puzzling enough – specifically, the apparent motion of the sun, moon, and so-called "planets," or wandering stars – that many civilizations attempted to model their quantitative behavior. This was in large part motivated by the (false) belief that the locations of these bodies at various times affected events on earth. According to this belief, accurate predictions would give those who could afford them an advantage in everything from romance to battle. Perhaps ironically, based on how things turned out, this led to essential sponsorship. In the 17^{th} century, building on the efforts of Copernicus, Kepler, and Galileo, the great Isaac Newton demonstrated that the force that caused objects on earth to fall to the ground could be used to explain planetary motions, with relative accuracy and elegant simplicity. Europe was electrified by the discovery that man could, through a combination of reason, mathematics, and observation, learn something truly new and useful about the nature of the universe. Many Europeans came to envision the Creator as a "great watchmaker" who set up the rules by which the universe operated, but was not actively involved in its day-to-day events. (This view was a subtle but critical part of the Enlightenment, influencing among others the founding fathers of the United States.) Neither the Bible nor any other historical records available at the time, however, suggested any evidence of human existence more than about four thousand years before the birth of Christ. The idea that the Creation might have existed for a longer period than this made little sense; what could possibly be the purpose of a world without man? (With the recognition that the world did indeed exist long before humans, Gould laments that the rationalization was easily changed to retain our essential role. In the revised view, while not present from the beginning, we are the result of a long and arduous process that had the primary purpose, or at least inevitable necessity, of producing us. (It must also be noted that the "young earth" view was not universal; Aristotle, for example, believed that it had existed forever.)

Newton's spectacular success stimulated others to try to develop quantitative models for the behavior of the earth and the things on it, including life and, of course, man. The fields that would become geology and paleontology came into existence, and many of Gould's essays describe key events or players in the context of their time. One of these key events was the discovery of "deep time," the recognition that the earth is far older than six thousand years, and was perhaps even millions of years old. (Today, we recognize the age of the earth as about 4.6 billion years.) Another was the recognition that what we today call "fossils" required a scientific explanation. Did these objects that resembled seashells or fish skeletons "grow" inside the rocks in which they were found, like crystals? Or were they the remnants of formerly living creatures? If the latter were true, there were additional puzzles: How did these mostly aquatic organisms end up inside rocks that were themselves found on mountains, often hundreds of miles from the sea? Further, many of these fossils were noticeably different from anything living today. Did this mean that extinctions occurred in nature? If so, what did that imply about the perfection of creation, or the infallibility of their creator?

"Species" certainly seemed to be real entities. There were many different kinds of fish, but each type was discrete; there were no "continuous transitions" between perch and bass, for example. It was ancient knowledge that animals such as dogs and goats could be bred for certain features, but they always remained dogs and goats. Despite their common appearance in mythology, no one had ever found a half-lion / half-eagle, or a half-man / half-bull. Beginning in the 1700's, several efforts were made to classify all living species according to various principles, such as their utility to man. One particular system, developed by the Swede Carl von Linne (who published under the Latinized version of his name, Linnaeus), developed a scheme in which species were grouped together based exclusively on anatomical similarity to each other. Those groups were hierarchically collected into larger groups, again based on similarity. For example, all birds were grouped together at one level, and then the entire group was collected into the larger group of vertebrates, which included mammals and reptiles, but not clams or insects. Each species could only be in one group at any level of this hierarchical structure; a whale, for example, could not be both a mammal and a fish. This type of “taxonomy” (a term that is associated with the rules and details by which objects are organized) would prove to be readily adaptable to evolutionary thought, with all members of a group descended from a common ancestor. However, Linnaeus did not believe in evolution; his view of life was entirely static. (Gould discusses this in his essay *Linnaeus’s Luck?*).

If species were real, static entities, it “made sense” to assume that each had been created, presumably at the same time, and had remained essentially unchanged since then. But then, what were these fossils (for example, trilobites) that were unlike anything living today? Even more troubling, the sediments that contained these unusual fossils contained virtually no evidence of any of the specific organisms living today. It was a puzzle, and the new Newtonian perspective required a search for solutions. Many proto-scientists, as well as many purely speculative “armchair philosophers,” proposed models. One group fell into the camp of what might be called “scientific creationists,” at a time in which this phrase was not an oxymoron. A literal interpretation of the Bible might allow for two creations, separated by the “mass extinction” event of Noah’s flood. Perhaps all the older fossils were a product of the first creation, while modern life was the result of the second. One problem with this approach is that there appeared to be multiple mass extinctions in the fossil record, not just one; so perhaps Noah’s flood was only the last of several such events. The second problem is that new species appeared to arise almost continuously throughout the process of sediment formation, with larger bursts occurring just after apparent extinctions. Perhaps God, or some mechanism set up by God, continually created new species at periodic or irregular intervals.

A second, smaller group, which included Charles Darwin’s grandfather Erasmus Darwin, speculated that the older species “transformed” over time into the newer species. Evidence from better microscopes and techniques showed that embryos clearly appeared to follow a developmental “plan”; if species themselves transformed over time, it made intuitive sense that this “development” also followed a plan, from the simple to the complex, or from the primitive to the advanced. A few scientists, such as Lamarck, tried to propose physically plausible mechanisms by which this process could occur, but there was little evidence to offer in support of them. Others offered notional mechanisms that involved unknown forces such as “vitalism,” but these were criticized on the (usually legitimate) grounds that they were a return to mysticism, and thus a step back from Newton’s great leap. At a larger scale, the implausibility of one creature changing into another over time, even with the discovery of vastly more time than was previously believed to exist, was still a scientific obstacle as well as a political and religious one. Nonetheless, the requirement for a satisfactory “scientific” explanation remained.

One of the most important, and most misleading, paradigms in Western thought – although today it is almost forgotten – is "the Great Chain of Being." Western intellectual history has long been obsessed with "ranking" the value of everything from minerals (copper was "higher" than tin) to types of divine angles; the same process was readily applied to biology. In this paradigm, which Gould discusses in several essays, sterile earth is at one end of the chain, and God is at the other. Animals are ranked higher than plants; within animals, vertebrates are ranked higher than arthropods and mollusks; within vertebrates, mammals are ranked higher than reptiles and fish; and so on. Man is ranked the highest of all life on earth in this paradigm, just below angles, since he is created in God's image. Other organisms are similarly ranked in terms of their similarity to man, with chronic debate over issues such as whether clams or snails were "closer" to us. (Much of the West's history of imperialism and colonialism, Gould laments in these essays, was formally justified via the further application of the Great Chain to races of humans – white Europeans at the top, Asians in the middle, and dark-skinned Africans, Indians, and Polynesians at the bottom. In many ways, these views were finally discredited only by the rise and fall of Adolf Hitler.)

If one operates under the paradigm that all life was created as is, and has remained unchanged since, then the Great Chain paradigm is merely useless to science. When the concept of evolution appears, however, it becomes a direct impediment. Early evolutionists (see Lamarck in Gould's essay *A Tree Grows in Paris*) fell into the trap of believing that the evolutionary process was, effectively, a progressive march up the Great Chain, "from monad to man." While the details of this paradigm are now ridiculed (if known at all), one of Gould's great themes is that the underlying assumption of *progress* in evolution remains. Many of his essays discuss the branching, diversifying "bush" model of the history of life, as opposed to the sequential, progressive "ladder" view. The classic example of ladder thinking is the sequence of fish to reptile to mammal to man; while technically true, this view ignores all of the other thousands of branching events, and implicitly places us at the top of some heap when, he argues, there is no "top."

Darwin's Worldview

This was the world that Darwin entered. Charles Darwin (1809 – 1882) was a not-too-promising member of the British establishment, who had the family resources and paternal blessing to pursue the career of a naturalist instead of a physician (like his father) or a member of the clergy. In part because he was unmarried, financially secure, and without career-oriented commitments, he accepted an offer to spend five years at sea on the *H.M.S. Beagle* beginning in 1831. He very much enjoyed collecting and studying the plants, animals, and geology wherever he went, if not the actual sea voyage itself. He collected thousands of specimens, returning crates of them to England whenever the *Beagle* made port. After the primary mission of surveying the Atlantic Ocean off the coast of South America was completed, the vessel spent an additional few years circumnavigating the globe via the Straits of Magellan. The *Beagle* stopped for several weeks at the Galapagos Islands in 1835 for more survey work. These volcanic islands, which were known to be quite young – five to ten million years old, by today's reckoning

– were full of life, including giant land tortoises. These creatures filled the niche of vegetation browser occupied by goats or sheep elsewhere.

More important, in the history of science, were the birds that Darwin found there. The first important group was the mockingbirds, which showed distinct differences from island to island. Darwin assumed these were mere varieties, as regional variations were widely observed in many species; one did not have to be an evolutionist to accept such variations. Later, after he returned to England and delivered the specimens to an expert ornithologist, he was deeply surprised to learn that they were actually separate species.

Darwin also collected another group of birds – the famous Galapagos finches – which were so distinct that he considered them to be in different genera (plural of genus, the taxonomic category above species), and in some case different families. This was in large part because their beaks were so different. Some had large, solid beaks, and cracked open hard seeds. Others had longer, narrower beaks, and used these to extract tender food from narrow crevices. Still others had beaks that were well suited to catching insects. Again, it was with surprise that he was told – after his return to England – that all were closely related, despite their wildly dissimilar appearances. "Species" appeared to be a more complex concept than he, even with his training as a naturalist, had appreciated.

One fact that did puzzle him while still at sea was that these finches were closely related to species living in the tropical areas of South America. What made this odd was that the Galapagos Islands, despite their equatorial latitude, have a climate that is relatively temperate, due to prevailing ocean currents. Also, of course, the islands were composed of fresh volcanic material, which again is quite different from the terrain of South America. In the creationist paradigm of the time, which he accepted, animals and plants were created "for" the specific conditions in which they would live. Why then, Darwin wondered, when these islands were created, had not birds more suitable to that environment been created as well? It seemed possible that the ancestors of all of the Galapagos finches had been blown the 600 miles from the mainland in one or more storms; but why had they not died out once there? Further, he was slightly puzzled by the fact that each island – each seemingly identical – each had its own unique variants of everything from birds to tortoises. He briefly considered the possibility that the ancestral South American stock had transmuted into different species on each island, based on the available food supply, but did not carry this speculation further until much later (as Gould discusses in his essays *Darwin at Sea – and the Virtues of Port* and *A Sly Dullard Named Darwin*).

Young Charles was in no way a radical; unlike his grandfather Erasmus, he went to sea as a confirmed creationist. In 1836, when he returned, he was still a creationist. One of the turning points occurred after learning the correct relational status of the Galapagos mockingbirds and finches, as discussed above. He came to wonder if species were somewhat plastic, and that they could change when placed in a different environment. If new species could "evolve" over space, was it not possible that they could similarly evolve over time? Once his mind was open to the idea, he quickly found evidence for this in some of the fossils he brought back – not always correctly, it turns out. He was no longer a creationist.

Darwin knew he was on to something, but would not go forward without a mechanism – one that did not require supernatural or inexplicable forces. He stumbled onto one after reading some documents that referenced Thomas Malthus's early 19^{th}-century essay *On the Principle of Population.* Malthus, who was more of an economist than a naturalist, noted that virtually all organisms can produce more offspring than can reach adulthood and themselves reproduce. Since the population can grow exponentially, he argued, it does not matter how much food is available; resources will eventually be exhausted. When resources become scarce, those with some sort of advantage – perhaps in terms of size, speed, or natural weaponry – would survive at the expense of others. With this as the key, Darwin developed his mechanism. He called it "natural selection," which he argued by analogy was an extension of the "artificial selection" humans used to breed pigeons, dogs, and livestock.

Natural selection is comprised of three postulates and one derived conclusion. The first postulate is that natural variation exists within all species. This was not a trivial point; Plato, whose views still held great sway at the time, had argued that each species was associated with a single, perfect "form," and that variations within species were attributable to different ways and degrees in which each individual fell short of that perfect ideal. Platonists argued that variation was an unimportant detail that naturalists simply needed to "average out," or address by finding what they believed was a near-perfect specimen. Darwin, on the other hand, recognized variation between individuals as a fundamental characteristic of populations and species, and therefore vitally important in and of itself. The second postulate is that parents could pass these variations, at least in part, to their offspring. In an age before any quantitative understanding of genetics, Darwin had to rely on empirical evidence. (One of the strongest technical arguments supporting evolution in general, and Darwin's theory in particular, is how well it has held up to the discoveries of genetics.) It was apparent that cats always gave birth to cats and never to dogs, and that children tend to resemble their parents. The third postulate is the contribution from Malthus: simply, not all of the offspring can survive all of the time. (The implication here is that the offspring would *compete with each other* for limited resources, although Gould notes in his essay *Kropotkin was No Crackpot* that other interpretations exist.) The derived conclusion, therefore, is that those offspring that vary in ways that give them an advantage in the local environment will have a better chance at survival and reproduction, while the rest are more likely to succumb. Whatever feature led to this selective advantage could, at least to an extent, be passed to the offspring. Over time, those finches that happen to be born with slightly larger beaks would be able to survive on an island with tough but loose seeds, but would lose out to others on an island with no such seeds but plenty of insects. On the first island, larger and tougher beaks are gradually but continuously favored. Over many generations, the offspring may differ considerably from their ancestors, eventually forming new species. This view differs strongly with the view of evolution as an internally-driven directive process, like the apparent development of an embryo.

This mechanism was an extension of breeding, or artificial selection, where the "selector" has been changed from goal-oriented breeders to survival-oriented nature. Yes, Darwin acknowledged, people have been breeding pigeons for hundreds of years, and they are all still just one species – they can still interbreed, and mixed breeds tend to resemble the documented ancestral stock. But nature has vastly more time available. Darwin argued that if the pigeon breeding processes were continued for thousands or tens of thousands of years, new species would result – just as they had (he argued) with the Galapagos finches and mockingbirds. Macroevolution – the formation or significant modification of important features, such as tail flukes in whales – was, in his view, was simply this "microevolution" (he did not use these terms) plus time. An essential implication of Darwin's theory was that evolution was a gradual and continuous process. This was required, he believed, because multiple structures would have to evolve in a coordinated way – for example, large antlers would require larger neck muscles and bones to support them. Since his theory excluded external "directive" forces, each part would evolve independently; thus, the number of stages required to produce a different *functional* organism would be large, and therefore the process must move very slowly. Other proposed evolutionary mechanisms such as Lamarckism, to be discussed, avoided this constraint by postulating coordinating (albeit unknown and mysterious) forces. Those postulating an evolutionary mechanism consistent with the platonic view of species as discrete states used the terms such as *transformationism* and *saltationism* to discuss the formation of new species in a single generation. Darwin's gradualist view was directly analogous to the new geological paradigm of his senior colleague, Charles Lyell.

Charles Lyell (1797 – 1875) is often credited as the father of geology, and appears several times in Gould's essays. He faced a serious problem in trying to turn the study of the earth into a science: there were dozens of speculative "models" that offered to explain the appearance of earth's surface, with its mountains, canyons, oceans, and so on. Producers of these models came to be known as "system builders" or "world makers," and virtually all of them drew on violent "catastrophes" in order to both explain Biblical stories and to fit the appearance of the modern world into the 6000-year timeframe that was generally allocated. One example Gould discusses is the striking of the earth by a comet. Comets had only recently recognized as heavenly bodies independently orbiting the sun; such an event, it was suggested, could change the tilt of earth's axis from perfectly upright to what we see today, giving us both seasons and other features such as mountain ranges. The problem with these models, as Lyell saw it, was that there was no direct evidence for any of these theories (other than the mere existence of seasons and mountain ranges), and no tests one could imagine to determine which of the numerous models – if any – was correct. How does one approach the problem of turning the study of earth's history into a science? Lyell's tactic was to capitalize on the relatively new concept of "deep time" – that the earth was actually far more ancient than the 6000 years usually allocated by the speculative world makers. It seemed clear that most sedimentary rocks had been deposited gradually rather than suddenly, and the erosion caused by a stream or river could be directly observed. If sufficient time is available, perhaps these gradual, uniform processes – which could be directly studied and quantitatively measured – could explain everything. Lyell was a lawyer by training, Gould tells us, and states that his three-volume work *Principles of Geology* (1830 – 33) was his "legalistic brief" against catastrophism *in all cases*. His perspective, which came to be called "gradualism" or "uniformitarianism," accepted floods, earthquakes, and volcanic eruptions of the magnitude that had been observed in recorded history, but nothing as speculative or miraculous as a catastrophic comet impact.

Darwin wholeheartedly concurred with this view, and applied it to his view of evolution. The fossil record, as alluded to earlier, did appear to contain sudden "mass extinctions," usually followed by the appearance of different groups. (These boundaries were so well-defined that they were used by geologists to compare the relative dates of one formation with another, leading to the terminology of Paleozoic, Mesozoic, Cambrian, and Jurassic used today.) Darwin was troubled by these discontinuities, and knew that he must explain them in terms that were consistent with his gradualist views. The approach he took was to argue that these transitions were *not real*, but rather reflected gross imperfections in the fossil record. Sometimes the rate of deposition would very high; it might later fall to zero for millions of years before returning (this is, in fact, usually the case). The result would appear to be an abrupt change, when in fact it was not. He predicted that, as more and better-preserved fossil strata were discovered, gradual but continuous evolutionary change over millions of years would be documented.

Darwin also believed that natural selection only worked to adapt the design of an organism to the local environment. For him, the "local environment" implied not only parameters such as temperature, sunshine, and rainfall, but all of the other species that formed the ecosystem; the "tangled bank," in his metaphor. Importantly, Darwin did not believe that natural selection was a "perfecting" process, merely an optimizing one within the biological constraints of the organism's lineage (see the section on adaptationism, below). Galapagos tortoises would become the best browsers they could be, but could be easily pushed to extinction if, say, goats were introduced to their island. The extinction or arrival of one species, therefore, would have an impact on the others. If the environment – including the flora and fauna – remained unchanged, he argued, natural selection would bide its time and all of the species in the ecosystem would remain evolutionarily static. Once the environment changed, however, the process would begin again, with evolutionary change proceeding gradually but continuously. Usually, he believed, the environment was perpetually changing, or at least changing sufficiently often that natural selection operated most if not all of the time, at its ponderously slow speed.

In Darwin's worldview, if the environment changed, the entire population of each species that lived in that environment would gradually change with it. When the climate turned cold, all northern North American mammals would (he predicted) slowly evolve to larger size (for heat conservation), become hairier, and collectively develop other features that would aid in cold-weather survival. The gradual nature of this process would manifest itself in the fossil record – if sufficient resolution could be captured – as one species appearing to "morph" into another. That is, Darwin believed, species were not "real" after all, but merely snapshots (in this pre-photographic age) in a continuously changing lineage. The technical terms used today for this concept are *anagenesis* and *phyletic gradualism*; Gould appears to use them interchangeably in his writing. Similar changes occurring in different (that is, non-interbreeding) species acquired the terminology of "trend." Trends – in this example, larger sizes in numerous lineages – are evidence of the power of natural selection, since it can produce similar adaptive results in different groups. When very different organisms develop similar features to address similar needs, the process is referred to *convergence*. A classic example is the porpoise, which is descended from terrestrial mammals but whose body has evolved into a form very similar to sharks and the extinct ichthyosaurs. While the details are always different, convergence is offered by advocates as evidence of the power of natural selection to create macroscopic evolutionary change.

Darwin's view of speciation – meaning the formation of a new species – became, therefore, an arbitrary demarcation of convenience on a continuous line. However, he did recognize that more than one new species could arise from an existing one. A species might be broken up into two or more non-interacting populations by processes such as migration or the sudden relocation of a river. Each population would then evolve to be better adapted to its own local environment, which would no longer be identical. Sometimes, a newly-evolved species might re-enter its ancestral range, where it might coexist with its sister species – or it might replace it completely. In the latter case, the fossil record of *one area* would show an abrupt change. It would be easy, he argued, to confuse this migration-and-replacement process with rapid evolution on one species into another, when this was not the case; another defense of gradualism in the face of a problematic fossil record. The closer two species were to each other, the more likely they would compete for the same niche – with one being favored, and the other either moving or becoming extinct. This, Darwin offered, explained why species at any moment in time appear discrete rather than continuous; the intermediate populations existed briefly, but were out-competed. Their (rare) fossils will eventually be discovered, he predicted, at least in enough cases to prove the point.

Darwin's theory of evolution by natural selection includes a particularly powerful philosophical implication. Since natural selection acts only on individuals trying to adapt to their immediate environment, it follows that evolution follows no "plan." Any order that we see in nature, therefore, in the form of food chains, complex ecosystems, or superbly adapted organisms, is not an indicator of design, but simply a side effect of each individual fighting for survival and for the chance to reproduce. There is no external guidance or coordination, divine or secular, leading to predictable results; only individuals competing. This is the metaphorical "unseen hand" of Adam Smith's market economy applied to nature, as Darwin openly acknowledged. In this view, natural selection does not lead to more intelligent or more complex life. He noted that parasites, which are usually simpler descendents of more complex free-living ancestors, are just as much a product of natural selection as birds and whales. In one early essay, *Darwin's Delay*, Gould speculates that the reason Darwin delayed publication of his theory for twenty years after he first developed it was not because the concept of evolution itself was so heretical; rather, it was the essentially godless "philosophical materialism" of his proposed *mechanism* that caused him to fear for his reputation and social standing. (Perhaps fortunately, then, as will be discussed below, *Origin of Species* actually *failed* to convince most readers that natural selection was the primary force behind evolution!)

Nonetheless, as Gould discusses, Darwin did believe in a form of progress over the history of life. He called on a secondary process for this, expressed in his "metaphor of the wedge" (referring to the metal tool used to split logs for firewood). In an unpublished draft of *Origin of Species*, Gould notes in his essay *The Wheel of Fortune and the Wedge of Progress*, Darwin wrote:

> Nature may be compared to a surface covered with ten thousand sharp wedges, many of the same shape and many of different shapes representing different species, all packed closely together and all driven in by incessant blows: blows being far severer at one time than at another; sometimes a wedge of one form and sometimes another being struck; the one driven deeply in forcing out the others; with the jar and shock often transmitted very far to other wedges in many lines of direction. . . . The more recent forms must, on my theory, be higher than the more ancient; for each new species is formed by having had some advantage in the struggle for life over other and preceding forms . . . . I do not doubt that this process of improvement has affected in a marked and sensible manner the organization of the more recent and victorious forms of life, in comparison with the ancient and beaten forms.

Yes, Darwin argued, natural selection optimizes species only for the local environment; but over time, some species are wedged out by others. He concluded that this process would eventually lead to an overall improvement in *all* wedges. He argued that this long-term trend – in the form of more complex (or in some other way more advanced) organisms – can be interpreted as a form of progress. However, he emphasized, this must not be confused with guidance or directionality.

If Darwin's view of the history of life did not offer the planning of divine creation or the inevitability of a directed unfolding of nature, it did offer something else: a *unique story*. At or near the beginning of life, there was a single, relatively simple organism. As time went by, the descendents of this organism diversified, eventually becoming the life we see today. Finches and sparrows share the common characteristics of feathers, a beak, and hollow bones because they share a common ancestor with those features. Finches and Galapagos tortoises have fewer features in common, but both have a backbone and a liver, features that no snail, insect, or earthworm has. They too shared a common ancestor, but one that lived far more distantly in the past. Creatures evolved in certain specific ways over time; things *happened*. In Darwin's view of the world, life on earth had a characteristic history, just as human civilizations did. This was fundamentally different than the paradigm of Newtonian physics, where every water molecule is essentially the same as every other water molecule across space and time, and planets travel in virtually unchanging orbits almost indefinitely. Darwin explicitly stated this in the very last lines of *Origin of Species*, which Gould also borrowed for the title of his monthly column:

> There is grandeur in this view of life, with its several powers, having been originally breathed by the Creator into a few forms or into one; and that, whilst

> the planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved.

Darwin's *Origin of Species* appeared in 1859. The book sold phenomenally well, and was very successful in convincing readers that *the similarities and differences between animals* suddenly "made sense" in the light of evolution, and that species, including man, did evolve over time. (The essential evidence that evolution occurred came from an important but esoteric field called *comparative anatomy*; Gould writes several essays about the origin of this field, and often noted that his office was in Harvard's Museum of Comparative Zoology, an important facility founded by the great Swiss-American naturalist Louis Agassiz in 1859. Unfortunately, this field focuses on details that require extensive training to appreciate. Those with professional training could see that Darwin was right about evolution, but those without it only saw odd bumps on teeth or slightly different shapes of complex bones. This, I believe, is the primary source of difficulty in appreciating, if not accepting, the reality of evolution in natural history.)

Some of the most convincing evidence he offered that life evolved were examples of what he called "contrivances." Rather than focus on the structures that seemed perfectly designed, such as a bird's wing, he instead turned to the large number of anatomical structures that appeared to be "kludges." He pointed out how often such features appeared to be modifications of structures that existed in older organisms, sometimes serving a completely different purpose. The modification of an existing structure to serve a new purpose, as opposed to the implementation of a new (and better) design, rendered the concept of "descent with modification" not only plausible, but sensible. (Again, this approach requires attention to detail, and thus is difficult to convey to those who are not willing or able to put in the required effort.) Gould used this same approach in several of his essays, sometimes calling it "the principle of imperfection." One of his most famous essays, *The Panda's Thumb*, is the prototypical example.

Although successful at convincing the scientific community (and, importantly, the British aristocracy) of the *reality* of evolution, he was largely unsuccessful in convincing the community that natural selection was the primary mechanism behind major evolutionary changes. Virtually all professionals agreed that natural selection *occurred*, and could and did act as the executor of unfit individuals. However, the majority did not accept the idea that natural selection could be a large-scale *creative* force. Natural selection might be able to "tweak" the beak of a Galapagos finch to survive on indigenous food sources, but it strained their credulity to think that it could produce a reptile from a fish, or a whale from a terrestrial mammal. They were now convinced that these things *had indeed happened*; but some other mechanism – either from an external source, or internal to the organism itself – must be responsible for them. Many proposed what were essentially the unquantifiable "vital forces" that most scientists had been trying to exclude from science since Newton. One quasi-scientific attempt at a model along these lines was called orthogenesis ("straight line creation" of new species). Orthogenesis argued that evolution did have a macro-scale, multi-generational direction (although no particular goal), as opposed to Darwin's view that evolution was only about adaptation to the local environment within the constraints of random variation. Still others fought for Lamarck's view that organisms could modify their own structure in response to external stresses, and then pass these modifications on to their offspring, much as humans can do with their culture. Both of these alternatives avoided the physical, as well as the philosophical, problem of coordinating "random" changes in several different structures simultaneously while maintaining a viable organism. A small but significant minority, including the other discoverer/inventor of natural selection, Alfred Russel Wallace, believed that natural selection could explain virtually everything. Their argument for selection acting as a creative as well as a destructive force was its ability to perpetuate an advantageous trend, which cannot change rapidly; the classic textbook example is that selection would favor a longer neck on a giraffe, gradually but continuously, over thousands of generations until the current form stabilized. (Gould notes in his essay *The Tallest Tale* that this is actually a very bad example; but the concept remains.)

In 1871, in *Decent of Man*, Darwin elaborated on a second adaptive-based evolutionary mechanism, which he called "sexual selection." In this view, a male peacock with an especially impressive display might be "selected" by a female to mate, despite the fact that the tail itself may be an impediment to such daily activities as feeding and avoiding predators. In this way, male peacocks might develop ever more impressive displays independently of, and perhaps even at the expense of, natural selection. This mechanism also met with limited acceptance in the professional community.

Mendel, Population Genetics, and the Modern Evolutionary Synthesis

The next essential piece of the puzzle was obtained around 1900, with the "rediscovery" of Mendel's genetics. (Two different scientists independently discovered the essential principles at about this time, and both found that an Austrian monk named Gregor Mendel had published similar work in an obscure and unread journal some 35 years earlier.) Mendel developed a model for inheritance that included four essential components. The first was that "genes," whatever they were, were discrete particles of some sort. (Today they are recognized as lengths of the molecule DNA.) The second was that each organism contained *two* complete sets of these genes, with one set obtained from each of its parents. This implies that there must be a mechanism in the reproductive process that reduces the number of these genes to a single set in the sex cells of each parent (today known as meiosis), so that when they fused to form the offspring's genome, two pairs (and not four) would be present. Third, the genes from each parent could be slightly different; today these different "versions" of the same gene are known as *alleles*. In the pea plants that he studied, one allele might produce tall plants while another produced short plants; one would produce purple flowers while another would produce white flowers; and so on. Fourth, Mendel noted that only one of each pair of genes was necessary for proper functioning; the other could be, and in his simplified model always was, inactive. His model stated, however, that the probability that one version of the gene would be expressed was not random (50-50), or always from either the father or mother; rather, certain alleles were "dominant," and if paired with the other "recessive" version would always express itself at the expense of the other. Only if both alleles were recessive would that character of the gene appear in the organism. While overly simplistic in certain ways – it was both easy and incorrect to infer that there were only a few possible alleles for each gene, for example, and that each gene influenced only one aspect of the developed organism – it was still a remarkable accomplishment, especially considering the limited academic and technical resources available to him.

There were some additional important implications for evolutionary theory in this model. First, it suggested that genes were metaphorical instructions, rather than little eyes, ears, and toes, or a complete little individual ("homunculus") that would be influenced in some way by the other parent. (Gould discusses the importance of this new way of viewing the problem in his essay *For Want of a Metaphor*.) Second, the discrete, particulate nature of these genes overthrew models in which genes were a continuously-varying fluid of some sort. The most popular pre-Mendelian models of inheritance involved the concept of "blending." In blending paradigms, it made sense that a tall mother and a short father would produce children of intermediate height. However, blending inevitably led down a path in which any new version of a gene would be "diluted" in a few generations to the point where it could have no effect generations later, thus effectively precluding it as an agent of evolutionary change. But Mendel's discrete, particle-based genetics with dominant and recessive alleles could not only explain the occasional "black sheep" from two white parents, it suggested a mechanism by which a single genetic mutation could spread throughout a population, perhaps eventually leading to new species. Many early geneticists, in fact, assumed that the mutation of a single gene could directly produce a new species. (The implication that a new species could arise abruptly via one or two mutations was in direct conflict with Darwin's position that evolutionary change was gradual and continuous.) Supporters called their theory "mutationism," which was a version of saltationism ("sudden jumps"). Early studies with fruit flies showed, however, that mutations led to increased genetic variability, but did not seem to produce new species.

While mutationism failed to prove itself as a valid evolutionary mechanism, Mendel's genetics was highly damaging to other mechanisms. It was very difficult to imagine a credible way in which the host organism could affect the presence of one allele over another via personal effort (Lamarckism), especially when the actual pattern appeared to follow the laws of random statistics; or that new alleles would sequentially change over time in such a way as to allow the host's lineage to follow some preferred direction over multiple generations (orthogenesis). However, the two-stage process of undirected allele combinations, followed by favorable or unfavorable "selection" (life or death) of the organism that developed from each pot of alleles, with the chance to "play again" awarded to the survivors – *that* was conceivable. Darwin's stock shot up; scientists began to regard him as a brilliant thinker ahead of his time, rather than a naturalist of limited intellect who wrote well but had some naïve ideas.

The modern evolutionary synthesis, as it would later be called – named for the fusion of genetics and natural selection – accepted another aspect of Darwinism: that the organism was the sole unit upon which natural selection, and therefore evolution, worked. The unseen hand of Adam Smith created high-level order purely from individuals acting in their own best interests; there were no "higher" forces directing populations or species to work for mutual benefit. How, then, does one explain the behavior of social insects such as ants, or altruistic behavior in humans? This became one of the most important problems for the modern synthesis, and was finally addressed by applying "game theory" to the problem. Game theory is a complicated branch of probability that, among other things, shows how sacrifices in the short term – which appear to be "anti-Darwinian" – can lead to larger gains in the long term, and are thus really consistent with the idea of self-interest. As Gould discusses in one early essay, *So Cleverly Kind an Animal*, the concept of "kin selection" was formalized by W. D. Hamilton and John Maynard Smith in the early 1960s. Darwin had argued that those organisms that survived and reproduced passed on those traits to their offspring; after Mendel, those traits were recognized as genes. Kin selection argues that, if the "goal" of an organism is to have its genome passed on to future generations, then sacrificing one's own life to save multiple siblings or offspring offers such a long-term benefit, mathematically. (Organisms do not perform any calculations, of course – the argument is that such behavior is selected for if it randomly appears.) Supporting evidence for the reality of this perspective comes from the unusual genetic makeup of most social insects. As discussed, the true significance of this perspective is that it offers a "self-centered" explanation for altruistic behavior, which in turn precludes the requirement to develop a separate mechanism to explain it. (In the early essay referenced above, Gould fully supported this concept. Later, he revised his worldview to incorporate evolutionary forces working directly on groups or species, but he never argued that kin selection did not occur.)

Another problem that the merger of Mendel and Darwin faced was that most attributes of organisms, including humans, appeared to vary continuously. It was true that babies were either boys or girls, but few other features appeared to be as "discrete" as the white or purple flower of Mendel's pea plants. However, genetic studies in the first decades of the 20th century showed that many features that appeared to vary continuously between certain limits among individuals, such as physical size, were actually a function of several different genes. It was then shown mathematically that if each of these genes were given a random distribution of available alleles, the resulting distribution of the characteristic would *appear* to vary continuously in a hypothetical population. In the 1920's, three mathematically-oriented geneticists – Sewell Wright, R. A. Fisher, and J. B. S. Haldane – are credited with inventing the field of *population genetics*. Within this construction, "evolution" is interpreted as the manifestation of changes in allele frequency within a population over time. This interpretation has several notable features. First and foremost, it is consistent with natural selection, and inconsistent with the other prominent mechanisms being considered at the time. Second, as formulated, it is also consistent with Darwin's view of evolution as a gradual, continuous process, since it still requires multiple structures to evolve in a coherent way via an incoherent (partially random) mechanism. It explicitly rejected saltationism.

Population genetics also recognized other mechanisms that could affect the average physical characteristics of a population over time. A process called genetic drift, for example, involved changes in allele frequency due strictly to random processes in reproduction. Each organism, as noted, contains two copies of each gene, and thus possibly two different alleles; but only one is included in any sex cell. (Different sex cells will contain different combinations of alleles.) The mathematical formulas behind population genetics show that the percentage of organisms with one particular allele can change over several generations based on nothing other than a sampling effect; that is, there is a certain degree of arbitrariness inherent in the process. Such processes are said to be *non-adaptive*, meaning that they involve changes in the structure of an organism over time (including, perhaps, the creation of new species) via a process other than natural or sexual selection. The relative importance of adaptive versus non-adaptive mechanisms in evolution, therefore, becomes an important issue in the further development of evolutionary theory.

Population genetics convinced most geneticists that natural selection was the dominant, albeit not exclusive, mechanism driving evolution. However, other important communities remained unconvinced. One group was the field naturalists, who objected primarily on the ground that natural populations appeared to possess far more variation than the geneticist's models assumed. In fact, they were correct in this. Work by Dobzhansky in the 1930's proved that the population geneticist's models could still work if more genetic variability and diversity were included. Dobzhansky also argued that natural selection would work to establish and maintain this genetic and morphological diversity.

Another important group that remained skeptical of the primacy of natural selection was the paleontologists. This community saw what they thought was evidence of steady progression in the fossil record, which was consistent with orthogenesis and/or Lamarckism. One of their most famous examples was the natural history of the horse, which appeared to move gradually and continuously from small, multi-toed browser to large, single-toed grazer over the span of tens of millions of years. G. G. Simpson successfully made the case in 1944 that the fossil record of the horse in particular was not, in fact, linear. The record actually shows a large degree of branching – in multiple directions, with browsers and grazers coexisting for extended periods – rather than a single, coherent trend. The same argument can be applied to other apparently-sequential lineages.

The coming together of the geneticists, field naturalists, and paleontologists in the mid-1940's formed the "modern evolutionary synthesis," or simply the modern synthesis. (Perhaps oddly, Gould writes few essays on the history of population genetics or the formation of the modern synthesis. He does discuss it in some detail in 2002's *The Structure of Evolutionary Theory*.) One of the key tenants of this new orthodoxy is that natural selection is by far the most important mechanism driving evolutionary change, although other adaptive (e.g., sexual selection) and non-adaptive (e.g., genetic drift) mechanisms may also play roles. Saltationism is excluded; macroevolution is, as Darwin proposed, essentially microevolution plus time, and evolutionary change is continuous (although it may occur at varying speeds, depending on the degree of environmental pressure). The modern synthesis also recognized, via the work of participant Ernst Mayr, that the formation of new species was far easier in small populations than in larger ones, in accordance with mathematical allele models. Speciation may thus occur when a small population becomes isolated from the parent stock, somewhere at the edge of its habitable range, and thus also subject to more extreme environmental pressures; this is called allotropic ("in another place") speciation.

Another of the important underlying assumptions is that all evolutionary phenomena – and in particular, the formation of new species – are consistent with genetic mechanisms that were *known and understood at the time*. In other words, while there might be debate over the relative importance of different mechanisms, supporters of the modern synthesis agreed that no additional mechanisms were required to explain evolution. (Since this time, mechanisms such as lateral gene transfer have been added, but for the most part the orthodoxy has remained intact at the microevolutionary level.) The rationale for this, Gould notes, is very similar to the one Lyell used to throw out catastrophic events in geology: currently understood mechanisms appear to be sufficient, and operating from this perspective precludes unnecessary and disruptive speculation.

Gould points out that the modern synthesis differed from Darwin's perspective in an important way. Darwin (as well as the earlier version of the modern synthesis, Gould states in *The Structure of Evolutionary Theory*) argued that natural selection was only one of several mechanisms driving evolutionary change. He also believed other adaptive mechanisms, specifically sexual selection, and non-adaptive mechanisms, such as the correlation of features (white cats tend to be deaf, for example) and other internal constraints of the organism's development could play roles in evolution. By the mid-1940's, however, the modern synthesis settled on Alfred Russel Wallace's view: natural selection, by itself, could explain almost everything. (Gould refers to this as the "hardening of the modern synthesis.") Proponents of this view borrowed Wallace's term and called themselves "Darwinists," "neo-Darwinists," or "strict Darwinists." In his writing, Gould also refers to proponents of this view as *adaptationists* (in that every feature of an organism represents an adaptation, via natural selection, to external conditions) or *functionalists* (in that every feature of an organism serves, or at some time in the past served, a function that led it to be favored by the selection process). Gould notes in several early essays that Darwin stated (in letters to Wallace) that he was not in this camp; he recognized natural selection as only one of several mechanisms, albeit an important one. That is, Gould states, Darwin was not a "strict Darwinist." This became important to Gould for rhetorical purposes, because early in his career he broke with this aspect of the modern synthesis.

An interesting and subtle consequence of the view that natural selection alone can explain virtually all aspects of evolution is that paleontology "ceases to matter." If natural selection is powerful enough to produce any feature (or the same feature multiple times, in the case of eyes or wings in different lineages), and if non-adaptive constraints play minimal roles, then it doesn't matter where you start – you will always end up at the same place, via convergence. Because natural selection produces optimal, if not perfect, solutions, the particular path taken to get there is reduced to details. These details may be interesting, the way stamps of different countries are interesting, but have no real significance to the *theory* of evolution. This conclusion, coupled with the Darwinian argument that the fossil record is so coarse and incomplete that it cannot provide the kind of detailed information necessary to study the evolutionary process, effectively reduced the field of paleontology to "the keeper of the record" rather than the potential source of useful information about the evolutionary process. Data to feed the complex mathematical models of the modern synthesis would come from genetic and morphological studies of fruit flies and *E. coli*.

Punctuated Equilibrium

Stephen Jay Gould (1941-2002), as he stated in several essays, was the grandson of Jewish immigrants who labored in New York City sweatshops. In the classic American tale of that time, they and their children (Gould's parents) managed to reach the middle class. He grew up in Queens, and attended public schools there. He fell in love with dinosaurs at an early age, and decided that he would become a paleontologist. He attended a small liberal arts college in Ohio, where he was exposed to a more humanities-oriented education that he might have obtained by majoring in science at a larger or research-oriented institution. In college and graduate school, he studied evolutionary theory – specifically, the modern synthesis, which he apparently fully accepted – with the vision of trying to bring its principles into his chosen field of paleontology.

As a graduate student at Columbia University, he chose to study the wildly diverse land snails of the Bahamas and other Caribbean islands. Snails offered the dual advantages that their shells captured the entire growth history of at least part of the organism, and that these shells were readily preserved as fossils. His goal was to identify shell features that could be quantitatively correlated with the immediate environment. That is, rather than merely describing fossils, he was trying to identify specific evolutionary *patterns* in the fossil record, and to use this information to study the adaptive process itself. Caribbean land snails in particular were well-suited to this purpose for several reasons. First, their diversity suggests that they are relatively susceptible to evolutionary forces. Second, individual snails do not move very far during their lifetimes (thus remaining in one environment), while each island has multiple environments, allowing comparison. Third, the isolation of islands generally can simplify the problem by largely eliminating the possibility of migration of a different species from elsewhere. The fossil beds, in the form of solidified sand dunes, also preserved an account of certain periods with high temporal resolution. (Gould discusses the details of his experiences and his findings in his essay *Opus 100*.)

Over time, and with help from David Woodruff and other colleagues, he identified two patterns in the data that caused him to question the established evolutionary worldview that he had been taught. The first involved the relationship of two major categories of snail shells, which he identified as "ribbed" and "mottled." He assumed at first that these categories each represented a separate lineage. But as he and colleagues examined the shells in detail (using numerous quantitative measurements and the recently-practical "personal computer" as an analysis tool), as well as the soft anatomy of the extant groups, it became apparent that the *actual* lineages were based on geographical location. It was surprising that the lineages had remained "in place" during the past several tens of thousands of years, considering the rising and falling of sea levels (connecting and separating islands) during periods of extensive glaciation. Also surprisingly, several lineages had each, apparently, gone back and forth between mottled and ribby forms (with many other features following along) multiple times, with the mottled members of each (distinct) species superficially resembling each other more closely than other members of their own lineage – until the anatomical details were closely examined. What this apparently meant, Gould inferred, was that certain patterns in microevolution, within a given group, were easier than others. Evolution tended to move species along certain *channels*, rather than in all directions with equal ease, as the modern synthesis implied. (The concept was not entirely new to Gould, who had written a senior undergraduate thesis on D'Arcy Thompson. In his 1917 classic *On Growth and Form*, Thompson argued that laws of form existed in biology that exerted a "force" on biological systems, analogously to the way gravity forces planets to be spherical. While Gould never accepted Thompson's central argument, he was attracted to certain details, particularly on how the physical form of an organism might *constrain* what natural selection could do with the offspring.) This line of thinking would eventually lead to his first book, aimed at his professional colleagues: *Ontogeny and Phylogeny* (1977). This path would also take him to his famous and controversial presentation on the spandrels of San Marco, which will be discussed in the next section.

The second theme that he extracted from the snail shell data that caused him to question the "big picture" was the fact that these changes in form, when they appeared, were abrupt – like most paleontological data. However, the fossil beds he was examining were detailed and complete over the transition period. Further, the limited size of the island – even when connected to others during times of low sea level – meant that he could identify every species of snail, living and fossil, in the entire region; no other species had migrated in that could have produced the false *appearance* of sudden change. Evolution had to work with what was on that small collection of islands, and nothing else. Why did he not see the extended, continuous transitions he was looking for? It puzzled him.

A fellow graduate student at Columbia, Niles Eldredge, was troubled by a similar pattern in trilobites. In addition to finding similarly abrupt changes in eye structure throughout well-preserved fossil beds from Ohio to New York, he was bothered by something else as well: during the periods between the transitions, there was virtually no change at all over millions of years. It had been established that the local environment had undergone the usual amount of change during this period, which – according to both Darwin and the modern synthesis – should have produced a certain amount of anagenesis or phyletic gradualism. The trilobites should have changed *somewhat* over time. Eldredge noted in frustration that they did not seem to *want* to change – except when they did so abruptly. Furthermore, in many cases the parent and daughter species *coexisted* for an extended geological period. Anagenesis argued that the entire parent population shifted towards the daughter form (due to the pressure from natural selection on all members of the population to adapt); how could both exist at the same time, if migration was excluded? In discussions, Eldredge and Gould began to question the gradual but continuous orthodoxy, and began to wonder if the fossil record might be telling them something important about how new species arose after all. Perhaps uniformitarianism was not always the correct way to view the history of earth and the life on it; perhaps species did arise relatively suddenly, via relatively abrupt "branching" off of a parental population rather than anagenesis, at least sometimes.

Gould completed his doctorate, and landed a position at Harvard. He and Eldredge remained in contact. Gould credits Eldredge with the observation and the analysis showing that if Ernst Mayr's widely-accepted view of allopatric speciation in small populations were true, it could directly explain the abrupt appearance of new species in the fossil record. Further, it would explain the coexistence, over extended periods, of the parent and daughter species. The very features that allowed the daughter species to evolve rapidly – small population size in a small, isolated region – would make it difficult to find a high-quality fossil bed in the place where the process took place, which was also consistent with the record.

In 1972, Eldredge and Gould produced an article entitled "Punctuated equilibria: An alternative to phyletic gradualism." The term "punctuation" was selected for its reference to the old cliché that a soldier's life was "long periods of boredom punctuated by short periods of terror." The paper and the title concept of punctuated equilibria – later, "punctuated equilibrium" or just "PE" – did not meet the fate of most big-picture concepts produced by newly minted scientists, which is to vanish without a trace. Instead, it received massive attention within the professional community, and was highly controversial. This appears (at least, to this outsider) to have been due to the way in which it was written. First, while it included the technical details of Gould's snails and Eldredge's trilobites, it went much farther and claimed the entire fossil record in support of its thesis. Second, and perhaps more importantly, the first several pages discussed, not data, but the way in which theory and data interact in people's minds (a theme that Gould would return to many times in his essays). There is no such thing as "purely objective" data, the paper stated; it quoted Darwin himself stating that all evidence must be viewed in light of some theory, some *worldview*, before it could be interpreted. The 1972 PE paper argued that, since the 1940's, phyletic gradualism had become the only acceptable speciation worldview. Therefore, it continued, no amount of new evidence would ever be able to overthrow this worldview *even if it were wrong*, on the grounds that none of the participants could *see* that it was wrong; there were no other viewpoints to compare it to. What was required is a competing worldview. Then the evidence – all of the fossil record, not just their data – might be used to evaluate which (if either) is the better paradigm. Few scientists noticed the extended periods of no or minimal evolutionary change before, they argued, because the very concept was outside the realm of their working paradigm. Paleontologists and evolutionary biologists look for *change*; when no change is observed, their worldview categorizes it as a non-event; "there is nothing here, let's forget about it and look elsewhere." (Gould discusses this concept in his essay *Cordelia's Dilemma*.) What Eldredge and Gould were claiming was that the lack of evolutionary change over these extended periods was apparently real, and required explanation; in their famous phrase, "stasis is data." The widespread appearance of stasis in the fossil record also implied that speciation via phyletic gradualism, while presumably still a valid mechanism, might not be as common as Darwin and proponents of the modern synthesis believed.

(All of Gould's major technical papers, and many other aspects of his professional work, are discussed in "Stephen Jay Gould: Reflections on His View of Life," edited by Warren D. Allmon, Patricia H. Kelley, and Robert M. Ross, and published in 2009. This book is a collection of essays written by his colleagues and several of his former students, and covers most aspects of his professional career. I will use "SJG:RHVL" to reference this book in the text that follows.)

The 1972 article concluded with some thoughts on other possible implications of PE to the larger field of evolutionary biology. One of these was that species could be thought of as "real" again, at least during periods of stasis, a view effectively abandoned by Darwin and the modern synthesis in favor of gradual but continuous phyletic change. This, in turn, implied that the field of paleontology could again serve a relevant source of raw data to the builders of theoretical evolutionary models; it would regain some of the professional stature it lost when the modern synthesis concluded that genetics alone would be a sufficient source of observable data. One can only gather data on the duration of stasis and the rate and conditions of branching from the fossil record itself.

(At first, Gould simply believed that PE was an important but straightforward modification to conventional Darwinism; an empirical argument that stasis was real and that evolution occurred with relative rapidity, when it occurred at all. It emphasized a "branching" bush-like geometry for the history of life, as opposed to a "ladder" view of one species changing gradually into another – an important distinction, but not [in his view, as well as others] really revolutionary. However, during the decade that followed, he came to recognize some additional and fundamental implications of PE. Darwinism identified macroevolution as microevolution plus time; but this, in turn, relied on continuous morphological change, with each tiny change favored by natural selection. If stasis truly existed, then the extrapolation of micro to macro became difficult to explain. Gould eventually came to develop a view in which the two phenomena, while related, were fundamentally separate. This revised view is discussed in the later section on hierarchical evolution, and lies at the heart of his final work *The Structure of Evolutionary Theory*.)

The 1972 article, as noted, produced quite a stir when it appeared. Certainly it was not surprising that hackles were raised by a couple of young guns telling the professional community that they fundamentally misunderstood the evolutionary process (because they lacked the perspective to view it clearly, no less!). On the other hand, it is difficult to imagine that their paper would have received the attention it did without such a direct, frontal assault. Gould and Eldredge were staking a significant fraction of their professional future by picking this fight. The fact that they drew on no new mechanisms, but rather explained PE in terms of a direct but unappreciated implication of Mayr's widely accepted work, made it difficult to dismiss out of hand. (Mayr, according to Geary in SJG:RHVL, acknowledged that he did not emphasize the concept of stasis in the parent population – which was precisely their point.)

The early battle that ensued was waged along two fronts, one specific and one general. The specific debate was, "Were Eldredge and Gould right about the frequency of stasis in the fossil record, or were these highly unusual islands in a sea of gradual, transformative anagenesis?" Data was offered in support of the view of long-term gradual transformation; but in some cases, others reinterpreted the data and concluded that there were two stable species present, one being slowly replaced by the other over time (in particular, see the essay *Ten Thousand Acts of Kindness*). Gould was careful to not claim exclusivity for PE. Both mechanisms, he stated, took place; what was important was the relative occurrence of each of these, within the "publication bias" framework of only reporting what seemed to be "results." One of Gould's essential points was that the PE pattern would only have to be found in the fossil record *a significant fraction of the time* to require an explanation. The modern synthesis had not predicted the common occurrence of stasis. The debate was long and often heated, but (almost everyone now agrees), fruitful.

The more general argument was, "Is PE a fundamental challenge to Darwin's theory of evolution itself?" Such charges were associated with the whiff of heresy and treason, with the tone carrying the suggestion that Eldredge and Gould might be radicals or crackpots. These concerns carried extra weight at that time, due to the resurgence of creationism in the political arena. They were always careful to state their belief that PE was within the Darwinian framework, and countered with the argument that some of their critics were not actually reading their work, or not reading it carefully enough. In some clever rhetorical thrusts, Gould noted several areas in which the views of the modern synthesis, at least as it stood at the time, were themselves inconsistent with Darwin, and that PE was, in these ways, closer to his vision. Throughout the rest of his career, Gould would always describe PE and his entire worldview, no matter how it evolved, as an *extension* of Darwinism.

In retrospect, looking back several decades after the concept was proposed, how has PE fared in the professional community? Several of the essayists in SJG:RHVL have weighed in on this. Allmon (p. 58) writes: "Although it remains difficult to put a firm number on its frequency, it is clear that morphological stasis is widespread in the fossil record, at least in many groups of benthic marine macro-invertebrates, and perhaps in many other groups as well, and may well be predominant in many clades under most circumstances. This was not predicted by the Modern Synthesis and was almost wholly unknown or appreciated prior to 1972." Geary (p. 131) writes: "Thus . . . it does appear that when large, relatively unbiased samples are compiled, the pattern of PE is dominant." Lieberman (pp. 229-30) writes: "Within sexual species, stasis appears to be the dominant mode, but important exceptions have been documented . . . . I have come to the conclusion that stasis is probably the rule, although exceptions also exist, and even in stable lineages oscillation does occur."

Adaptationism and the Spandrels of San Marco

In a parallel but distinct line of thought, Gould was also struggling with a second inference about evolutionary theory that he believed he saw in his Caribbean land snail studies. The modern synthesis implied, he wrote, that the mechanism of natural selection was so general and so powerful that, if a species could be represented as a metaphorical "billiard ball" sitting on a pool table, it could be pushed in any direction by the pool cue of natural selection. In this view, the porpoise-shape-with-fins design appears in sharks, reptiles, and mammals because it is "the right answer," and natural selection is powerful enough to create it repeatedly, albeit with a record of the raw material it started with in the form of tiny details. (This metaphor dates back to the 19th century. Another way to view it is to envision the table surface as, instead of perfectly flat, rather "rubbery," with numerous peaks and valleys that change with time, representing changes in the environment. The metaphorical billiard ball then rolls – that is, the species "evolves" – via the adaptive process of natural selection, easily and without resistance in whatever direction leads "downhill" at that moment.) In this context, the observation that numerous details of the Caribbean land snails seemed to go back and forth between the same complex states posed a problem for him. Some of these features were apparently adaptive – shell thickness or ribbing (for strength), for example; but there were just too many of them, and most of them – a bump here, a different coiling ratio there – did not appear to offer any selective advantage. According to evolutionary theory, while general trends could reappear via convergence, specific details should never reappear; the odds of evolution producing the same *detailed* structure twice were infinitesimal. Yet, that is what appeared in some cases in the fossilized sand dunes.

Gould's interpretation was that the organism had certain built-in evolutionary "channels" that it preferred to transverse in the presence of changing environments. This was also not a new argument; Gould, being a student of the history of science as well as science itself, was aware that Francis Galton, Darwin's cousin, had proposed this idea in 1869. In the metaphor of the pool table, Galton suggested that the billiard ball was not really a sphere, but rather a complex polyhedron. Such an object would resist small amounts of adaptive pressure, and then would move only in certain directions (and not necessarily exactly in the direction of the adaptive "force") in the presence of higher pressures. (Gould explicitly discusses this metaphor and some specific examples involving dog breeding in his essay *A Dog's Life in Galton's Polyhedron*.)

Other 19th and 20th-century thinkers had also developed ideas that emphasized the relative importance of the morphological form of an organism as a *constraint* on what evolutionary paths its descendents could follow. One of the most important of these was Ernst Haeckel (1834 – 1919), who became one of Darwin's prominent advocates in Germany. Haeckel believed that there was a direct, one-to-one correlation between the evolutionary history of a lineage (technically called "phylogeny") and the *development* – a technical term that includes the emerging field of embryology – of the living descendents of that lineage from fertilized egg to adult (technically called "ontogeny"). His theory that the developmental process of an organism "recapitulates," or repeats, the evolutionary history of the entire lineage came to be referred to as *recapitulation theory*, and is associated with the obtuse phrase "ontogeny recapitulates phylogeny." The classic example is the appearance (and later re-absorption) of gill slits in developing mammal embryos; in recapitulation theory, the embryo "re-lives" its entire evolutionary process during its development, with all steps present and in the same order, and with new developments being tacked on only at the end.

(This theory, as Gould discusses in several essays, was widely accepted in western culture and rapidly applied to the history and races of man. In recapitulation theory, the transition from child to adult is considered to be part of the evolutionary process, as was the cultural development of humans over many generations. It was directly inferred that today's children were, in many ways, "equivalent" to *adults* living hundreds or thousands of years ago. Further, the argument was readily extended to view different races of man as developing at different rates – Caucasians were always found to be most advanced when the studies were performed, with Asians in the middle and Africans bringing up the rear. In the context of recapitulation theory, adults of other races were "like" white children – and needed to be taken care of, for their own sake. This argument was used to justify colonialism and imperialism, and was so widely accepted in the west that it became almost invisible in the home countries. Haeckel himself did not intend for his ideas to be applied in this way, but it happened nonetheless – a general problem that concerned Gould greatly. He presented a general critique the biological arguments against the equality of different races in his essay *Human Equality is a Contingent Fact of History*.)

Haeckel overreached; recapitulation theory proved to be fruitless in advancing the understanding of evolution. Further, the central tenant of "recapitulation" – all the same events in exactly the same order – itself proved to be incorrect. However, it is now appreciated that there are nuggets of truth in his views. In particular, the evolutionary pathways that organisms follow during their embryological and youthful development do reflect "channels" that natural selection can influence relatively easily. One of the most important examples, observed in many phyla, is the retention of child-like features into adulthood, technically referred to as *neoteny*. Other non-developmental channels have also been empirically identified, such as *scaling laws*. A classic example of a scaling law is the so-called "mouse to elephant curve," in which the ratio of brain weight to body weight is plotted for (in this case) all mammals. Generally, the points fall on a broad line – although the line is not straight, but instead follows a logarithmic formula. The fact that there is a correlation of these two biological factors, however, suggests that the two are *not independent of each other*. This stands in direct contrast to the "billiard ball" argument of the modern synthesis that natural selection can guide the evolving organism in any direction – such as a small body and a large brain, or vice versa, at least within some range.

Gould studied the evidence surrounding patterns of both development and scaling, as well as his own evidence on the apparent channels of evolution that his land snails appeared to follow, and came to the conclusion that natural selection was not as dominant a force as the modern synthesis implied. To be sure, he believed in natural selection, and his early papers on snail evolution discussed what he identified as selection-based adaptation. Nonetheless, he became very interested in the *channels* and *constraints* – his choice of terminology – that an organism's form and development placed on microevolution. If the view that natural selection could produce any possible structure was called "adaptationism" (a term that he used and associated with strict Darwinism), then he came to refer to the view that the internal biological and developmental constraints were of *comparable* (not necessarily greater) importance as "formalism" or "structuralism." Gould spent years studying the past and present of these fields, and published his first book on this subject in 1977. The book was titled *Ontogeny and Phylogeny*, in deference to Haeckel's catchphrase, and was intended for his professional colleagues rather than a more general audience; it is very technical. Allmon in SJG:RHVL states that this book "may well end up being one of his most lasting and influential scientific contributions . . . ."

1977 was also the year that *Ever Since Darwin*, Gould's first collection of his essays from *Natural History* magazine, was published. This collection contains several essays that express completely orthodox neo-Darwinian positions on the power of adaptation, as well as several on formal and developmental constraints. During this period, however, Gould was apparently becoming increasingly frustrated with the views of the evolutionary community at large – dominated by population geneticists – which downplayed or ignored the roll of constraints on the history of life. He and colleague Richard C. Lewontin wrote a presentation condemning what they perceived as the closed-mindedness of the adaptationist community to any mechanism other than natural selection. In 1977, he went into the lion's den to pick a fight at an important meeting in England. The presentation, entitled *The Spandrels of San Marco and the Panglossian Paradigm*, was similar in approach, but even more provocative in tone, than his earlier publication on punctuated equilibrium.

"Spandrel" is an architectural term that refers to the curvy "v"-shape that the bottom edge of a domed ceiling follows when it necks down between two supporting arches at right angles to each other. If the architectural design calls for a dome to be placed directly on arches, with the dome extending down to fill in the gaps, then spandrels are produced; this is straightforward if somewhat arcane geometry. Because they are elevated and mostly vertical, and because the arches themselves are usually "open," it is common to decorate spandrels with impressive art. Gould toured one such spandrel-laden building in the city of Venice (specifically, San Marco), and came up with a metaphor for the relationship between constraint and adaptation. If one knew nothing about architecture, he argued, one might conclude that these beautiful spandrels were the key design feature of that part of the building; metaphorically honed by natural selection to optimization, if not near-perfection. However, he continued, biology is all about the architecture; and in architecture, spandrels are merely an inevitable side effect of domes on arches. One might as well decorate them, but these decorations should not be confused as being an essential part of the design. Biologically, spandrels represent a *constraint* that is not the optimization of anything; they are not, metaphorically, *adaptive*. Evolutionary history and current biological designs, he argued, are full of beautifully decorated spandrels. These spandrels may have been tweaked by, but they were not *produced* by, natural selection.

Had this been the only metaphor in the presentation, he probably would have escaped unscathed – but the presentation would have had little impact. So Gould drew on another non-biological reference, this one from 18th-century French literature. Dr. Pangloss is a character in Voltaire's 1759 satire *Candide*. As horrible events plague the characters, Dr. Pangloss continually expresses the view that, while these results do not represent perfect or even good outcomes, they do represent the best that *could be achieved* compared to all possible alternatives, in the big-picture scheme of things. (Pangloss is identified as an "optimist," when this term still literally referred to the view that an outcome would be "optimal.") Pangloss's mantra is, "All is for the best in the best of all possible worlds," a reference to the German philosopher Leibniz. After explaining this concept to his audience, Gould proceeded to tell them that they were all being "Panglossian" with their adaptationist "Just-So Stories" (a reference to Rudyard Kipling's book of stories for children with titles such as "How the Leopard Got His Spots" and "How the Camel Got His Hump"). Opponents viewed Gould's remarks as not just provocative but anti-Darwinian; and, in the sense of "strict Darwinism," they were.

Gould was careful to acknowledge that adaptation via natural selection occurred. He further acknowledged that the adaptationist approach of looking at a feature and asking "what does this do to help its host?" has been fruitful in determining the function of such features from the pituitary gland in the brain to one-way valves in blood vessels. What he charged them with was invariably assuming that any feature or structure *must* serve, or in the past have served, some purpose that was favored over many generations by natural selection. In this view, for example, when ancestral humans lost most of their body hair but retained their eyebrows, their starting point would be that eyebrows serve (or served) a *function*, leading to favorable treatment at the hands of natural selection. All that remained was to come up with a "just-so story," Gould charged, to explain what that function might be. Lip service might be paid to non-adaptationist arguments, but in practice it was almost always assumed – usually with no evidence – that the form of any given structure in an organism was the result of natural selection working on highly plastic material. Here and elsewhere, he essentially accused the adaptationist orthodoxy of replacing the all-powerful and optimizing God of "natural theology" – another popular topic in these essays – with natural selection as His secular equivalent. This paper, which was both relatively free of jargon and deliberately provocative, served its purpose: while not winning many converts and producing a lot of genuine anger, it did induce the community to reexamine its adaptationist assumptions. (Allmon, in SJG:RHVL, references members of the community noting that "fanciful Just So stories are now, thankfully, rarer.") Many of Gould's essays discuss individual cases where the constraints of natural history played the dominant role in a structure, with natural selection only working within the available envelope to shape what it could. Blood is red, he noted, not because organisms with red blood out-competed those with green blood; it is red because the essential molecule, hemoglobin, is based on iron.

It might appear that the difference between the adaptationist and the formalist viewpoints is only a matter of degree. Both communities recognize natural selection, and both acknowledge at least a few non-adaptive, "legacy of form and quirk of natural history" processes. Thus, the entire debate may appear to be a technical tempest in a teapot; the factions are only debating relative importance. This appearance is deceiving. The underlying and usually unstated reason why the issue is so highly charged is because – like everything in evolution – it must eventually involve *Homo sapiens*. Specifically: is our large brain, and by extension our language-capable mind, the direct result of adaptive processes? That is, did a larger brain offer our ancestors a selective advantage over our primate and hominid relatives? Or is it instead a *non-adaptive side effect* – a spandrel – of some other process? Could it be that civilized life, which is so dependent on our huge brain and highly-developed mind, is merely a capitalization on a fortuitous happenstance? This debate, and others that appear to be about technical details and methodology, is at least in part about man's place in nature. Is man the inevitable result or the directed culmination of something, divine or secular? Or are we simply one species out of a million (albeit with the unusual ability to contemplate the distinction), a lucky accident, who too will also pass away, unmourned, like all of the others? Gould repeatedly argues in these essays that all evidence suggests the latter (and he, for one, is OK with that); the former, in his view, is misleading and counterproductive "hopeful thinking."

His views on the "happenstance" of human existence illustrate perhaps the most fundamental aspect of his worldview: the reality and importance of *contingency*. He repeatedly calls out the resistance that most people – including many scientists – have to adopting this concept. Conceptually, contingency is the opposite of determinism. The latter assumes, usually tacitly, that whatever happened *had to be* what happened, while the former argues that it could have been otherwise. Since history – natural or human – can only happen once, no controlled experiments can be performed, and thus it is very difficult for one faction to convert the other. Proponents of the contingent view argue that, if your great-great-grandfather had been born female instead of male – statistically, the probability was 50% – then someone else, *and not you*, would be here instead. Some people find this perspective incomprehensible, others distressing, and still others merely absurd. The most common counter to this argument is very simple: what happened, happened, and it would again. The same is true for the history of life on earth. (Such debates often drift over into discussions of predetermination, predestination, and the existence of free will.) A somewhat softer version of the deterministic view is that, say, had dinosaurs not become extinct, intelligent life still would have evolved (via contingency); perhaps an intelligent dinosaur would be reading these words instead of an intelligent mammal.

Contingency, Gould states, is often mischaracterized as "randomness," with the implication that *anything* could have happened, which is practically the definition of absurd. Contingency *includes* a genuinely random component, he writes, and this is important; but this component is only one part of a larger, largely deterministic process that operates via the rules of physics and chemistry. Regarding the great-great-grandfather / grandmother argument, Gould clearly believed that his existence was indeed that tenuous; but rather than be dismayed over this prospect, his view was one of humble joy that it was "he" who won the cosmic lottery and had the opportunity to experience life as a human on earth, at least for a little while.

Reductionism, Selfish Genes, and Evolutionary Psychology

Gould was involved in another important struggle within the adaptationist / structuralist debate, over what he called *reductionism* or *atomism*. The essence of this struggle is the independence of features in an organism with respect to natural selection. That is, how easily can natural selection modify one structure while leaving all others alone? Can natural selection "fine tune" each part of an organism individually, or are features so highly correlated that changes in one feature invariably lead to other significant changes as well? Reductionists postulate that correlation between different components is relatively small in most cases, and therefore argue that organisms can be "reduced" to their individual components. If valid, this perspective would permit evolutionary biologists to approach problems with some of the techniques of analysis (literally, "taking apart"), which are commonly used in fields such as mathematics, physics, and chemistry. Gould accepted a certain amount of reductionism; in his essay *Mozart and Modularity*, he references an important argument (dating back to the 19th century) that evolution itself is not possible if organisms are so integrated that one structure cannot change without all other structures changing in a corresponding way. That said, he did not believe that the degree of reductionism proposed by the adaptationist community was realistic, and doubted that the reductionist approach would ever be very fruitful. Also, he believed that there were almost certainly additional rules – all still measurable and testable, at least in principle, and therefore scientific – that appear only when the components are assembled. He discusses this "holistic" view most explicitly in his essay *Just in the Middle*, where the essay's subject, E. E. Just, demonstrates that living and recently-deceased cells behave in some fundamentally different ways. (Similar processes *do* occur in physics and chemistry in more complicated situations, and are often associated with the phrase "nonlinear phenomena.")

The struggle between reductionism and holism quickly found its way to the field of genetics. If individual genes correlate directly with individual features, the reductionist argument would greatly strengthened; "selecting" a feature would be closely correlated with selecting a gene. But genetics suggests that, with a few notable exceptions, one gene can influence many features, and each feature is usually affected by several genes. In these cases, even if the selective advantage of an organism is due to a single modified feature, many genes are effected; similarly, a mutation in one gene may affect an array of features, some of which may offer the host an advantage while others lead to a disadvantage. (A surprisingly large number of genetic changes lead to no detectable change at all, and are therefore said to be selectively neutral.) As a result of this ambiguity, the debate moved to a more technical level. Reductionists, in general, continue to argue that there is a strong, if not perfect, correlation between groups of genes and the structure of individual components. Holists, on the other hand, argue that the connection between an organism's genome and its final form is so complex and indirect that individual genes cannot be selected for, with very few exceptions. Gould was in this camp. He argued that an organism's genome *documented* much of its evolutionary history, but did not *drive* it.

This view placed him at the center of another conflict, this time with Oxford scientist Richard Dawkins, who wrote the 1976 best-seller *The Selfish Gene*. Dawkins' argument is that genes, not individuals, are actually the primary unit of selection in Darwin's theory. (A somewhat oversimplified understanding of this perspective can be obtained from the old joke, "A hen is an egg's way of getting to another egg," with the implication that better eggs will produce better egg-layers via natural selection.) If the reductionist view of a direct, linear relationship between genes and biological structures is accepted, then it is indistinguishable whether the gene or the structure is being favored by natural selection; it is simply two sides of the same coin. This also implies that the magnitude of change in the genome is proportional to the magnitude of change in the resulting organism. If only a few parts of the organism's structure are "evolving" at any given time, in this view, it implies that only a few alleles are being swapped out at the genetic level. If so, then "inferior" alleles can eventually be completely removed from the genome via natural selection. Gould strongly disagreed with this perspective. If the connection between genome and organism is complex and multifaceted, he argued, then favoring one feature affects many genes and many alleles. The genome lives (that is, reproduces) or dies as a complete, jumbled set; alleles cannot be individually selected for. Again, this may appear to be a major fight over a minor issue; but Gould (and, I believe, Dawkins) believed that this was actually a proxy battle in the larger adaptationist – structuralist war. If Dawkins is correct, then individual features can be, to a large degree, independently selected for via direct changes to the genome, and natural selection can explain almost everything in evolutionary history. If Gould is correct, then indirect and non-adaptive processes, including contingency, play a large role in the history of life. In Gould's view, Dawkins is actually the ultimate "strict Darwinist." Gould presents his critique of Dawkins' arguments in his essay *Caring Groups and Selfish Genes*.

Even before publication of *The Selfish Gene*, a related debate spilled over into the public forum with the publication in 1975 of E. O. Wilson's book *Sociobiology*. Gould supported the conclusions of the majority of this book, at least at the time, but vehemently disagreed with the book's last and most influential chapter. Wilson's thrust was that behavior – primarily of insects and other animals, but also (in that last chapter) of humans – was strongly correlated with individual genes. Using what Gould identified as reductionist and adaptationist arguments, Wilson postulated that human behavior – collectively, if not individually – was largely under genetic, rather than cultural, control. Human behaviors, he argued, have been shaped via natural selection for optimal performance as hunter-gatherers, just as (he also claimed) our physical bodies have been.

Gould responded pointedly and forcefully to his more senior colleague at Harvard. His primary line of attack was methodological, emphasizing the genetic problems with the reductionist approach discussed above. In his essay *Biological Potentiality vs. Determinsim*, he argued that it was definitely premature and probably incorrect to argue that there was a gene "for" any given behavior such as xenophobia or aggression. We are unable to predict, based on the genome, how tall an individual produced from that genome will be; the field is not sufficiently mature be identified as a science (with the implication that it might never be). It was more likely, Gould continued, that what is in human genes as it relates to human behavior is the *potential* to behave in any one of a large number of ways. That is, what we "get" from our genes is *behavioral flexibility*. He acknowledged that he could not prove this position, but countered that his opposition could not prove theirs either; they simply assumed its validity. Nonetheless, as Gould feared, Wilson's book led to the creation of the field of evolutionary psychology.

The intensity of his reaction, he openly acknowledged, was not only due to his scientific objections; it was also social and political. Astronomy may be considered apolitical today, in the cultural sense, but Gould always recognized that politics is inherently intertwined with any scientific field that involves man – his origin, his relationship to the environment, and especially his nature. As David Prindle argued in his 2009 book *Stephen Jay Gould and the Politics of Evolution*, any scientist in this field who does not recognize that politics comes with the territory is either naïve, or is taking a political position himself. Prindle identifies Gould as a political leftist, by which he means a "modern liberal" or "humanist," as opposed to (as some have charged) a Marxist. Perhaps the single most important value held by this loosely aligned community, Prindle states, is the concept of equality (of humans) – in Gould's case, equality of opportunity, not equality of result. (He was a tenured professor and best-selling author, after all!) This theme does recur throughout Gould's essays. Thus, it is consistent that his political objection to Wilson's argument is that evolutionary psychology is easily co-opted by social conservatives. Groups looking to preserve their power have referenced the work of "intelligent, apolitical scientists" to justify their positions throughout modern history, often to rationalize the non-equal treatment of people based on race, gender, and class as "natural"; see the earlier discussion on recapitulation theory. Importantly, he notes, these borrowings come regardless of the intention of the researchers themselves. Gould was always forceful in stating that we must not shy away from objective truth, even if it supports politically unpalatable conclusions. (Darwin's view of evolution via natural selection, he noted, has been and remains more politically useful to the political right than the left, despite the odd usage in America today.) But especially if the science is not sound, Gould argues, the scientific community has an obligation to society as a whole to recognize that its results can be used or misused by others, and to take some responsibility for what others do, or could do, with their models.

Hierarchical Evolution

At a technical level, by the end of the 1970's Gould found himself at odds with two distinct but related components of mainstream evolutionary theory. One was his view that adaptationism is insufficient to explain microevolution. The second was that, because of the phenomenon of stasis, macroevolution cannot simply be an extrapolation of microevolution. Combining these and a few other ideas, he published a paper entitled "Is a new and general theory of evolution emerging?" in 1980. The paper critiqued the modern synthesis, and presented his thoughts on what its replacement (or modification) might look like. Bambach (in SJG:RHVL), who summarizes Gould's most important professional publications, notes that this is the beginning of his 20-year effort that culminated in his final work, *The Structure of Evolutionary Theory,* which appeared posthumously in 2002. Importantly, as Gould himself notes, he did not succeed in developing a paradigm as complete as that offered by the modern synthesis. Perhaps his final book should have been called "The Status of Evolutionary Theory," as it summarizes the history of evolutionary thinking and what we have learned through the end of the 20th century, while acknowledging that there are still too many things that we do not know or understand. Gould seems to have offered it in the spirit of, "This is as far as I got, and these directions look most promising to me."

One of the two most fundamental features of his revised partial evolutionary paradigm is the concept of *hierarchy* (the other being contingency.) To explain: if punctuated equilibrium, and in particular the phenomenon of stasis, accurately reflect a significant part of the evolutionary process, then macroevolution *cannot* be an extrapolation of microevolution. In the worldview of phyletic gradualism, adaptive pressure – for example, a change in climate – leads to evolution by selectively favoring those individual offspring that vary in ways that offers them an advantage. But if stasis is real and sufficiently powerful, the offspring will only be able to change a small amount; new species with anatomically different features will not result. So, then, how does macroevolution occur? Gould argued that new species, including the development of new structures or new ways of using existing structures, arose during the brief periods of punctuation. There is an important distinction between what happens during these punctuations and a rapid version of "natural selection." While Gould did not use the terms that follow (see Thomas in SJG:RHVL, who does), the mechanism of natural selection is an "equilibrium process," one in which the morphological or functional state of the organism moves directly in the direction of better design. Gould's view – partially following an idea considered decades earlier by Sewall Wright, one of the founders of the modern synthesis – is that speciation *is not an equilibrium process*. That is, new species are produced that may be better adapted or less well adapted than the parent species. Those that are less well adapted do not last long; those that are better adapted may coexist with their parents and/or each other for some extended period of geologic time, but one may eventually displace the others completely. This is a subtly revolutionary view. Darwin and the modern synthesis rested on the fundamental assumption that competition between individuals was so powerful that any false evolutionary step would selectively preclude reproduction. In this orthodox view, a species that is not superior, at least in its local niche, *cannot come into existence*. Gould's revised view is that a species that is merely "good enough" can arise (relatively suddenly, via PE), and may even be able to survive for an extended period, if it can simply find a niche in which to dig in and hang on. The contingent nature of these non-equilibrium states is implied; he discusses these thoughts in his essay *The Great Seal Principle*.

Gould's view is that species play a role in evolution that is analogous to organisms, at least in some ways, but at a higher level. Individual organisms are born and die, and cannot change genetically during their lifetime; in PE, species come into existence relatively abruptly, and then do not change genetically very much ("stasis") until they become extinct. An organism can produce offspring that resemble it to a large degree, but contain some intrinsic, random variation; in PE, a parent species may spin off a number of daughter species, which are similar but also vary genetically – and, Gould offers, to some degree randomly. Finally, organisms compete with each other for limited resources, and those that vary in advantageous directions are favored by natural selection. In PE, Gould came to believe, the distribution of species that are produced in punctuations may, to some degree, also compete with each other. (Gould writes no essays on this, but this clearly leads to a different and more direct interpretation of altruistic behavior, at the expense of kin selection.) Gould disliked the term "species selection," preferring the term "species sorting" (to not overemphasize the similarities). "Trends," defined as different species experiencing similar changes over time, were offered as evidence of the power of natural selection to produce macroevolutionary changes. Even in their 1972 paper, Eldredge and Gould offered the alternative view, again analogous to natural selection, in which those new species – produced in a partially random process during a punctuation – that varied in more favorable directions tended to last longer and speciate more. That is, they argued, trends could be explained in either paradigm.

Both Darwin and the modern synthesis argued that the organism was the only level at which evolution, via natural selection, acted; so did Gould in several of his early essays. Now, Gould was arguing that macroevolution was a separate phenomenon. Importantly, however, he emphasized the similarities, or analogies, of the macroevolutionary process to the micro process. Rather than claiming that PE overthrew Darwin's theory, he argued that it was an *extension* of it. Punctuated speciation, inherent and non-optimal variation, and species selection / sorting were fundamentally "Darwinian" in nature; they just operated at a different level. He referred to this multi-tiered evolutionary viewpoint using the term *hierarchy*, and suggested that both organisms and species should be identified as "Darwinian individuals" (discussed in his essay *A Humongous Fungus Among Us*). Organisms and microevolution constituted the first *tier* of this hierarchy, with populations or species and macroevolution constituting the second, higher tier.

Interestingly, Gould rarely discussed his hierarchical view of evolution in his essays, and the terms "hierarchy" and "tier" rarely appear there. He did, however, discuss some of the ways in which the two tiers could interact. In 1982, he and colleague Elizabeth Vrba wrote a paper "Exaptation – A Missing Term in the Science of Form," which was summarized in his essay *Not Necessarily a Wing*. This paper notes that there is an important distinction between a structure that has always been shaped (by natural selection) to serve a particular function, such as an eye for seeing, and a structure that initially served one purpose and was then co-opted to serve another. Both processes have been referred to in the literature as adaptations, the paper stated, but the latter reflects a discontinuity. The two offer the term "exaptation," as opposed to "adaptation," as a descriptor for this second phenomenon. The example chosen was the wing; it had always been a problem, they noted, to explain the origin of this structure when (say) 10% of a wing would be of 0% utility for flight. Darwin himself, Gould noted, addressed this problem by suggesting that the pre-wing structure probably served another function – perhaps the regulation of body temperature. The essay discusses some experimental data that shows that this particular transition was possible. In another essay, *An Earful of Jaw*, he discusses the evidence that the ear bones of terrestrial vertebrates were "exaptations" of jaw bones. (Exaptation appears to be a derivation of the spandrel concept. While the term seems not to have caught on, "co-optation" does appear today and seems to mean the same thing.) Gould also discussed the concept of a structure that was initiated for one reason – or no reason – that is usurped to serve a very different function in *Tires to Sandals*. He also argues that such changes in usage are one of the most powerful pieces of evidence we have that the process of evolution – regardless of mechanism – actually occurs in nature in perhaps his most famous essay, *The Panda's Thumb*, which emphasizes that such exaptations are often quite apparently sub-optimal.

Within the essential construct of population genetics, which Gould never questioned the validity or importance of, how does one explain a major morphological change associated with a punctuation? The perspective of the population genetics community was that speciation was the manifestation of numerous small genetic changes over an extensive period of time; "mutationism," the saltationist perspective that a single or small number of changes could produce a new species, had been explicitly excluded. Gould attempted to argue his way around this problem by resurrecting some of the ideas of geneticist Richard Goldschmidt. In the 1940's, Goldschmidt presented evidence that not all genes were "equal"; that some genes appeared to control the function of a number of others. Based on this, he argued that macroevolutionary change might be initiated by a single or small number of changes to these "regulatory" genes, rather than a large number of regular genes. His work appeared at the same time that the modern synthesis was trying to establish itself, and Gould argues that Goldschmidt was unfairly vilified as a saltationist. (In fact, Gould writes in his essay *Return of the Hopeful Monster*, Goldschmidt did not argue that the new "species" appeared fully formed; only that the significant morphological change that resulted from a relatively minor genetic change would serve as a starting point for the conventional natural selection process.) Gould was himself attacked as a saltationist for his support of some of Goldschmidt's views, and genetic evidence was offered that such changes did not occur. In what must have brought an "I-told-you-so" smile to his face, the 1980's and 1990's proved very good to Gould in this field. First, as Dorit notes in SJG:RHVL, better genetic analysis tools showed that the older ones were biased towards finding smaller degrees of change rather than larger changes. Second, as the function and operation of the so-called HOX genes, found in animal life, became better understood, it became apparent that the regulatory-gene paradigm of (certain) small genetic changes producing major changes to the resulting organism was valid after all. Third, it appeared that changes in the HOX genes manifested themselves most readily in directions that were associated with the embryological development of the organism – exactly the subject of Gould's 1977 book *Ontogeny and Phylogeny*. Gould was not a geneticist, but this book is often credited as playing a role in the founding of the dynamic field of evolutionary developmental biology, or "evo-devo."

Gould was careful to argue that his hierarchical, two-tiered view of evolution required no new or unknown mechanisms. It may not be clear what is happening inside those punctuations, or what the relative importance was of the several different mechanisms that could plausibly lead to stasis, but he was convinced that no new "physics" or biochemical processes were required. However, he continued, while it was important to recognize that while physics and chemistry were necessary to explain life, they were not sufficient; additional processes operating at higher levels must also be involved. This was an extension of his argument that macroevolution was not an extrapolation of microevolution, and drew on his views of emergence or holism described earlier. For a man who loved to invent metaphors, it is perhaps surprising that he never drew on his favorite sport of baseball to illuminate this point. If I may: the laws of physics and chemistry are like the rules of baseball and the recorded statistics of all of the players. Even with a perfect understanding of all of this information, one cannot predict with certainty at the start of the season which team will win the World Series; "that's why you play 'em," as the expression goes. In this metaphor, the history of life is like the outcome of a baseball season; the rules and individuals matter, but other factors that only "emerge" at the team level – an effective manager, better on-field communication, or bad personal relationships in the clubhouse – can also affect the outcome. (Gould's other major theme, contingency, also plays a role; sometimes a key player gets injured, and sometimes the ball just rolls between Bill Buckner's legs.) One of the most important aspects of this view to the professional community is that the only source of data on these emergent mechanisms is the fossil record itself; genetic studies cannot, by themselves, tell you whether any given group will be successful. (Perhaps Gould never considered this metaphor because, during his youth, no matter how the season started, everyone knew that in the end that the Yankees would win!)

Catastrophe and Mass Extinction

The relatively rapid nature of punctuational change led Gould into conflict with the "gradualist" orthodoxy of his community in the 1970's, as has been discussed. Both Darwin and the strict Darwinists argued that evolutionary change must occur gradually, because otherwise the different changing parts would not "match up." (Gould was always careful to note that his punctuations were rapid only on a geologic timescale; it still took hundreds to tens of thousands of years, far too slow for any "participant" to recognize what was happening.) Gould, historian of science, recognized that Darwin's views on gradual evolution were directly influenced by Lyell's uniformitarian argument on geology, which eliminated speculative "catastrophes" in all cases from mainstream consideration. There is a significant overlap between geology and paleontology, and accepting universal gradualism in one implies its validity in the other; thus, Gould occasionally argued for the occasional "catastrophe" in *geology* as a second front on those that argued for gradualism in all cases. (One such essay from 1978, *The Great Scablands Debate*, discussed the vindication of a scientist who argued that a set of canyons in Washington state was formed abruptly.)

Then, in 1980, a remarkable discovery was made. Hard scientific evidence was unearthed that proved that the earth had been hit by a large asteroid or comet, and that the date of this impact matched the end of the Cretaceous period (and the Mesozoic era), when the dinosaurs and many other forms of life vanished. The discoverers of this evidence – some of whom, importantly in terms of how the debate played out, were physicists rather than geologists or paleontologists – argued that the timing of these events was not a coincidence. The dinosaurs, and much of the rest of life on earth, they boldly (rashly? arrogantly?) claimed, had been wiped out by – there was no other word for it – a catastrophe. (Gould discussed the news in contemporary terms in his 1980 essay, *The Belt of an Asteroid*.) The geologists and paleontologists pushed back, presenting their evidence for a multimillion year decline; even if an asteroid had hit the earth, they argued, it would have been devastating only regionally. Within a few years, however, as the *possibility* of a sudden global catastrophe caused the community to re-examine their assumptions and the geologic and fossil record, most members became convinced that the proponents were correct. One mass extinction, at least, appeared to be real after all; *it was not* an artifact of the incompleteness of the fossil record. That was all it took; if one was real, then it was at least no longer out of the mainstream to consider that others might be also. Further, if the Cretaceous mass extinction was real, then it became reasonable to ask if the apparently sudden appearance of new species and higher taxonomic groups afterwards might be real as well. The single biggest impediment to the acceptance of, or at least the serious consideration of, punctuated equilibrium had been shattered. Gradualism certainly occurred, but the argument that “only” gradualism occurred began to disappear.

(Gould’s luck with external discoveries and events that supported his worldview struck again, in 1994, when the fragmented comet Shoemaker-Levy 9 impacted Jupiter. It was clear to everyone by this time that the impact 65 million years ago had had a global effect; nonetheless, to many it still seemed fantastic that a single object 10 kilometers across could devastate a planet 12,000 kilometers in diameter. Most scientists predicted that the Shoemaker-Levy fragments, all significantly smaller than the K-T object, would have little effect on Jupiter. The results, however, were dramatic; huge “bruises,” some of greater diameter than earth, appeared on the surface, and remained visible for months. The implications for an asteroid or comet collision with earth became viscerally apparent in a way that it never could have from calculations or computer models alone. Only rarely in the history of science are one’s unorthodox worldviews validated so profoundly in the proponent’s lifetime; this happened to Gould not once, but several times. It is estimated that a comet of that size or larger hits Jupiter less than once every 5000 years.)

At first, Gould was highly pleased that the K-T asteroid impact convinced the community, and the world at large, that gradualism was not the exclusive mechanism for geological or (by implication) evolutionary change. Mass extinctions seemed like a godsend for the theory of punctuated equilibrium; catastrophes, followed by periods of rapid production of new groups, looked like tailor-made “punctuations.” Perhaps stasis was the normal mode of existence most of the time; then, when a catastrophe opens up thousands of niches – so his initial thought process went – the brake comes off, and evolution can occur at its unconstrained rate. Within about ten million years, whales had filled the niches left by ichthyosaurs, and mammals filled the large terrestrial herbivore and carnivore roles.

However, as Gould studied the results and considered the implications of mass extinction, he came to appreciate that the situation was, once again, more complex. In the 1970’s, a number of Gould’s colleagues had worked with him to produce relatively simple computer programs that modeled how speciation and changes in diversity would appear if phyletic gradualism were the dominant paradigm, and if punctuated equilibrium were the dominant paradigm. The object was then to compare the output of these models to the details of the fossil record, to determine under what circumstances each fit the data better. The results were often ambiguous, in part because neither model “worked” across the boundaries of the five great mass extinctions in earth’s history (at the end of the Ordovician, Devonian, Permian, Triassic, and Cretaceous periods). Additionally, as Gould emphasized, the model of PE that he and Niles Eldredge developed was intended to work during “normal times.”

Mass extinctions became a booming field of research, and the team of Sepkoski and Raup studied the details of groups (at the taxonomic level of *family*) as they were formed and became extinct. What they found, Gould discusses in several essays (culminating in *The Wheel of Fortune and the Wedge of Progress*), was surprising. First, there were a number of smaller events in addition to the "big five." Second and third, they were larger in scope (number of families eliminated) and more abrupt (even without evidence of external events such as asteroid strikes) than had previously been appreciated. This was no doubt partially due to the sway of the previous worldview that played down the significance of these odd events. Finally, and perhaps most importantly from Gould's perspective, the patterns of extinction – the types of groups that survived and went extinct – during these events appeared to differ from those of normal times.

Gould came to argue that there were three different processes one could consider when trying to understand how the diversity of life changed across a mass extinction event. The first was that the stress induced by whatever was producing the event would simply cause natural selection to operate at a faster rate. He referred to this as "turning up the gain" on the normal process; one would expect to see the fittest survive and the less fit perish, only more quickly. The second involved pure chance; those species (and families and orders) that happened to live where conditions were worst would die, and this would be completely independent of whether they were better adapted. He referred to the third, which he found most intriguing, as the "different rules" model. In an environment that had changed abruptly, there might well be definite, knowable reasons why one group survived while another did not, but these reasons had nothing directly to do with natural selection. For example, if the asteroid impact at the end of the Cretaceous period led to a collapse of the food chain (perhaps due to sunlight being blocked via a persistent dust cloud), then smaller animals might survive at the expense of larger animals – simply because they needed less to eat, and could "hang on" until the ecosystem began to recover. At the time of the event, there were no large mammals, and no small dinosaurs. This did not mean that mammals were better adapted than dinosaurs; there was no way that natural selection could "adapt" mammals in preparation for such an event. If this speculative (but reasonable) hypothesis is valid, mammals survived via the "different rules" paradigm. Other mechanisms were no doubt also involved – Gould always argued for the *relative* importance of mechanisms – but he came to believe that the different-rules mechanism was the key to understanding changes in life's diversity over the apparently numerous extinction events. He acknowledged being attracted to it in part because of the large degree of contingency involved. He also liked it because it implied that mammals did not "out-compete" his beloved dinosaurs; had the asteroid missed, mammals would likely still be exclusively small today.

Gould considered microevolution and macroevolution in "normal times" to be the two tiers in his hierarchy of evolutionary processes. The former is controlled by natural and sexual selection, as well as – in his view – a number of important non-adaptive processes; the latter, by the selective sorting of new species produced in the occasional successful punctuation. Importantly, based on the arguments above, he concluded that mass extinctions were not simply "big punctuations"; they were too different, although there are clearly some analogies. Instead, he came to argue, mass extinctions and the large-scale adaptive radiations that follow represent a *third tier* in the evolutionary hierarchy, above the level of macroevolution. These rare events, he argued, further disrupt or redirect any large-scale trends that Darwin's microevolutionary wedge of progress might still possibly produce. (Allmon, Morris, and Ivany, in the fourth essay of SJG:RHVL, note that this argument "has generally not fared well" within the community to date.)

Gould thus came to recognize three tiers of evolution. Oddly, there is a fourth as well that he discusses in his essays, but does not seem to formally consider in his official hierarchy. This is the lower level of genetics. Many fascinating experiments, starting in the 1960's, proved that the majority of DNA in any eukaryotic organism does not seem to actually "do" anything, in the sense that it does not code for proteins or act as a regulator. Francis Crick, the co-discoverer of the structure of DNA and general savant, published a paper in 1980 speculating that the DNA was following an analogous "Darwinian" process; those strands of DNA that left more copies of themselves in the next generation were "favored" over those that did not, as long as no significant harm was done. Gould discusses this paper in his essay *What Happens to Bodies if Genes Act for Themselves?*, noting the extensive differences between this view and Dawkins' "selfish gene" concept.

Trends in Natural History

In the early 1980's, Gould was riding high. Shortly after the publication of his third collection of essays from *Natural History*, however, he was diagnosed with cancer. This essay is not intended to be a biography, so I will not dwell on the details; he survived, living another twenty years before succumbing to a different form of cancer. One feature that is relevant to this essay, however, is how his worldviews discussed thus far changed as a result of facing his own imminent mortality. The answer, I think it is safe to say, is that they did not change at all. In particular, his views on the contingency of human existence – including his own – never even skipped a beat; we all remain, in his view, just lucky to be here.

In the late 1980's, he began writing what would become his biggest seller, *Wonderful Life*. While consistent with his views of punctuated equilibrium, the bush versus the ladder view of evolution, and the contingency of history, the book was not about his own work, or about ideas that he himself had developed. Rather, the subject was Harry B. Whittington's reinterpretation of the Burgess Shale fossils, unearthed by Charles Walcott several decades earlier. In one essay, Gould writes: "I regard this reinterpretation of the Burgess Shale as the most important paleontological conclusion of my lifetime."

The facts of the case are as follows. Walcott discovered the Burgess Shale formation in British Columbia, Canada, in 1909, and quarried it extensively in 1910 and 1911. This particular fossil bed is important for two reasons. The first is that it was produced by a relatively gentle underwater landslide that entombed, yet did not "smash," part of an entire ecosystem. Due to the absence of oxygen in the region of deposition, the sediments preserved not only the hard parts of the organisms, but the soft parts as well; this is very rare, and offers unique insight into the anatomy of the fauna (many of which have no hard parts at all). The second reason is that it captures a moment in time only a few million years after one of the most puzzling events in natural history, the so-called Cambrian explosion. It was during this geologically brief period that most, if not all, of our modern phyla made their first appearance in the fossil record. (There are several definitions for the taxonomic term "phylum," which technically lies below kingdom and above class, but in general it refers to a unique body plan. A vast majority of species today fall into one of five phyla: arthropods, annelids, mollusks, echinoderms, and chordates – the last of which includes vertebrates, including mammals and humans. Overall, the total number of phyla – which changes from time to time as new information becomes available and as debates are won and lost – is about 35.)

Darwin was aware of the apparent discontinuity at the beginning of the Cambrian period; at the time, there were no known pre-Cambrian fossils at all. The sudden appearance of fossils in the geologic record troubled him, for the same reasons that mass extinctions troubled him – they both challenged the gradualist perspective. He was convinced that further exploration would lead to the discovery of pre-Cambrian fossils. (In fact, numerous such fossils have been found – but most are microscopic, and represent single-celled organisms. Some macroscopic fossils – the Ediacaran fauna – have been discovered in the late pre-Cambrian, but their relation to modern groups remains tentative at best. It does appear that the Cambrian explosion, whatever its cause, represents a real event.)

Walcott recognized the significance of this find, and examined the fossils carefully – when time allowed. He named them, and identified the (modern, extant) phyla to which each belonged. Walcott's perspective on trends in the history of life was entirely mainstream: after multicellular life first formed, he believed, it split up into several distinct body plans, or phyla, and in particular into the major phyla we know today. At first, each such group was represented only by a few species – metaphorical "twigs" – that then "grew" (diversified) into the present branches of life. It was possible, even likely, that other, smaller (less diverse) phyla branched off from the main trunks over the eons. This paradigm, often called the "cone of diversity," can be conceptualized as an upside down triangle on an x-y plane. The y-axis represents the passage of time, and the x-axis – the increasing width of the triangle, or cone – represents the increasing number of species within each phylum. Working under this paradigm, Walcott's preliminary descriptions classified each of the organisms according to the phyla we know today. Walcott was an incredibly busy man; he was the Secretary of the Smithsonian Institution and President of the National Academy of Sciences (simultaneously!), and was involved in many other projects as well. As Gould discusses in *Wonderful Life*, Walcott stored the fossils away at the Smithsonian, intending to describe them in detail as his grand retirement project. But he died "with his boots on" in 1927, and the fossils languished.

Finally, starting in around 1970, Cambridge University professor and trilobite expert Harry Whittington reexamined Walcott's fossils with the goal of formally describing them. Whittington came to realize that many of the animals preserved in the Burgess shale were truly odd. While ancestors to modern phyla were clearly present, he concluded that Walcott had been wrong in his belief that *all* of the fauna could be placed into modern categories. Perhaps the most impressive "oddball" was *Opabinia*, a twoinch-long organism with segments and feathery gills like an arthropod, but no legs, five stalked eyes, and a grasping structure on the end of a long tube attached to the head. Whittington, along with graduate students Derek Briggs and Simon Conway Morris, concluded that many – perhaps a majority – of the Cambrian fauna could not be placed into *any* existing phylum. This pattern continued into the next taxonomic levels. For example, today there are four major subphyla of arthropods, with trilobites representing an extinct fifth. The Burgess shale, however, include fossils of more than a dozen others, none of which are represented today. Nonetheless, each of the Burgess phyla appear to be represented by only a handful of species; this is far different from today's world, where there are on the order of 100,000 species of vertebrates, and over a million species of named arthropods.

Whittington drew two dramatic conclusions from this data. The first is that the Cambrian explosion was even more abrupt and more "explosive" than previously believed; many, many new body plans were produced in a geologically brief amount of time. Further, the variation of these designs greatly exceeds what we see today. (Gould's professional work references a 1987 paper by Bruce Runnegar, who argues that the term *disparity* should be used to describe the degree of difference in body types, as opposed to the commonly-used *diversity*, which refers to the number of species within a group. The problem, of course, is how to quantify "disparity.")

The second conclusion is that this period of creation was followed by a *decimation*; many, if not most, of these body plans were extinct by the end of the Cambrian period. Those that survived diversified, and established themselves as the groups we know today. Gould argues that this evidence supports a real and perhaps unexpected trend in the history of life: what he refers to as "early experimentation and later standardization." Graphically, this is very different than an inverted cone of steadily increasing diversity. Also importantly, in the scheme of things, there appears to be no obvious reasons why certain groups survived when others, perhaps most, did not. He argues once again for the contingency of history with his "tape of life" argument: If the tape of life (in this age of analog tape recorders) were erased, re-wound, and played again, it is likely that a different set of survivors would emerge from the explosion / decimation process. There is no reason to believe, he continues, that a chordate would be among the fortunate again. There is only one known chordate represented in the Burgess shale, he notes, called *Pikaia*; it is rare and was first thought to be a worm of some sort. Had *Pikaia* (or whatever chordate our ancestor turned out to be) not survived, then perhaps the most "intelligent" organism on earth might be a mollusk of some sort, such as an octopus. The title of his book – *Wonderful Life* – is a pun that plays on this concept. On the one hand, it refers simply to the amazing organisms of the Burgess shale, such as *Opabinia*. On the other, it is a reference to the 1939 film, "It's a Wonderful Life." In this movie, the character played by Jimmy Stewart is shown how different the world would have been if he had never been born.

By this time in his career, Gould was certainly no stranger to controversy. However, he did not expect the resistance he received from *within* the scientific community to *Wonderful Life*. He had found Whittington's reinterpretation of the Burgess Shale fauna to be startling, but he assumed that the rest of the community would accept his conclusions, as he had. But many – perhaps most – did not. Many biologists argued that Whittington had gone too far, and that the Cambrian fauna were not nearly as unusual as he argued; that is, in essence, Walcott had been basically correct. A faction of the community argued that the ancestors of the Cambrian fauna were probably represented in the Ediacaran (pre-Cambrian) period, and that the Cambrian "explosion" was not really much more significant an evolutionary event than any other period of similar duration. Gould was surprised at this, and concluded that the community's affection for gradualism was perhaps even greater than he had appreciated.

Gould suffered a tactical setback on this front when one of the "weirdest" of the Cambrian animals, *Hallucigenia*, was found to actually be a relatively conventional member of an existing phylum. The source of the problem was that Simon Conway Morris, a key member of Whittington's team, had interpreted the animal "upside down," thus appearing to walk on what turned out to be protective spines. To his credit, Gould had reserved judgment on this interpretation. He writes in *Wonderful Life*, regarding the possibility that *Hallucigenia* is actually a broken-off appendage of some larger animal: ". . . I am rooting for Conway Morris's interpretation (but if forced to bet, I would have to place my money on the appendage theory)." Nonetheless, when the truth was recognized, opponents of the "early experimentation" perspective quickly noted that "Gould was wrong," implying that the entire book was so full of errors that it was not worth reading. Perhaps ironically, Conway Morris himself came to oppose Whittington's (and Gould's) perspective on the unusual nature of the fauna. In Conway Morris's revised view, it was only a matter of time before all of the Burgess shale fauna could be fit into existing categories; he challenged Gould's position in articles and books. Gould took all of this in stride, writing one essay on the subject (*The Reversal of* Hallucigenia) and participating in one exchange with Conway Morris in *Natural History* magazine. He then moved on, maintaining Whittington's perspective.

His tape-of-life argument is, apparently, at least partially responsible for the heightened emotions on the subject of the Cambrian explosion within the community. Conway Morris argued that human-level intelligence would have occurred in any event, as the result of the process of convergent evolution (the process that produced very similar hydrodynamic shapes in sharks, dolphins, and ichthyosaurs). In his essays, Gould argues that such views ultimately reflect *hope*, not science; the hope that there is a design, a plan, or at the very least some sort of an inevitability to our existence, and perhaps by extension some sort of significance to our lives other than fortuitous happenstance. He collectively refers to all such views, which are not new, as anthropocentrism. Many scientists, he states, including physicists and cosmologists as well as biologists, are taken with these views. Some of his essays present his arguments against them (in particular, *Mind and Supermind*), which center on the position that anthropocentric hypotheses are inherently untestable, and thus inherently unscientific; they are at best comforting speculation.

Since Gould's death in 2002, the community has developed a new interpretative consensus about the Cambrian explosion, involving the concepts of *crown groups* and *stem groups*. In this perspective, the group that would eventually become (for example) arthropods branched off from a common ancestor with nematodes (small, ubiquitous, wormlike creatures), probably sometime in the late pre-Cambrian. This clade – or evolutionary branch – had some, but not all, attributes of arthropods: perhaps a segmented body, but perhaps not jointed legs. The clade proceeded to branch several more times; one of these branches, which continues to exist today, is the phylum of Arthropoda. This is an example of a crown group. Most of these other branches, one of which might include *Opabinia*, died out without descendents; these are called stem groups. This taxonomic mechanism allows the "weird wonders" of the Burgess shale to be grouped with existing phyla, rather than their own unique phyla, and thereby reducing – its proponents claim – the need to draw on "unusual evolutionary mechanisms" to explain the Cambrian explosion.

What would Gould make of this? My guess is that he would have no objection to most of the new consensus. He would certainly agree that *Opabinia* shared a common ancestor at some point with everything from nematodes to humans, and that branching of these groups occurred. He would, I imagine, appreciate that this view recognizes two of the points about the Cambrian explosion that he felt were most important: the high disparity of body plans in the early Cambrian, and the extinction of many of these groups by the end of the period. On the other hand, as a stickler for words and their meanings, he might object to labeling *Opabinia* as a "stem arthropod." *Opabinia* has no legs (in addition to five eyes and a proboscis), and therefore is not an arthropod – a word that literally means "jointed leg" – by any meaningful definition. On a larger scale, he might consider this consensus to be little more than a re-definition of the word "phylum" to include stem groups, which up until this point had been *defined* as separate phyla. As with the other objections to the themes he presented in *Wonderful Life*, my guess is that he would be somewhere between discouraged and mystified that so many scientists would be genuinely *troubled* by the thought that the Cambrian explosion was not "business as usual."

Besides the *Wonderful Life* observations of early disparity of body plans, followed by a massive decimation, Gould often noted a third important factor in the fossil record: *no new phyla have appeared since the Cambrian explosion*. This implies another fairly radical interpretation: after the Cambrian explosion, not very much has happened at the highest, "big picture" view of life on earth. Some interesting new classes appeared when life first moved onto land around 400 million years ago – reptiles, mammals, and birds, to name three – but these all apparently share a common marine ancestor of the same phylum. Meanwhile, the number of classes of echinoderms (the phylum that includes starfish) has decreased from about 21 to five. Overall, Gould argues, if one does not focus on any one particular group – specifically, us – then most of the action in the history of life takes place during one five or ten million year span more than 500 million years ago. He admits he finds this deeply puzzling. He *likes* Darwin's metaphor of the wedge, which argues that even though natural selection itself only adapts organisms to the local environment, over time the result should lead to a better overall class of life. It makes sense; yet "progress" of this sort is rarely, if ever, observed. Mollusks and starfish today, while highly diversified, do not seem to be more *advanced* in any measurable way than those that lived 500 million years ago. (Gould touches on this in his essay *An Awful, Terrible Dinosaurian Irony*.)

He went on to argue that a similar important event occurred in the more distant past, when prokaryotic life such as bacteria first appeared. Excluding the rules by which DNA codes for amino acids, there is probably nothing more fundamental than an organism's *metabolism* – the mechanisms by which it acquires and uses energy to drive its internal functions. At some point early in life's history, prokaryotic organisms with several very different metabolisms appeared. One particular strategy that drew on the metabolic process of *respiration* (the use of oxygen to liberate energy by certain chemical reactions) produced organisms that were apparently capable of merging with each other to form larger, more complex eukaryotic cells, and one or more groups of these led to multicellular life (and ourselves); but other types of prokaryotes and eukaryotes are still with us today. That is, he argues, in the distant past something "happened" and many types of prokaryotes appeared; since then, in the big scheme of things, little has changed.

He captured the logical conclusion of this train of thought in his next book, *Full House* (1996). The fundamental theme is that the concept of *progress* – an evolutionary trajectory toward more complex life over time – is not really a valid trend in the history of life after all. Instead, he argues that there is an inherent *variation* in the possible complexity of life on earth, and that it began near the simple end of this distribution. Since it could not become simpler – oddly, he does not discuss viruses here, which would seem to bolster his point – then the later formation of more complex life gives the *false appearance* of a progressive trend. In fact, the width of the peak – the range of *variation* of complexity – is increasing, but the mean, or highest point on that distribution, is not moving to the right (more complexity). The peak remains fixed on prokaryotes, such as bacteria. We are watching one edge of the distribution, he argues, when we should be watching the mean and the width, which gives a more accurate representation of the system as a whole.

How then does one explain the large brains of mammals, and the even larger brains of humans in this paradigm? First, Gould begins, one must be careful about using "increased complexity" and "larger brains" as if they are interchangeable; this does not necessarily follow. Second, and more specifically, he notes via the "mouse to elephant" curves that he has used in his essays since the beginning that brain size scales (albeit not linearly) with body size, and that the primary difference in vertebrates is whether the animal is warm-blooded or cold-blooded (although carnivores within each group also have larger brains than herbivores of the same body mass). The fossil record also shows fairly clearly, he continues, that the brain sizes of mammals that lived 100 million years ago still fall on the appropriate curve, indicating that mammal brains as a function of body size are the same then and now. That is, mammals are not getting relatively "brainier"; some mammals now have larger brains because they inhabit larger bodies, due to the current absence of dinosaurs. Dinosaurs, too, he notes in his essay *Were Dinosaurs Dumb?*, had brains that fell on the appropriate curve. Humans are indeed relatively and absolutely "brainy" by these criteria, a point he notes in his early essay *The History of the Vertebrate Brain*. However, he argues, this reflects an unusual variation, and not a global trend. We have these enormous brains, and as a result – of this he has no doubt – our conscious minds, unique in the history of life on earth. But this is almost certainly the result of an odd set of contingent events, he argues, rather than the result of an inevitable trend. "Early experimentation and later standardization," with the occasional decimation thrown in, may be the best we can do in terms of long-term trends in the history of life. Why evolution should behave in this way, rather than progressively, is a problem that he thought about but never really resolved. Possibly, he speculated, the nature of punctuations and mass extinctions "reset" any wedging progress that might occur if phyletic gradualism was the only mechanism by which evolution occurred.

Gould on Science, Creationism, the Humanities, and Religion

Gould was first and foremost a scientist; this was where his professional training lay, and this pursuit landed him a position and, later, tenure at Harvard. But he was also a historian of science, and a philosopher of science. Two of his key publications – on punctuated equilibrium and spandrels – were as effective as they were because he was able to mix these areas of study. Gould had strong views on "science" itself, as a field of human endeavor, and a remarkably large fraction of his essays focused on this. His motivation for repeatedly returning to this subject appears to have been, at least in part, his belief that many of his fellow scientists – not just the general public – actually misunderstood, in a subtle way, what science *is*. The source of his different view stems directly from his study of the history of science, something few scientists actively study.

In his "philosopher of science" mode, Gould proudly recognized the formalization of rational though in its various guises – in particular, science – to be one of man's greatest achievements. However, he cautioned, science is not, as many scientists in particular believed, a linear march toward "truth," where here this tricky term may be defined as an absolute and perfect understanding of the external universe around us. More specifically, Gould non-concurs with the perspective that science is based on the *objectiveness of observation*. Certainly, he agrees, direct observation is an essential component of science, and is a primary difference between this method of "knowing things" and others, such as appeals to authoritative sources (for example, Aristotle or the Bible), internal contemplation, or divine inspiration. However, he continues, while observation is necessary, it is not sufficient. Many scientists believed (and believe) that if they observe something, it becomes a part of the body of scientific knowledge. This is not necessarily so, for three reasons. The simplest is that the mind can play tricks on us; "eyewitness testimony" has come to be recognized as notoriously unreliable, and Gould writes several essays – for example, *Muller Bros. Moving and Storage* – where he has discovered his own personal recollections to be faulty. A second reason is that the mind has certain "built-in" analysis algorithms that we tend to default to. One that Gould refers to in several essays is "dichotomization": the placement of an object into one of two categories, such as different-same, changing-static, and one-many. This categorization process can be very useful, but can also be misapplied – especially to systems that vary continuously. He also notes in several essays that humans do not, in general, deal very well with the concepts of probability; most people believe, or at least *suspect*, that the universe is deterministic. This manifests itself in many ways, from 20-20 hindsight on completed sporting events ("that upset was inevitable!") to our conscious and subconscious perceptions of fate or destiny. Interpreting processes that include an aspect of true randomness via the mechanism of our determinism-loving minds is usually difficult. As another important example, he notes that we prefer our narratives of history in "story" form, with a definite beginning, middle, and end. We prefer decisive events to amorphous sequences, and we struggle when reality comes closer to the latter than the former.

The third and most subtle reason is that, perhaps contrary to common sense, there is invariably more than one way to interpret a supposedly objective observation. Data and theory are, and must be, fundamentally intertwined in our minds; one of Gould's favorite quotes from Darwin is, "How odd it is that anyone should not see that all observation must be for or against some view if it is to be of any service!" (This is from a letter that Darwin wrote to Henry Fawcett, and is mentioned in several essays, most notably *Dinosaur in a Haystack*.) Two people, operating under different paradigms, can look at the same object or event and see it completely differently; different aspects are emphasized or downplayed. (He presents two interesting examples in his essay *The Sharp-Eyed Lynx, Outfoxed by Nature*.) This was the underlying argument that he and Eldredge drew on in their first paper on punctuated equilibria; scientists were not "seeing" stasis.

It is easy to dismiss older paradigms as unimportant on the grounds that they have been superseded or proven false. Gould cautions against this perspective, drawing on two lines of reasoning. The first is that the ability to understand well-thought-out paradigms *in their own terms,* even if obsolete today, can help us to at least *consider* that our own paradigms may be incomplete or even incorrect as well. This, at least in principle, can allow a working scientist to increase his sphere of thought; to "think outside the box" (a phrase that Gould never used and likely detested). Most of Gould's "biographical essays" are really about the paradigms that the subjects held, and how they came to develop them. The second line of reasoning is that some of these older paradigms may contain important nuggets that are difficult to perceive in current models. Gould drew on these alternative perspectives to see "catastrophism" in geologic history when others had dismissed it, as well as regulatory genes from the dismissed work of Richard Goldschmidt, the limited relationship between ontogeny and phylogeny (leading to his book of that title), and to question the universality of the Malthusian assumption in natural selection (in his essay *Kropotkin Was No Crackpot*). Sometimes, he pointed out, old problems are not fully resolved, and old insights are not always accommodated in a new way; sometimes, they are merely forgotten.

Gould often argued that scientific process does not move in a straight line; rather, it moves in fits and starts, zigzagging, going down numerous dead ends. A fundamental aspect of his argument is that science *cannot* move in a straight line, because science *must* involve theory, and theories are human constructions, just as art and music are. Importantly, some of the "raw material" of a scientist's creation is the very culture that he is a part of; Gould and numerous others have noted that Darwin was as influenced by Adam Smith's "unseen hand" as he was by the Galapagos finches. Adults usually form new ideas via metaphors; a new thing "is like" something else that we already "understand"; our theories, therefore, reflect the metaphors available to us as well as the data itself. Gould's general view was that we should, therefore, acquire as many metaphors as possible, even obsolete ones.

As he discusses explicitly in his essay *A Foot Soldier for Evolution*, a theory is not simply an obvious inference drawn from a sufficient number of facts; theories are large conceptual frameworks that incorporate many different facts, and not all with perfect ease. Newton famously created a theory of gravity; it accommodated a wide variety of facts, but not all. Eventually, Einstein developed a different and vastly more complex theory of gravity, which is fundamentally different than Newton's. It accommodates a larger array of facts, but still leaves some physicists wanting more. In order to construct better scientific theories (or models, or paradigms, or worldviews – the terms are interchangeable in this context), one must indeed make observations, perhaps based on repeatable experiments; "arm chair speculation" will not suffice. But with observations in hand, his point is that different theories can be constructed. The key to recognizing the flaws in a paradigm, however, does not come simply from more observations; it comes from using the paradigm to make predictions about what other facts *that you have not yet observed* should be found. Then, and only then, will an unexpected fact cause you to recognize that the model may have a problem. It is therefore *testability*, Gould states, rather than observation, that is the essence of the scientific method. (The historical sciences are subject to test as well as the hard sciences, even though repeatable experiments are not available. He discusses some of the standard approaches to historical sciences in his essay *Worm for a Century, and All Seasons*).

Will we ever produce "perfect" scientific theories or paradigms to explain the universe around us? This is a question that he carefully sidesteps. He states in his complex essay *Shields of Expectation – and Actuality* that a combination of additional data and revised thinking can and does lead to scientific progress, in that as a result our understanding of nature can improve. But as to whether we can asymptotically approach "the truth," in an absolute sense, he implies that he simply doesn't know.

Many professional biologists felt and expressed unease with Gould's arguments about science because they felt it played into the hands of the creationist movement. Gould responded to these concerns, not by toning down his views on the nature of science, but by becoming one of the most prominent public critics of creationism. This culminated in his testimony in the case *McLean v Arkansas Board of Education* in 1981. The ruling overturned a recently-passed Arkansas state law that mandated the teaching of creation science in public schools, specifically in science class. This ruling was not appealed, but a similar case from Louisiana – *Edwards v Aguillard* – was. The Supreme Court found the law unconstitutional in 1987, on the grounds that it attempted to advance a particular religion. The underlying rational the Louisiana court judge gave in his ruling pleased Gould greatly. The Creationist argument in its modern form is based on Biblical literalism, and is therefore on faith, and is therefore not *testable*, and is therefore not *science*. (Others, including Gould in his essay *Genesis and Geology*, also noted that Genesis is inconsistent with the geologic and paleontological observations.)

Gould's powerful dislike of the creationist community is not based, however, on their incorrect understanding of science. Most of the scientists in Darwin's time were creationists, and Gould clearly bears them no animosity. Gould's dislike was instead due to their intellectual dishonesty, something that he did find personally offensive. In his essay *The Freezing of Noah*, he writes: "Modern creationists . . . do no fieldwork to test their claims (arguing instead by distorting the work of true geologists for rhetorical effect), and they will change not one jot nor tittle of their preposterous theory." In *Evolution as Fact and Theory*, Gould tells the story of how his own work on punctuated equilibrium (with Niles Eldredge) in the early 1970's found its way into a creationist pamphlet entitled "Harvard Scientists Agree Evolution Is a Hoax." Interestingly, when Gould saw how they were using their paper, he responded with some op-ed pieces in popular newspapers. These responses were both "political" and written so clearly that non-professionals could readily understand his scientific arguments. Ironically, these events may have played a role in his becoming a monthly columnist in *Natural History magazine*.

Regarding the motivations of modern creationists, Gould leaves no doubt of his views in this extended quote from his essay *A Visit to Dayton*. He writes: "[The leaders of the creationist movement] are a motley collection to be sure, but their core of practical support lies with the evangelical right, and creationism is a mere stalking horse or subsidiary issue in a political program that would ban abortion, erase the political and social gains of women by reducing the vital concept of the family to an outmoded paternalism, and reinstitute all the jingoism and distrust of learning that prepares a nation for demagoguery."

His essay *Evolution as Fact and Theory* also attacked the creationist argument that "evolution is just a theory." It *is* a theory, he states, but in the sense that Newton's model of gravity, and later Einstein's, are "theories" – but the term means "overarching model," not "unproven hypothesis." The *fact* that evolution occurs is now accepted by all professionals in the field, for reasons that Gould summarized in that essay. The *theory* of evolution, in terms of the process and mechanisms behind it, are what Gould and his colleagues are wrestling with. By analogy with gravity, there may be debate between Einstein's theory and other possible theories, but no one denies that the phenomenon exists. That life evolves is as certain as, if not as obvious as, gravity.

In addition to "scientist," one of the terms most commonly associated with Gould was "humanist." Humanism means different things to different people. To some, it refers to a love of the humanities: literature, art, languages, history, and so on. Gould certainly fit this definition; he may have been the most well-read scientist on the planet. He valued all intellectual pursuits, and regretted (while accepting) that he lived in a society that did not share this perspective. A related aspect of his humanism, therefore, was the willingness to produce monthly essays for his fellow intellectual travelers.

Intellectual or not, Gould loved most, if not all, of humanity; he was a city kid, and loved walking around in cities wherever he went – hanging out in African marketplaces at the expense of seeing a lion on the savannah. Yet at the same time, he also believed that humans, one species of a million or so on this planet, are not inherently superior to any other. One thing that truly angered him in Western culture was the view that man had been given dominion over the rest of the world (either by God, or by the inevitability of a secular evolutionary process) to do with as he pleased. Gould had no problem with a good steak, and he certainly had no sympathy for those who considered the existence of cities to be a crime against nature. What angered him was the sense of *entitlement* that so many of his fellow humans hold when it came to exploiting resources, and the associated soft contempt that they often held for the natural world and the carelessness with which they treated it. He resented the perspective that earth and the life on it had no value other than to serve us. Gould was grateful for every species that existed, and humbled that he had the opportunity to cohabit the earth, if not his apartment, with them. In a manner of speaking, he was a "life-ist" as much as a humanist.

Gould was a humanist in another way as well. His worldview that we – as individuals, and as a species – are here in large part by chance, rather than by destiny, is an aspect of what religious fundamentalists sometimes refer to as "secular humanism." Gould ended several essays by acknowledging that many are distressed by the perspective that our lives and individual suffering mean nothing to the universe as a whole; he recognized the need for joy and solace, but wished that we could all find it in ways other than assuming, for example, a 6000-year-old earth or the inevitability of our lives. Gould was certainly proof that one could be a "secular humanist" and still find joy in life.

His humanistic perspective on science is directly related to his views on the role of science in society. Gould *of course* believed that science was an important and valuable endeavor; he worked hard to be able to do it for a living, and never regretted it. Having said that, he often wrote about how scientists operating under a false sense of certainly offered those in power justification for brutal racist and imperialist policies. It was in this context that he protested so strenuously against E. O. Wilson's view that human behaviors were under genetic control; whether true or not, those in power could easily latch on to such an argument to justify everything from exploiting the poor to denying equal rights to women or non-whites. If the science actually supports the conclusion, he wrote, we must support it even if it is unpalatable; but in most cases, the science was bad, and in some important cases even fraudulent. His book *The Mismeasure of Man* details many important cases in which scientists inappropriately leant their research and their credibility to such policies. His fundamental thesis in this regard is that scientists have a very unimpressive track record regarding the application of "science" to questions of morality, and should recognize this and show restraint. (One of his personal favorite essays, *Carrie Buck's Daughter*, was on this subject; when Gould died, *Natural History magazine* chose to reprint this one as a memorial.) Scientists should resist the urge to think of themselves as a new priesthood.

Gould's view of formal religion was complex. Although a self-described agnostic, he was proud of his Jewish heritage, and an avid reader of the Bible and of biblical studies. In the first essay of his first collection of reprints, he clearly identified the mechanistic aspect of Darwin's theory as a fundamental disconnect between the scientific and religious communities. But for most of his career, he labored to establish a philosophical truce between science and mainstream religion. He was always careful to separate creationism from religion. Again in his essay *A Visit to Dayton*, he stated: “They [modern creationists] have been disowned by leading churchmen of all persuasions, for they debase religion even more than they misconstrue science.” He argued that science and religion are not natural opponents, but allies; both face the common opponent of literal, intolerant dogmatism. His thesis, which he called “non-overlapping magisteria” or NOMA, was that science and religion (he lumps ethics and political policy on social issues in with the latter) address different needs of human nature. (He discussed this construct in his essay *Non-Overlapping Magisteria*, and his 1999 book *Rocks of Ages*.) Modern religion, he says, can offer nothing useful on such topics as the origin of the earth, of life, or of mankind – and he adds that most religious authorities, including the Pope, agree. Gould and many others have noted that many mainstream religious organizations officially sided with the scientific community during the two “scientific creationism” court cases from the 1980’s discussed above. Similarly, he argued that science should play at most a limited role in our debate over how to construct a society, or what “justice” or “morality” should mean. Certainly, he stated, we should not attempt to find justification or rationalization for any sort of moral behavior in nature itself (a point he discussed in his essay *Nonmoral Nature*).

His NOMA construct thus attempted to integrate four of his positions. First and foremost, it attempted to establish a sustainable peace between science and mainstream religious believers, whom he respected. (He also openly acknowledged that if people are forced to choose between one and the other, science will lose in the vast majority of cases.) The others were: to remove and keep fundamentalism out of politics and education; to establish that scientists can be as dogmatic as anyone else, and in as much need of humility; and to keep the traditional conservative political powers from misusing science to justify non-egalitarian policies. It appears that NOMA made few converts on either side during his lifetime, as both sides found it unappealing. As Allmon notes in SJG:RHVL, most people of faith are unwilling to completely abandon the concept of a caring God with supernatural powers, which largely limits religion to ethics. Likewise, many scientists believe that questions such as “What happens to the mind when the brain dies?” are legitimate subjects of scientific inquiry. Perhaps some form of NOMA that “descends with modification” from this initial species may someday establish itself.

Summary

Allmon, Morris, and Ivany note in the fourth essay of SJG:RHVL that, early in the general course “History of Earth and Life” he taught at Harvard every year, Gould would write four words on the blackboard that he identified as obstacles to a better understanding of natural history. These were: Progress, Determinism, Gradualism, and Adaptationism. If he had chosen to select four words that *aided* in the understanding of natural history, I think they might have been: Stasis, Constraint, Hierarchy, and Contingency. Gould himself offered an “office door” summary of a large part of his worldview – way too long to fit on a bumper sticker, of course – in his essay *Can We Complete Darwin’s Revolution?* It reads as follows:

> Humans are not the end result of predictable evolutionary progress, but rather a fortuitous cosmic afterthought, a tiny little twig on the enormously arborescent bush of life, which, if replanted from seed, would almost surely not grow this twig again, or perhaps any twig with any property that we would care to call consciousness.

On the more technical issues of punctuated equilibrium and contingency in the fossil record, how does the professional community view Gould's worldview several decades after the first appearance of punctuated equilibrium? While surely not a universal view, I will offer the last word to Richard Bambach, a long-time colleague of Gould. Bambach closes his essay in SJG:RHVL (p 124) with a reference to two publications that appeared some years after Gould's death. He writes: "Steve [Gould] is not cited in either report. . . . But he doesn't need to be. Punctuated equilibrium and contingency are well-established concepts now; as ideas they are no longer news. But Steve made both types of study central to modern biology and paleontology. Now we all work in Gould's world."