Eight Little Piggies

ELP 1. Unenchanted Evening

The purpose of this essay, Gould begins, is to present a twist on the reporting regarding the tragedy of human-induced extinction. In the process, he provides an enlightening discussion of the rate of evolutionary change. The victims in this case are the dozens of species of the land snail *Partula* that are native to Tahiti, Moorea, and neighboring volcanic islands. The essay's title is a pun on the song "Some Enchanted Evening" from the 1949 Rodgers and Hammerstein musical *South Pacific*, which also takes place in Tahiti.

Snails of the genus *Partula* are noted for the diversity of their shape and coloring, with each species living in a small and distinct geographical area. They live on fungus that grows on rotting vegetation, and leave plants, including cultivated crops, alone. Unfortunately, the large African land snail *Achatina* is not so innocuous; it eats just about everything. As in many other places, this snail was deliberately imported by Europeans to Tahiti as the main ingredient of snail soup. And, as in all of those other places, it quickly escaped (both to the rest of Tahiti and the neighboring islands) and began to decimate the colony's crops. The response to the disaster associated with introducing a non-native species of snail was to introduce another species of non-native snail: *Euglandia*, famous for its unusual habit of feeding on other snails. *Euglandia* had also been introduced elsewhere, with very limited success in terms of its ability to eradicate *Achatina*. The result was the same here – but there was the predictable (and predicted) side effect that, while doing only minor damage to the *Achatina* populations, it was highly successful in wiping out almost every species of the indigenous *Partula*. Gould could have left this story at this: another example of man's carelessness and stupidity leading to the extinction of most of a genus. But that is not his style. Instead, he uses the history of the study of *Partula* to present the loss from a different perspective.

One of the reasons that the process of evolution is so difficult to understand is that it does not appear to operate on the timescales of human lifetimes [see LSM 22]. However, land snails living on volcanic islands may come closer than any other macroscopic organism to providing a laboratory for observing the evolution in action. Volcanic islands provide several key requirements. One is geologic youth, and with it the lack of established species and the absence of predators. Another is the wide range of environments on such an island (altitude, windward versus leeward, and so on). Further, most such islands incorporate a series of ridges that run from the peak to the shore, which can isolate one population from another even on the same island. Snails offer key features as well, perhaps the most important being that most are hermaphroditic. Because of this, the arrival of a single snail (as opposed to a mating pair) can produce a local population. Within the land snail family, the genus *Partula* is particularly noted for its large variation in shell shape and color, features that are much easier to study statistically than anatomical features that can only be studied with a dissecting kit and a microscope.

The attributes of *Partula* and Tahiti allow scientists to explore, to a degree, the importance of environment, as opposed to randomness, on the variation of species. Specifically, they can address the question of whether the shape and coloring of each distinct species is correlated with some aspect of the local environment. If it is – if, say, larger shells are correlated with higher rain rates – then we have evidence that natural selection shapes developing species in a way that presumably optimizes survival. If, however, no such correlations can be identified, this may imply that most variations are actually random (within certain constraints), and may be incorporated into a new species as long as they are not explicitly harmful. This question highlights one of the most important debates within the evolutionary biology community during the twentieth century: is natural selection the primary (or only) force that shapes each part of each organism, or is it simply an executor of the unfit? Adaptationists, also sometimes known as formalists, strict Darwinists, or neo-Darwinists, argued (and argue) for the former. Darwin argued for the latter [see TPT 4]. [Gould discusses his early research on a different genus of land snails, and his evolving thoughts on adaptationism, in HTHT 10, TFS 11, and DIH 27].

So which is it? The first man to explicitly enter the fray was John T. Gulick (1832-1923), who worked with the land snail genus indigenous to the Hawaiian Islands. Gulick was a missionary, and was opposed to the idea that the environment completely controlled the species on religious and philosophical grounds; he believed that this position would imply, by extension, that there was no free will. He concluded that was no correlation between the shape of the Hawaiian land snails and the local environment of their native valleys; the same vegetation, moisture, and temperature appeared to produce significantly different results. Alfred Russell Wallace, co-discoverer of natural selection and the original “strict Darwinist,” argued that what might appear to us to be identical conditions might be very different to the snails themselves. The continued debate caught the attention of Henry Edward Crampton (1875-1956), a legend among “snail men” such as Gould. Crampton spent fifty years studying the more diverse *Partula* on Tahiti and the surrounding islands, producing three massive tombs in 1917, 1925, and 1932. Focusing on this question with an open mind, his conclusion firmly supported Gulick’s: identical conditions produced different results every time. He personally measured several dimensions of hundreds of thousands of snail shells during this period, and performed statistical analysis on the data (without computer or calculator) to quantify not just the average size of each species, but the variation within it.

Crampton collected his data before the *Euglandia*-induced extinction event, and it remains invaluable. However, Crampton was trying for more than a single snapshot in time. His second goal was to establish a baseline of *Partula* morphology. This would permit future researchers to observe evolutionary changes over decades or centuries, if it occurred on that timescale, with a statistically significant sample of historical data as a reference point. In fact, there were scientists who followed in his footsteps over the decades, trying to do just this. It was these people who first recognized the disaster that was befalling the *Partula*. This leads to Gould’s alternative perspective on the nature of the tragedy: it is not just the species themselves that are lost, it is Crampton’s great foundation. The fifty years of painstaking data collection and analysis that Crampton performed leads only to a snapshot, and not to a movie.

Gould tells us that the reason most people, including most biologists, have not heard of Crampton is that his work appeared at the beginning of a long period in which the functionalist (or adaptationist) viewpoint held sway. Gould tells how he himself used to be one, and a bit about how he came to change his mind. [He elaborates on this in DIH 27.]

ELP 2. The Golden Rule: A Proper Scale for Our Environmental Crisis

As happens occasionally, the writings of Stephen Jay Gould are employed by others in the service of an argument that he himself opposes. The relevant issue is the existence of a small population of red squirrels that exist only on one mountain in southern Arizona, and the desire of a nearby University to clear part of the remaining habitat for an astronomical observatory. Gould found himself dragged into this conservation versus development debate via a pro-development op-ed piece that appeared in the *Wall Street Journal* with the provocative title, “No Red Squirrels? Mother Nature May Be Better Off.” The author references work by Gould and colleague Jack Sepkoski to argue that not only will the species in question eventually become extinct anyway, but that this will lead to a larger diversity of new species in the future. The primary purpose of this essay is to address the all-too-common misunderstanding that leads from Gould’s writing to the op-ed author’s conclusion, as stated in its title. Gould also discusses his actual views on the subject of development versus conservation, and on this case in particular.

First, Gould does acknowledge that most species exist for no more than a few million years, so it is virtually inevitable that the red squirrel will someday go extinct – as will we. He also “admits” to writing (along with many others, including Darwin) that extinctions in general can open niches for the development of new species. Further, he has noted [see TFS 16] that there do appear to be a larger number of species now (albeit fewer phyla and classes) than in the geologic past. The flaw in the op-ed argument, Gould states, is that it fails to account for the time scales involved. The amount of time for life on earth to recover its diversity after a mass extinction event, such as the one that wiped out the dinosaurs, is on the order of ten million years. This is a thousand times longer than the amount of time from the end of the last ice age (and the beginning of agriculture) to now. Any enhanced diversity that may result from contemporary human-induced extinctions will be, by human standards, infinitely far in the future. He adds that the argument that the squirrels in question must eventually become extinct is analogous to not giving a child medicine for a curable disease because he will eventually die anyway.

As to the particulars of this issue, he notes that the red squirrel is not a unique species, but rather a subspecies; the latter tend to ebb and flow. His view is that conservationists (and he included himself in this group) should not fight to defend every subspecies, on the grounds that such a position will not maintain popular support and will thus be self-defeating. He does, however, side with the conservationists in this particular case, because the mountain that the red squirrel lives on is an “island forest.” Deep in what is now a hot, dry desert, the altitude preserves the remnants of a forest ecosystem that was widespread in the region during the last ice age. Thus, the red squirrel serves as an “indicator species,” much as the Panda does for the threatened bamboo forest ecosystem in China.

So, what sort of general rule can we come up with for determining when to take a stand against a particular development project in order to preserve an ecosystem? Gould argues that it is not really about protecting the planet – it will look after itself in the geologic long run, no matter what we do. However, there are advantages to humans in preserving species, forests, and polar ice caps that are both ethical and practical, and that are connected to the time scales of our own lives. Gould suggests an approach in which we recognize the power that earth actually holds over our lives, and then follow the golden rule – treat it and its ecosystems with the same degree of stability and "decency" that we ourselves require. On the human timescale, this is simply enlightened self-interest.

ELP 3. Losing a Limpet

Naturalists came to recognize that extinction was a real phenomenon in the 19th century [see HTHT 7]. Species with limited geographical ranges and/or food sources, such as the dodo, the Galapagos tortoise, and the panda are all clearly vulnerable. But creatures with large ranges, such as the passenger pigeon, may also succumb under certain circumstances. However, with the exception of a few species of vertebrates, it was widely assumed that sea life was immune from human-induced extinction. Local populations of oysters or crabs may crash to the point where they are no longer commercially viable, and entire local populations may be wiped out, but the sea is so vast that some members of the species – so the argument goes – would always survive somewhere. This informal law has held up remarkably well. However, a 1991 article by James T. Carlton and others in the official journal of the Wood's Hole Institute, the *Biological Bulletin*, states that a species of limpet from the Atlantic Ocean – *Lottia alveus* – does appear to have gone completely extinct. Limpets are mollusks, actually a type of snail. *Lottia* lived along the northeastern coast of North America, and the last one was seen alive in 1933. As Carlton's paper describes, it appears to have gone extinct when the plant it lived on, a species of eel grass, was itself decimated. The source of this attack was a protist, and so apparently had nothing directly or indirectly to do with man. The eel grass itself survived because of its extensive geographical range, and because it had a wider tolerance for salinity than its attacker and survived in the brackish waters near shore until the epidemic passed. Other creatures that depended on the eel grass were also able to survive, albeit at reduced populations, by turning to other sources of food. But *Lottia* could only feed on the one species of eel grass, and could only survive in a narrow range of salinity – and so apparently perished completely. What we observed here, Gould tells us, is an example of natural extinction; a species coming to the end of its multi-million year existence, a process which occurs "all the time" in geologic timescales. *Lottia* was particularly vulnerable to extinction due to the small size of its ecological niche. Nonetheless, he cautions, humans should be aware that no ecological area is invulnerable to extinction.

ELP 4. Eight Little Piggies

Plato believed in the paradigm of "divine ideas" or "forms," perfect shapes that living organisms strove to achieve but could only approach. Richard Owen [also see LMC 6 and LSM 9], the great 19th-century naturalist and vertebrate anatomist, modified Plato's paradigm into the related concept of an "archetype" for vertebrate design. Owen's archetype was not so much a goal as an abstract tool kit that contained all basic parts that could be modified as required to form any amphibian, reptile, mammal, or bird. Owen, who came to believe that "transmutation" occurred but was an outspoken critic of

Darwin's theory of natural selection, considered the archetype to be an abstraction. Darwin, however, essentially took Owen's idea as literally true; in his view, the archetype was manifested in a flesh-and-blood common ancestor. Either way, the concept of the repertoire-of-parts metaphor remains useful, and is used today.

Owen's archetype of the terrestrial vertebrate contained a spine with a skull at one end, and four limbs, each of which ended in five digits. Some members of this group might contain a less-than-complete complement of components – horses have only one toe, and whales only a scrap of bone for their rear limbs – but all can be seen to belong to the overall group. None of the lobe-finned fish that are candidates for the role of ancestor to the first tetrapod (the group that contains amphibians, reptiles, mammals, and birds) is limited to five proto-digits, so it had long been held that the first terrestrial vertebrate had this configuration. Our hand, with its four fingers and opposable thumb, is considered second only to our large brain in making us "human"; we should be appreciative, therefore, that our tetrapod ancestor developed a non-specialized limb with five digits.

The contemporary fossil record included three candidates for this ancestral tetrapod. Two, *Ichthyostega* and *Acanthostega*, were first collected in Greenland by a Danish expedition in 1929, and date back to the end of the Devonian period (about 340 million years ago). While the ends of the limb bones were not sufficiently well-preserved to count toes, it was assumed that each would have five. Then in 1984, a third late-Devonian tetrapod genus, *Tulerpeton*, was discovered by a Soviet paleontologist. The fossil was well-preserved – and clearly showed *six* digits on each limb. Additional fossil material on the other two tetrapods was unearthed in 1987, and it was discovered that at least the rear legs of *Ichthyostega* contains *seven* toes, and at least the forelimbs of *Acanthostega* contain *eight* (hence the essay's title). Thus, it appears that there is nothing archetypical about five toes after all. While this discovery does not alter the general conclusions about the importance of "about five" digits to the development of terrestrial vertebrates (including humans), it now appears that our five-toed architecture is a secondary stabilization rather than a primary attribute.

Gould then notes that frogs and other amphibians generally have five toes on their rear limbs, but only four on their front limbs. Up until this point, it had been assumed that at ancestral amphibians had five toes on all limbs and then lost one on the forelimbs, but the above discoveries call this into question. Our common view of evolutionary history is that lobe-finned fish evolved into amphibians, and the reptiles then evolved from one group of amphibians. However, paleontologists have not been able to identify which genus of amphibians led to reptiles. Further, there are no amphibian fossils that positively predate the appearance of Amniota (collectively, the group of vertebrates that includes reptiles, mammals, and birds; the term refers to a common attribute of their eggs). Perhaps, it has been recently argued, amphibians and the Amniota diverged early and then evolved independently from a common tetrapod ancestor. In light of the variable-digit argument presented above, it becomes plausible that amphibians did not "lose" a toe on their front limbs, but rather stabilized at four from the very beginning.

Gould proceeds to discuss some additional research in the field of embryology on the formation and development of digits. Since the early days of the field, it was recognized that the parts of the limb nearest the body develop first, and the digits last. It was assumed that the axis of formation ran down through one of the digits, and much of the debate focused on which finger represented this axis. Some powerful research published in 1986, however, shows that actual path of limb development is significantly different: it does proceed down the limb toward the "pinky" (actually the ring finger), but then turns along the bones of the wrist towards the thumb. Thus, each of the digits is actually a side branch off of this main axis (the pinky actually branches off "backwards").

Next, Gould asks why five should end up being the canonical number of digits for at least the Amniotic group of terrestrial vertebrates. There are two schools of thought on this. The first school, adaptationism, begins with the assumption that is that there is or was some selective advantage to five toes. For example, fewer toes might not allow sufficient stability, while more might lead to other problems. The other school of thought, to which Gould (and Darwin) belong, is that of historical contingency. In this view, five digits just happened to be what one key ancestral tetrapod possessed, and it was "good enough." If this animal had had four or six digits, then perhaps so might we.

Considering how powerful the forces of natural selection can be, Gould notes, it is perhaps puzzling that the number of digits has remained so stable in the Amniota. In an extended parenthetical statement, he speculates that there may be a connection between this remarkable stability and one of the most important puzzles in natural history: why no new phyla have appeared since the Cambrian period ended more than 500 million years ago.

ELP 5. Bent Out of Shape

This essay overlaps two important themes in evolution: convergence and irreversibility. "Convergence" is the term evolutionary biologists use to refer to similar structures that evolved independently in different lineages, such as the wings of birds, bats, and insects, or the eyes of squid and fish [however, see LMC 17!]. One of the most famous examples is extinct aquatic reptile group Ichthyosaur, which bears a striking morphological resemblance to a modern dolphins and swordfish. The full degree of the similarity between these groups was not recognized until the 1890's, when high-quality specimens that included the creature's outline (including soft tissue) were discovered in Germany. These fossils clearly showed not only the bony, fish-like paddles, but also a previously unknown dorsal fin and caudal (tail) fin. These fins were the same size and in the same place as comparable fins on large fish, and clearly demonstrate the power of natural selection to find similar solutions to solve the same problem. These fossils showed that the last third of the Ichthyosaur's vertebral column bent sharply down to form the leading edge of the lower half of the symmetrical tail fin (the upper portion was boneless). In fish, the vertebral column ends at the beginning of the tail fin; in sharks, it follows the upper lobe. (In whales and dolphins, the tail fluke is horizontally-oriented, rather than vertical.) This sharp downward bend is unique to ichthyosaurs, and led many earlier observers to believe that it represented a point of consistent post-mortem fracture. It also provides the title for the essay.

So the convergence aspect of ichthyosaurs is clear; but there is another important observation in these fossils as well. Reptiles, including ichthyosaurs, are descendents of tetrapods, which are in turn descendents of certain lobe-finned fish. However, ichthyosaurs are easily identifiable as modified reptiles. That is, evolution did not "regress" these creatures back to a more fish-like ancestral state, but rather "progressed" forward to extend the reptilian digits to superficially resemble a fish's paddle, to create a dorsal fin out of apparently only skin (fish usually have bones in their dorsal fins), and the unique tail fin structure. The concept that complex evolutionary processes are irreversible is known as Dollo's law, after Louis Dollo (1857-1931), an important Belgian paleontologist [also see TPT 3]. This is not a true law, but a statistical one; it argues that the number of mutations that must be selected for is so large that the odds of reversing all of them are virtually nil. The ichthyosaur may come to physically resemble its distant ancestor, but the anatomical structures associated with life on land are not, and cannot, be completely erased. These remnants of the creature's phylogeny (evolutionary history) are one of the strongest pieces of evidence that organisms do, in fact, evolve.

ELP 6. An Earful of Jaw

One of the most difficult challenges that Darwin's theory of evolution must satisfactorily explain is how a new organ or structure can arise. Since (say) half a wing is of zero utility for flight, there would be no evolutionary advantage to the individual to "improve" it to 51%, no selective disadvantage if it fell to 49%. [This specific example is discussed in BFB 9.] To add to the challenge, the origin and development of new structures is only rarely preserved in the fossil record. One important exception to this, and one of the great success stories of long-term evolution captured "in the act," is the development of the middle ear bones in tetrapods and their modification in mammals. [See DIH 28 for another successful case, and BFB 11 for an important example that turned out to be largely incorrect.] The discovery of the process by which this transition occurs actually came from embryology, and predates Darwin's theory by several decades. Gould tells the story in this essay.

Fish can hear; they have a cochlea (inner ear) that converts sound waves in water into electrical signals that travel to the brain. What fish do not possess is the middle and outer ear of land-based vertebrates; instead, they have a "lateral line" down each side that contains acoustic sensors. These sensors do a fine job of detecting high-pressure sound waves carried by the incompressible medium of water, but are ineffective in dealing with low-pressure sound waves in the highly compressible medium of air. Thus, when some lobe-finned fish evolved into tetrapods at the end of the Devonian period [ELP 7], the formation of a new structure was required in order for these land-dwellers to hear effectively. The outer ear – specifically, the eardrum – appears to have formed independently in several lineages, and Gould does not discuss that topic in detail here. The importance of the eardrum is that it has a much larger diameter than the opening into the liquid-filled cochlea, which allows it to collect acoustic energy over an area large enough to be effective. What is still needed is a structure to convert large-amplitude, low-pressure vibrations of the ear drum into low-amplitude, high-pressure vibrations in the inner ear (cochlea). In most land-dwelling vertebrates, this is accomplished with a single delicate bone that connects the two, and works via the provocatively-named "stiletto heel" principle. However, in the mammal ear, there are three such bones. How could natural selection produce these completely novel structures?

The answer is that the bones already existed, but were serving another function – they were part of the jaw. As long as these bones were required for proper jaw function, little could change. However, the bones became "available" for another role when the ancestral organism developed an alternative way to address those requirements. Gould makes the point that it is the redundancy, the "slop" associated with the natural evolution of complex organisms, which makes this sort of evolution possible. Bacteria are, in many ways, optimally designed, with little excess genetic or organic material; but after some 3.5 billion years, they are essentially unchanged. More complex creatures are not nearly so well optimized, and carry less-than-optimal, jury-rigged solutions. It is the ability of one structure to serve multiple purposes, and multiple structures to serve the same purpose, that makes it possible for the descendents of aquatic fish to develop acoustic sensors that work in air.

Much of the essay is spent on the specifics, which are well-documented in both the embryological development of modern vertebrates and in the fossil record. Early fish had gills but no jaw, as lampreys do today. The first jaws are known to be a series of modified gill arches (the front one may be a homologous structure). The upper branch of one such gill segment evolved into a heavy brace to help connect the upper jaw to the brain case. This bone, which becomes the stapes ("stirrup"), happens to lie near the fishes' inner ear. Recent discoveries of well-preserved stapes in the early fossil tetrapod *Acanthostega* shows that this bone, while not yet reduced to the delicate role it would take on later, was located and constructed in such a way that it could also provide some limited capability as a functional middle ear bone. (It was the report of this discovery that induced Gould to write this essay.)

While amphibians, reptiles, and birds employ this single-boned middle ear, mammals have developed a middle ear with two additional bones (the "hammer" and "anvil"). Embryology and the fossil record clearly show that these two structures correlate to parts of the jaw in other vertebrates. (Mammal jaws are each composed of a single bone.) Further, the evidence shows that they originally started out as the upper and lower parts of another gill arch. In the multi-boned jaws of many (non-mammalian) vertebrates, these bones actually form the jaw hinge. The fossil history of mammals, however, shows that the anterior ("front") bones in the upper and lower jaws grew backwards over an extended period, and eventually formed a new joint. The two now-redundant rear jaw bones, called the quadrate and the articular, detach and become free-floating. In still later strata, they are seen to migrate towards the ear, eventually forming the hammer and the anvil bones. If this were speculation, it might not pass muster; but the fossil record on this is remarkably rich, and this is precisely what is observed. [Gould discusses the role of "initiations" in ELP 26.]

ELP 7. Full of Hot Air

As a historian of science, Gould is drawn to "fruitful mistakes." These are errors that eventually lead to deeper understanding, either by being right for the wrong reasons, or being wrong due to the falsity of an underlying assumption. One of his more famous lectures to his students at Harvard is based upon the incorrect conclusion that the lungs of terrestrial vertebrates evolved from the homologous structure in fish, the air bladder; Darwin himself makes this error in *Origin of Species*. The record actually show that air bladders evolved from lungs! The utility of presenting this case study is that it highlights a common, underlying false metaphor: that the evolution of life is a ladder, as opposed to a bush. In the "ladder" view of evolution, fish evolved into amphibians, which evolved into reptiles, which evolved into mammals. In this paradigm, it makes perfect sense that lungs evolved from air bladders, since the first terrestrial tetrapods evolved after the first fish. However, while this path probably occurred [but see ELP 4 regarding amphibians], it was in fact only one of many; life is a bush. What we collectively call "fish" are actually a far more diverse group than terrestrial vertebrates; further, they continued to evolve after our branch diverged. The most common type of fish today, the ray-finned teleosts, actually appeared rather late, well after land-dwelling vertebrates with lungs existed on land. The teleost line followed a different, but equally good, contemporary path to success – by optimizing the supposedly advanced "lung" implementation for what we – incorrectly, Gould says – think of as the primitive, and thus by implication inferior, "air bladder" implementation.

Our ancestors were lobe-finned fishes, not the ray-finned teleosts; there are several other classes of "fish" as well, including sharks and the extinct armored fishes. The ancestor to all of these groups had both lungs and gills; some, such as lungfish and the famous coelacanth, still do. Teleosts, with a few exceptions, have lost the ability to use the structure as a source of respiration, and instead use the structure almost entirely for buoyancy. Other groups, such as the shark, have lost the structure altogether (and instead have oversized oil-filled livers which provide buoyancy instead), while all terrestrial vertebrates except amphibians have lost the gills. When viewed in this way, it becomes more apparent that modern fish are as "evolved" as modern reptiles and mammals. It should also be clear that lungs are not more "advanced" than air bladders, but simply represent a different set of selection-based optimizations to a homologous structure.

While Darwin was wrong about the evolutionary sequence of lung and air bladder, Gould notes that he was absolutely correct about how the organ illustrates the solution to one of the more difficult conceptual challenges of evolution via natural selection. Fully-formed lungs work for some vertebrates; fully-formed air bladders work for others. But how do you get from one to the other? The answer is found in the concept of *redundancy*, which he divides into two categories: two-for-one and one-for-two. As an example of the former, he uses this example: many early vertebrates had two organs that served the single function of respiration (lungs *and* gills). In such cases, macroevolution may occur when one organ completely takes over the role, thus freeing up an existing structure for a new purpose [also see the previous essay]. As to the latter, an organ can simultaneously serve more than one function. Gould details how air bladders today serve not only as sources of buoyancy, but are also used in some species of fish as depth sensors, and sound sensors, and as sources and amplifiers of sounds. Importantly, both forms of redundancy are quite common in animals. This is "because," Gould points out, these organs were not designed "for" one purpose or another; in fact, they were not "designed" at all, but rather *evolved*. It is the very existence of this "slop" or ambiguity in these structures that allows many examples of macroevolution to occur, and it is the very non-optimization of the structures that is one of the clearest pieces of evidence we have that evolution actually occurred.

ELP 8: Men of the Thirty-Third Division: An Essay on Integrity

Eugene Dubois (1858-1940) was the Dutch anatomist famous for discovering Java Man in 1891, the first true pre-*Homo sapiens* fossils of man. He named the species *Pithecanthropus erectus*, although today it is recognized as *Homo erectus*. The fossils consisted of a femur comparable in both size and construction to modern man (indicating that it walked upright), and a skullcap that suggested a brain size about two-thirds that of *Homo sapiens*. Dubois is also infamous for his odd behavior in the decades that followed. In this essay, Gould tells the "official" version of the story repeated in many books, but then adds the context – almost always missing – in which Dubois worked. In science, where tomorrow's data can undermine anyone's theory, all the participants can really have is the integrity and self-consistency of their models, based on the information that is available to them at the time. Thus, he laments, it is doubly unfortunate when isolated parts of a scientist's model are taken out of their context, in addition to being proven wrong by later discoveries. This happens all the time, he notes, in large part because scientists are so busy that they do not have the time (or perhaps desire) to read their colleagues' writings with the care they often deserve. Placing the scientist within the framework of his own worldview is the "integrity" of the essay's subtitle.

The canonical story – Gould quotes several references – is that Dubois received much praise for his discovery, but also much harsh criticism as to the validity and significance of the fossils. He responded poorly to this criticism, locked up the fossils, and sulked for 25 years. When he finally succumbed to pressure to make the bones available for scientific scrutiny again, he did so – but this time, instead of claiming the fossils were from an ancestor to man (as he had claimed earlier), he instead claimed that they belonged to a giant gibbon! The impression one comes away with is that he was cantankerous, antisocial, and at least a little crazy.

While Dubois was sensitive and did, in unprofessional defiance, make the fossils unavailable for 25 years, he did not hide and sulk during that period. First, Gould notes, he retained his posts as a professor in Amsterdam and curator of the Teylers Museum in Haarlam, and published numerous papers during this period. The focus of his work was the establishment of a useful scaling law for brain size to body size in animals. Whales have the most massive brains, while shrews – due to their tiny size – have the highest brain-to-body mass ratio of any animal; what is the proper relationship? In 1891, Otto Snell developed the power-scaling law that we still use today – the so-called "mouse to elephant curve" [see ESD 22 and 23]. But it was Dubois, in his classic 1897 paper, who provided the first extensive data set in support of this model – in the middle of his supposed "sulking period." (Gould references a recent biography of Dubois by Bert Theunissen entitled *Eugene Dubois and the ape-man from Java*.)

This work was not unrelated to Java Man or human ancestry – in fact, it was completely motivated by it. Dubois believed in evolution, and it was his belief in it that led him to look for ancestors of mankind in Indonesia. However, he disliked Darwin's theory of natural selection. Instead, he believed (as many in Europe did at the time) that evolution was *directed* (toward greater complexity and higher intelligence), and *internally powered* rather externally selected for. He also believed in the non-Darwinian view that evolution occurred in discrete jumps. His next contribution – which would turn out to be incorrect, but is essential to understanding his work – is that the brain-to-body ratio of the mouse-to-elephant curve came in discrete, quantized amounts. Further, these ratios followed a consistent doubling pattern: if this parameter was set to one for humans, then apes were at one-fourth on this power scaling curve. Dubois extended this trend to other animals: one-eighth for most carnivores and hoofed herbivores, one-sixteenth for rabbits, one-thirty-second for mice, and one-sixty-fourth for shrews. Evolution, according to his view, occurred via these discrete acts of brain-to-body ratio doubling.

Notably absent from this sequence is an animal with the corresponding ratio of one-half. Dubois was motivated by the desire to prove that his fossil find, *Pithecanthropus*, was in fact this "missing link" between apes and humans. However, the femur showed a creature of about the same size as a modern man, but the skull cap suggested a brain of two-thirds, not one-half, of the size of modern man. It was this problem that led Dubois to propose that *Pithecanthropus* had the proportions of a gibbon, with longer arms (relative to the femur) and a much larger chest; these proportions would produce the correct brain-to-body mass ratio of one-half that he was looking for. Seen in context, Dubois's odd claim of a gibbon-like fossil was not a step away from considering Java Man to be an ancestor of man, but rather a step toward it. While Dubois was incorrect, and guilty of interpreting data to match a pre-conceived theory, he was not the crazy old coot that the canonical version of the story makes him out to be; the context matters.

Dubois extrapolated his model into the invertebrate world as well, and concluded that the original single-celled life on earth had the equivalent of a brain-to-body ratio that was thirty-three factors of two less than humans. Thus, humans are the thirty-third division (or multiple), so the title of this essay is an acknowledgement of this obsolete paradigm, rather than a reference to military service.

ELP 9. Darwin and Paley Meet the Invisible Hand

This is an essay on natural theology in general, and specifically about William Paley's 1802 book entitled *Natural Theology: or, Evidence of the Existence and Attributes of the Deity, Collected from Appearances of Nature*. Natural theology argues that the organization that is observed at all levels in nature is evidence both of a designer (invariably taken as God), and of His goodness. [Gould addresses problems with the latter part of this argument in HTHT 2.] This primarily English school of thought goes back to at least John Ray's *Wisdom of God Manifested in Works of the Creation* (1691), and continues at some level to this day in the form of "Intelligent Design." [Gould discusses the contribution of Robert Boyle, writing in 1688, in LMC 15.] Today the argument has its political and popular supporters, but no intellectual credibility. As he often does, however, Gould examines the theory of natural theology within the context in which it was created; he then compares it to Darwin's theory of natural selection.

Paley's argument begins with a two-part postulate. The first is that both the components of animals (organs and other structures), and the combinations of these parts (the entire animal) are, in fact, designed. The second part is that there is a *purpose* associated with each design: wings to fly, the heart to pump blood, and so on [see HTHT 6 for a discussion of "purpose."] Paley follows with an inference: that good design implies a designer. That is, these well-designed structures, so much more complex than a pocket watch (his famous opening example), could not have come into existence on their own. (Gould notes that modern theological thought rarely draws on examples from the material world as evidence for the existence of God.)

Paley continues by refuting what he believes to be the only two possible alternatives to his theory. The first is that good design exists, but that it was not created for the purpose it currently serves. There are many such cases, he allows, and gives the example of how rough, abrasive dogfish skin could be (and was) used as sandpaper; surely the creator did not design it for this purpose. But this argument cannot be valid for more complex structures; what possible purpose could an eye serve other than seeing? The second alternative is that good, purposeful design exists, but that it arose via a (guided) evolutionary process rather than in a single act of creation. (Gould reminds us that the concept of evolution existed long before Darwin, whose theoretical contribution was the mechanism of natural selection.) Paley then refutes an essentially Lamarckian evolutionary theory, based on the concept of the inheritance of acquired characteristics and the disappearance of unused structures. His specific counter-arguments include the fact that men have nipples despite having no use for them, and that male Jews continue to grow foreskins despite generations of circumcision. He also presented the important theoretical argument that half of a design is of roughly zero percent utility [see BFB 9]. One alternative that Paley does not consider, Gould notes, is the view that animals are not so well-designed after all, but merely kludged together; the product of evolution via the messy, waste-filled, and uncaring mechanism of natural selection.

In Paley's theory, good design is not limited to material structures; it incorporates behaviors as well. Using the example of birds, Paley argues that the pleasure obtained in sexual activity is a mark of good design, in that it indirectly but powerfully motivates the species to perpetuate itself. But what about the mother bird sitting on the nest for weeks on end, which would appear to involve the very opposite of pleasure? This must also be designed behavior, Paley argues, for the opposite reason: it *is* unpleasant, and thus indicative of a higher principle at work. (Paley makes a related argument that a man might suffer gout in order to better appreciate his pain-free hours. Gould notes here and elsewhere that Voltaire satirized this view of life via the character Dr. Pangloss in

Candide, published several decades earlier.) Of the bird's nest-sitting behavior, Paley writes that he recognizes the presence of an "invisible hand." This phrase caught Gould's attention, for it is the very one used by Adam Smith in his 1776 work *Wealth of Nations*, written a generation earlier, to describe laissez-faire in free-market economics. The irony, Gould points out, is that Adam Smith's use of this term is much more like Darwin's theory of natural selection than Paley's theory of natural theology.

Darwin was clearly influenced by Smith's argument that an orderly economy can emerge from situations in which each member of society is merely acting in his own self-interest, with no awareness of his role in a larger structure, and recognized the analogy of market forces to natural selection. While society eventually objects to the brutality that unchecked free markets can apply to its members, there is no corresponding analogy in nature. Paley could not conceive of, and (Gould argues) would not have accepted, a version of evolution in which every change was the result of repeated decimations – Gould uses the term *hecatombs* – of the "unfit" and unlucky. Paley's invisible hand was real, and belonged to a caring deity. Darwin's invisible hand, like Adam Smith's, is not real; it is an allusion, a way of thinking about order arising from what appears to be only chaos. Kindness and the best interests of the community at large are fictions in this paradigm. Gould writes: "Smith's invisible hand is the *impression* of higher power that doesn't actually exist at all. In Darwin's translation, the invisible hand dethrones the God of natural theology."

As always in these sorts of essays, Gould tries to close on an upbeat note. Yes, he agrees, we lose a sense of comfort when we abandoning Paley's view of nature, a sense that our lives are an essential part of a grand design. He writes: "But think what we gain in toughness, in respect for nature by knowledge of our limited place, in appreciation for human uniqueness by recognition that moral inquiry is our struggle, not nature's display. Think also what we gain in increments of real knowledge – by knowing that evolution has patterned the history of life and shaped our own origin." We gain something priceless by simply understanding the way nature is, not the way we might like it to be.

ELP 10. More Light on Leaves

Scientists, like members of all professional communities, tend to guard their turf against those not recognized as members of the guild or fraternity – even if they are recognized as brilliant in another field. We might look back to an earlier age with the hope that things might have been better in a less specialized time, but they never were. Gould laments this, and offers two arguments in favor of participation by talented scholars from other fields. He identifies the first, "universalism," as the weaker of the two; this view holds that the minds of good thinkers all work in pretty much the same way, so any assistance offered on thorny problems should be appreciated. The second and more important argument, he continues, is "special insight." This refers to the ability to someone who is an expert in a different field to bring a new and possibly fruitful perspective to a field or issue, one that the community itself may not capable of generating.

Moving from the general to the specific, Gould identifies Johann Wolfgang Goethe (1749-1832) as such a man. Goethe was recognized in his own day (and in ours) as a great poet, author, and artist, but he also performed notable work in the fields of anatomy, botany, geology, and optics. He was always considered an outsider in these fields, even after some noteworthy successes, and he always resented it. The perspective he offered is more common in artists than in scientists: what Gould refers to as a holistic, rather than a reductionist, viewpoint. Goethe looked for, and sometimes saw, underlying laws of unity beneath the apparent endless diversity of living organisms. He won an early victory by predicting the existence of a small bone in the human jaw, based on its existence in other vertebrates; it was later found via embryology, and is still sometimes referred to as "Goethe's bone."

Goethe's most important work in the field of biology, translated, is called *An Attempt to Explain the Metamorphosis of Plants* and was published in 1790. (He is credited with coining the term "morphology.") This was not a scientific work in the standard sense; it described no plants in detail, and was composed of 123 numbered passages expressing his thoughts and insights in the form of aphorisms. Like Richard Owen [ELP 4] and Etienne Geoffroy Saint-Hilaire [LMC 17], he believed in underlying "archetypes of design"; an abstract set of components shared by a group of organisms. Goethe referred to the fundamental, archetypal component of plants – at least the green parts and flowers – as the "leaf." (This turned out to be an unfortunate choice, Gould notes, because it was easy to misconstrue his abstract ideal as a literal structure, a position that exposed him to a certain amount of ridicule.) To this concept of an underlying unity of structure, he added two more themes: progressive direction and repetitive cycling, two of the great metaphors in Western thought (and the central subject of Gould's 1987 book, *Time's Arrow, Time's Cycle*, he adds). The directional process involves the refinement of sap from the first shoot to the flower. The cyclical process involves three specific cycles of expansion and contraction – seed to sprout (first expansion), leaves to the sepals at the base of the flower (first contraction), and so on. While incorrect in most specifics, Goethe's book was thought-provoking, and his errors "fruitful" (Gould acknowledges the pun). Most botanists of the time were focused on describing the details, and thus the differences, of each component; Goethe's work presented a perspective of underlying similarity. He suggested unifying "laws" to connect all plants, inspiring others to seek patterns in the overwhelming diversity of nature. [Today, flower pedals and other structures in plants are recognized as being, literally, modified leaves.]

ELP 11. On Rereading Edmund Halley

Gould promised himself that he would not write an essay about Edmund Halley when his namesake comet came around in 1986, since so much else was being written about it. But the fact that so little attention was paid to Halley's special contribution to geology, he claims, forced him to revise his position. Halley (1656 – 1742) was a contemporary and friend of Newton, and made a wide variety of scientific contributions. Of particular interest to Gould is a paper entitled: "A short account of the cause of the saltness of the ocean, and of the several lakes that emit no rivers; with a proposal by help thereof, to discover the age of the world." As the title suggests, Halley argued that if the ocean were originally salt-free, and salts were added in minute amounts each year from the rivers that fed them, and that the ocean was not yet saturated (as evidenced by the greater salinity of the Dead Sea), then one could obtain an estimate for the age of the earth by measuring the change in ocean salinity over time. This paper is generally credited as the first attempt to use measurable data, rather than more speculative inferences, to determine the age of the earth.

Halley did not have the ability to accurately measure the amount of salt in the rivers that fed the oceans; he also recognized that the material contained in them would vary by river, and probably over time as well. Instead, he measured ocean salinity as best he could, and then noted that another measurement in a century or two might be able to detect a difference. He lamented that neither the Greeks nor Romans had done this, as the two thousand years since then might have allowed (he thought) an accurate measurement. (John Joly, an important Irish geologist, did attempt to use Halley's data and strategy at the end of the 19th century to perform this calculation. He came up with an estimate of about 100,000 years, recognized today as much too short.) As we now know, Halley's approach cannot work, because the salinity of the oceans is actually in equilibrium; there are both biological and sedimentary mechanisms that remove salts from the sea at roughly the same rate that they are added. Nonetheless, Halley is credited with inspiring others to develop what we would today call "scientific" methods for dating the age of the earth. (This problem was not truly solved until the discovery of radioactivity and its associated processes in the early 20th century.)

It is commonly assumed today that Halley's interest in the age of the earth was associated with proving that it must exceed some minimum age – and in particular, the 6000 or so years offered by Biblical scholars (see the next essay). While it is true that Halley did not interpret the six days of creation literally, but instead as six extended periods of time [a recurring concept discussed in BFB 27], his motivation was actually the opposite – he was trying to prove that the universe was not eternal! In part as a result of Newton's work showing the stability of planetary orbits, many thinkers were reconsidering Aristotle's position that the earth had existed *forever*. Like his contemporary Thomas Burnet [ESD 17 and Gould's 1987 book *Time's Arrow, Time's Cycle*], Halley objected to the concept of an eternal earth on the grounds that it would render history, and all human activity, meaningless. (If the world lasts forever, then how can any event have significance, and how can a life have meaning?) Halley was motivated to find an *upper* limit for the age of the earth, not a lower limit.

ELP 12. Fall in the House of Ussher

James Ussher (1551 – 1656), Archbishop of Armagh and Primate of All Ireland, is known today for identifying the moment of earth's creation as noon on October 23, 4004 B.C. The fame of Ussher's date and timeline comes not from its sanctification by any branch of the Church – and certainly not the Pope, since Ussher was a Protestant – but from the fact that his chronology was incorporated in sidebar fashion in the King James Bible [completed in 1611]. The Gideon Society maintained this practice until the mid-1970's, and plays and movies about the Scopes "Monkey" trial [HTHT 20] invariably include a Darrow-Bryan exchange ("Was that Eastern Standard time?!") on the preciseness of the identification. As a result, Ussher is commonly assumed to be a "fundamentalist" of his era, attempting to hold back scientific progress a couple of generations before Newton. This is not the case, Gould states, and proceeds to discuss the significance and methodology of Ussher's efforts. He credits a 1985 article by James Barr in the *Bulletin of the John Rylands University Library* entitled "Why the world was created in 4004 B.C." for many of the details that follow.

Gould makes four broad points. The first is that Ussher was not alone in attempting to develop a chronology of all history (believed to be only about six thousand years at the time). He was representative of a school of scholarship (or "house," leading to part of the essay title's Poe-based pun) in his time. Proposed dates for creation ranged from 3761 B.C. (based on the Jewish calendar, still in use today) to around 5500 B.C., so Ussher's date was in the mainstream. It did, of course, rest on an error – the inerrancy of scripture – but this was a standard assumption of the time, and progress can (and must) be made in the presence of such errors. Gould's second point was that Ussher's task was far more complex than counting up the "begats" in the Old Testament; the Bible by itself is woefully inadequate for this. One obvious problem, for example, is that it ends several hundred years before the birth of Christ. Further, there were different versions of the Bible in existence at that time, with inconsistencies between them.

Gould's third area of discussion focuses on Ussher's reasoning for the specific date and time of creation. In addition to his painstaking calculations, the year 4004 B.C. also reflects a popular belief that the six days of creation were related to the six thousand years that the earth was expected to exist before the end times. Contemporary research proved that King Herod of Judea had actually died in 4 B.C.; if he was to have met the Magi, Christ would have had to have been born at least four years before Year One [see DIH 2 for a discussion on the absence of the year zero]. Unlike other scholars who argued that Jesus was born in spring, Ussher argued for autumn (thus completing the title pun). He decided that the first Sunday after the equinox was a reasonable assumption, and corrections for the change from the Julian to the Gregorian calendar moved this to October 23. The time of noon was apparently picked arbitrarily; but Gould notes that it reflects a time in which travel across time zones was virtually unknown.

The fourth and final point is that the community that Ussher was a part of was attempting to do far more than establish the moment of creation. They were, in fact, trying to establish an entire historical chronology. To accomplish this, they drew not only on scripture, but on every document available to them; only about one-sixth of Ussher's treatise, it is reported, was drawn from the Bible itself.

ELP 13. Muller Bros. Moving & Storage

One of the most common misunderstandings about science, Gould begins, is that the reason for its success is that it is based on direct observation. Not so; the key to science, he states, is testability, not observability. No one has ever directly observed an electron or a black hole; their existence must be inferred. Similarly, no one has ever directly observed evolution, or the processes of any of the other historical sciences from geology to cosmology. Further, he notes, observations themselves – both the seeing aspect and the remembering / recalling aspects – are loaded with pitfalls. Numerous psychological studies have identified the surprising unreliability of eyewitness testimony in criminal cases. Gould relates two personal stories from his youth where he vividly recalls events that could not have occurred. First, he draws on his memories of Sunday walks with his grandfather in Queens when he was about five. He remembers the walks vividly; however, upon retracing the path as an adult, incorrectly. (One of the locations on their walks is a building that was not the Forest Hills tennis stadium, a dominant landmark of his neighborhood, but a warehouse sporting the sign that is the essay's title.) Second, he recalls an automobile trip with his family as a teenager. One of his most powerful memories was watching Devil's tower, a famous and visually impressive geological formation in Wyoming, appear from miles away over the Great Plains. In repeating this trip later with his own family, he discovered that the actual terrain was mountainous, and could not allow such an observation. He had apparently juxtaposed it with Scotts Bluff, Nebraska, a landmark for pioneers but not nearly as imposing an image. Eyes and memory can play tricks on us; as scientists, we must remain humble and vigilant. [He returns to the theme of direct observations leading great minds astray in LSM 2.]

ELP 14. Shoemaker and Morning Star

Gould reflects on the human longing for long-ago times. There are small towns in the United States which capitalize on their 18th or 19th-century history by dressing up in costume and carrying on old crafts in the old ways. He discusses a pleasant time he spent in the Amana colonies, Iowa, where many of the old crafts remain (although the largest employer in the area is the company of the same name that makes refrigerators and other appliances). The slower, simpler life there seemed nostalgic and appealing – until he came upon what he refers to as the "Great Reminder": graveyards full of dead children. What has changed the death of a child from a grim prediction to a rare tragedy, he notes, is as much due to a better understanding of nutrition and sanitation as it is of modern medicine. While acknowledging the downside of contemporary technology (circa 1990), for the reason associated with the Great Reminder alone, he would not choose to live in any earlier age, even if he could do so as a wealthy man.

He closes this essay by noting that the large amount of change in society that has occurred over the past few centuries is due to the fact that human culture can evolve by Lamarckian mechanisms ("the inheritance of acquired characteristics") rather than the vastly slower Darwinian mechanism of natural selection. Both mechanisms, however, allow for the existence of *history* – that is, something other than the almost endlessly repeating cycles of the physical sciences. As Darwin noted in the closing paragraph of *Origin of Species*, planets travel in essentially endless orbits as eons go by. But life evolves, and although it is slow and essentially directionless, each moment is unique. Darwin writes, "There is grandeur in this view of life . . . ." The essay's title, taken from the English translations of two Amana tombstones -- Schuhmacher and Morgenstern – reflects this difference. The first, "shoemaker," is a humble but human occupation; the second, "morning star," is a beautiful but sterile heavenly object.

ELP 15. In Touch with Walcott

Gould begins with a mention of his fondness for authenticity. He owns two original "calling cards" of famous people, he tells us: those of Charles Darwin and of Charles Doolittle Walcott, the latter best known today for his discovery of the Burgess Shale in 1909. (The latter card, he discovered after the essay had appeared in print, actually belonged to Walcott's wife.) The primary topic of this essay is a continuance of this theme; Gould expresses his strong, albeit mysterious even to him, desire to meet someone who has, himself, met Walcott. (In a six-degrees-of-separation story, he tells us of his connection to Charles Darwin: his thesis advisor was Ned Colbert, who as a young man met Henry Fairfield Osborn [BFB 29], who in turn met either Darwin himself or – depending on the version of the story – Darwin's colleague Thomas Henry Huxley.) Several months after the publication of his book *Wonderful Life* in 1989, which was about the fossils Walcott discovered in the Burgess shale, Gould received a letter. It came from T. H. Clark, a 97-year-old well-known geologist and emeritus professor at McGill University in Montreal. Clark informed Gould that had met Walcott when he was a young man in 1924, at the Burgess Shale quarry itself. Gould was invited to an upcoming presentation involving Clark on the Burgess Shale material at McGill – put together in response to a flood of requests since the publication of *Wonderful Life* – and to discuss Walcott. Gould accepted immediately, eager both for the discussion, and to "touch" Walcott with the minimum one degree of separation.

Most of the remainder of the essay is a biographical sketch of Walcott, of the importance of the Burgess Shale, and of the reinterpretation of the fossils that Walcott discovered there; that is, it is a very brief summary of *Wonderful Life*. Charles Walcott (1850-1927) was the most politically active and powerful scientist of his generation, and was at one time the Secretary of the Smithsonian Institution, President of the National Academy of Sciences, Vice Chairman of the National Research Council, Chairman of the Executive Committee of the Carnegie Institute of Washington (which he helped found), and more – all simultaneously! He was also a very good practicing paleontologist, with an eye toward discovering new, important fossil beds. It was in this role that he discovered the Burgess Shale in British Columbia, Canada. [Gould discusses this story in BFB 16.]

The Burgess Shale captures a snapshot in time during the early Cambrian period, shortly after the "Cambrian explosion" in which most if not all modern animal phyla first appeared. [It appears that few if new phyla have arisen since that time; see DIH 9.] The Burgess Shale is also critically important because the fauna's soft parts are preserved as a carbon film; this is very rare, and allows priceless insight into their anatomy. Many of these animals had no hard parts at all, and are only known from this location [and more recently from a few other sites, including the Chengjiang formation in China]. Walcott named and made a cursory study of the creatures found there, classifying all of them in terms of modern phyla; but he was too busy to analyze them in detail. He stored them away, intending to perform this task as a grand retirement project. However, he died 1927 while still secretary of the Smithsonian, and the fossils remained largely untouched for several decades. Finally, starting in the 1970's, Harry Whittington of Cambridge commenced a study of the fossils, and reinterpreted them in a much different way; it was this reinterpretation that motivated Gould to write *Wonderful Life*.

As noted, Walcott believed that all of the organisms found in the Burgess Shale belonged to phyla that existed today: arthropods, mollusks, and so on. Whittington's reinterpretation was that a large fraction of the specimens did not belong in to any living phylum. Instead, the Burgess Shale represents an initial radiation of body types, which was followed later in the Cambrian by *decimation*. [In BFB 16, Gould writes that "fifteen to twenty Burgess creatures cannot be placed into any modern phylum . . . ." He adds that this trend also exists *within* the largest phyla, such as arthropods. Today, all arthropods can be placed into one of four major groups: one that includes insects, a second that includes spiders, a third that includes centipedes, and crustaceans. While there are very few species of arthropods present in the Burgess Shale compared with the hundreds of thousands today, those that are there represent an additional twenty or so major groups.] Regarding the late-Cambrian decimation, Gould notes that the survivors do not appear to be more advanced or better adapted than those who did not. Perhaps, he suggests, the decimation was a lottery-like process; survival did not go to the strong or smart, but simply to the "lucky." [Gould elaborates on these views in ELP 21 & 22.] He points out that the phylum that includes vertebrates is poorly represented in the Burgess Shale, and therefore it may be pure chance that our ancestor survived when so many others did not. He expresses his famous view that if the "tape of life" were rewound, erased, and played over, it is likely that no vertebrates, and as a result no intelligent life (in the reading, writing, and arithmetic sense), would have evolved. In his words: "Conscious life on earth is this tenuous, this accidental."

Would Walcott have recognized the true uniqueness of what Whittington found, had he had the opportunity to study the fossils more closely? Gould argues here and in his book that he probably would not have. Walcott was a devout Christian, and believed that God had created the laws of evolution such that the coming of man was inevitable. Gould writes: "Walcott, from the depths of this traditionalism, was fiercely committed to a view of life's history as predictably progressive and culminating in the ordained appearance of human intelligence." Thus, Walcott's worldview would inevitably have led him to believe that all of the Burgess Shale creatures must be precursors of today's fauna. [Gould was surprised by the fact that the "inevitability of intelligence" argument remained, and manifested itself in the form of professional resistance, in spite of the passing of the overtly fundamentalist perspective from the scientific community. He regards such views as non-scientific anthropocentrism (TFS 26).]

Gould closes with a story from his meeting with T. H. Clark. Clark. Clark surprised him; he politely but firmly argued that Gould was wrong. Had Walcott had the time to examine the fossils as carefully as Whittington did, Clark stated, he undoubtedly would have come to the same conclusions.

ELP 16. Counters and Cable Cars

This is an ode to two of Gould's favorite concepts, and how they apply to cities: authenticity and community. He has determined, he writes, that there are three types of authenticity. The first is authenticity of *object*: the cast of a dinosaur bone might be visually indistinguishable from the real thing, but there is something special about the one that was part of an animal that walked this earth 80 million years ago. The second is authenticity of *place*; seeing a giraffe on the savannah is more impressive than seeing the same animal in a zoo. (He wrote this essay in San Francisco in 1989, shortly before the World Series that was delayed by an earthquake. He uses this authenticity-of-place argument to expresses his appreciation that the Series is played in the same venue as the regular season games, rather than a neutral site.)

Finally, there is authenticity of *use*. He offers two examples from his visit to San Francisco. The first are the famous cable cars, which possess both object authenticity and place authenticity (he states that riding a perfect replica on an artificial hill in Disneyland would mean nothing to him, but that he was thrilled to ride them here). But they also have use authenticity; before the tourist crowds get too thick, he discovered that there are still a large number of people who use them for their original purpose: commuting. He appreciated the uniqueness of San Francisco at no time more than when he was riding along with the locals on their way to work in this way. The second example came while eating breakfast at a small but famous local diner. He had eaten there before, with a group and at a table, but this time he dined alone – and sat at the counter (hence the essay's title). Again, as part of the early morning crowd, he found himself among a group of regulars. These were not people who are visiting from out of town (like himself, he acknowledges), but locals who routinely use the diner for its original purpose: breakfast. He discovered that his waitress new most of them, and they interacted like people would in a small town; "I'll have the usual," "How's your wife?" and so on. He loves this.

Looking for the larger picture, he acknowledges that certain things have to be "homogenized" to make modern civilization possible; it greatly helps to have downtown streets laid out in a grid, for example, and public buildings need a degree of efficiency that almost requires standardization. But the spaces in between the major thoroughfares, he writes, should ideally be filled with establishments that reflect the local or regional traditions – while still welcoming the respectful visitor, of course. What he dislikes about chain stores and fast food restaurants is that they force standardization at the wrong level. Local distinctiveness leads to healthy local communities, he argues, and to authenticity. Fast food chains force out local distinctiveness, much like flocks of pigeons in cities displace the indigenous bird populations.

He uses this last example to transition to the theme of natural history. He is often asked, "Why do we need to save all these species anyway?" Besides the "standard" answers of possible medicinal or agricultural use, genetic diversity, the interconnectedness of ecological webs, and so on, he offers an aesthetic one. Referring to evolutionary biologists, he writes: "We relish diversity; we love every slightly different way, every nuance of form and behavior – and we know that the loss of a significant fraction of his gorgeous variety will quench our senses and our satisfactions in any future meaningfully defined in human terms. . . ." Diversity, in the form of unique local ecosystems (communities), produces sublime "authenticity."

ELP 17. Mozart and Modularity

While visiting London, Gould toured a special exhibition on Mozart at the British Museum. One of the items on display was a 1770 article published in the prestigious *Philosophical Transactions of the Royal Society of London* by a scholarly member of the lesser nobility, a lawyer named Daines Barrington. The article discussed, not the adult Mozart, but rather the 8-year-old child prodigy. The article, published some years after a meeting that Barrington had with the young Mozart (who was born in 1756), was one of many arranged by Mozart's father. All who were exposed to the young Mozart were amazed by his musical talents, including his abilities to sight read and to memorize and improvise on command. The thesis of the paper that appeared before the British scientific community was on the modular nature of genius: Mozart was not, Barrington wrote, a 25-year-old man in an 8-year-old's body, but rather a boy, ordinary in every way but musically. It struck him as of general importance that one aspect of a human could develop differently than others. Gould uses the term "dissociation" to refer to the concept that we can be thought of as "an amalgam of separable components," as opposed to entirely integrated wholes.

Gould appreciates Barrington's observations, and concurs with his conclusion. He then proceeds to generalize the principle of dissociation to address one of the thorniest criticisms that all evolutionary theories are faced with. This criticism was well presented by Georges Cuvier (1769 – 1832), the great French naturalist and paleontologist, writing more than 50 years before Darwin published *Origin of Species*. Cuvier [HTHT 7], who used his extensive knowledge of animal anatomy to classify vertebrate fossils, argued against "the transmutation of species" on the grounds that a change in one anatomical structure would require corresponding changes in many others in order for the organism to continue to function, which is statistically impossible. Gould agrees with Cuvier's logic, but not with the underlying assumption. Cuvier was essentially arguing that an organism had to be considered as an integrated whole; Gould, via analogy with Mozart's single area of difference, that an organism's parts – and thus their evolution – can be considered separately. In human evolution, for example, our ancestors stood erect well before the size of their brains began to increase. Gould notes that Darwin wrote on this theme as well, from his early jottings in the so-called M Notebook to his later book *The Expression of the Emotions in Man and Animals* (1872). Gould presents several other examples, from a variety of fields, to support the view that complex systems (including living organisms) can, to an extent, be considered in terms of their parts. By implication, evolution can act on these parts individually, and the rest of the organism can – at least in some cases – follow along.

[In several earlier essays – most notably TPT 8, HTHT 13, TFS 25, and BFB 8 – Gould expresses considerable support for the holistic, as opposed to the reductionist (or dissociative, or modular) viewpoint in biology, especially as it relates to the connection between genes and behavior. This essay shows the other side of his views on this topic.

His worldview thus apparently incorporates both holism and reductionism simultaneously, to different degrees and at different levels.]

ELP 18. The Moral State of Tahiti – and of Darwin

Darwin's first official publication was a short "op-ed" piece, co-written with *Beagle* captain Robert FitzRoy, which appeared in a South African newspaper in 1836 when the *Beagle* docked there. The article, entitled "The Moral State of Tahiti," joined an ongoing editorial battle on whether Christian missionaries helped or hurt the indigenous communities they joined. The FitzRoy-Darwin article comes down squarely on the pro-missionary side, arguing that the natives of Tahiti were sincere in their Christian beliefs, and that they behaved in a considerably more civilized fashion as a direct result of missionary intervention. The paternalism of this article is unmistakable, Gould tells us: European civilization is superior, indigenous cultures are inferior, and it is our duty to help those less fortunate become more like us. For modern fans of Darwin, it is somewhat embarrassing to read.

Were the views Darwin stated in this article simply a manifestation of his youth? There is a term for such early, crude creative efforts, Gould tells us: *juvenilia*. (As an example of his own juvenilia, he offers a poem about dinosaurs he wrote as an 8-year-old and sent to Ned Colbert, curator of dinosaurs at the American Museum of Natural History, and a "boyhood hero." Much later, Colbert became Gould's graduate thesis advisor, rediscovered the poem, and read it in public! [One has to be impressed that an 8-year-old would even know the name of a museum curator, much less idolize him. How many 8-year-olds who want to be astronauts know the name of the director of manned space flight at NASA?]) Several hagiographical biographies of Darwin suggest that, in his maturity, he viewed issues of race in a way that is similar to most Westerners today. Quoting repeatedly from Darwin's later writing, Gould argues that this is not really so; he retained a large degree of Victorian paternalism his entire life, although he did come to better appreciate the flaws of his own culture.

However, Gould reiterates, it is important that we not judge Darwin by our standards, but rather by those of the world he lived in; we learn far more that way. Victorian paternalism was universal at that time, but came in two major strains: those who believed that the differences between Westerners and other races were cultural, and those who believed they were inherently biological. The former group viewed non-Europeans as fellow humans, who (with the White Man's help) could be improved. The latter tended to essentially view them as intelligent farm animals, with slavery as an appropriate and necessary institution by which to manage them. Darwin was squarely in the former camp, a devout abolitionist in an era where many believed this made him disloyal to his class. He was always comfortable discussing topics of interest to him with anyone whom he could learn from, perhaps regardless of class. On his *Beagle* voyage, he routinely talked to slaves as well as slave-owners when docked in countries where slavery was legal, such as Brazil.

Gould includes an interesting aside in this essay. It turns out that Captain FitzRoy had been to Tierra del Fuego, near the southern tip of South America, some years before. On this trip, he "acquired" four Fuegians and brought them back to England, with the goal of showing how members of this most primitive culture could be made into Englishmen with the proper instruction and experiences (a la Shaw's *Pygmalion*). Of the three that survived, all did learn some English and some etiquette. FitzRoy had promised to return them – with linen and china – and was prepared to do so at his own expense when his well-connected family intervened with the Crown and obtained government funding for what would become the *Beagle* expedition. So, Gould notes, paternalism is partially responsible for the very existence of Darwin's voyage! The three remaining Fuegians quickly returned to their native ways, to the dismay of Capt. FitzRoy; but he was able to reestablish contact with one of them a year later on yet another voyage. The Fuegian remembered both FitzRoy and Darwin kindly, and asked FitzRoy to bring him a gift: "two spearheads made expressly for Mr. Darwin. Regarding the Fuegians specifically, Darwin had written: "I believe if the world was searched, no lower grade of man could be found." Yet he also spent enough time with them on the Beagle to convince himself that they were no less human than he was, and he clearly made a favorable impression on them as well.

ELP 19. Ten Thousand Acts of Kindness

This essay begins by discussing an irony of natural history, as seen through the lens of punctuated equilibrium. It then argues that the same irony is present in human history. In both cases, Gould notes the vast majority of actual events are either mildly positive or innocuous. Yet it is the turbulent times – often involving natural catastrophes or wars – that produce the tree of life, and the outline of history. Are we, as people or as species, defined by the largely predictable "everyday," or by the rare and violent upheavals?

Gould begins with natural history. Niles Eldredge and he developed the theory of punctuated equilibrium primarily to explain the apparent paradox that, where any type of fossil occurs in quantity, the species apparently remains unchanged over millions of years. On the other hand, where fossils are rare (indicating small populations), a much greater degree of diversity is found. That is, small populations are associated with evolutionary branching, while large populations show virtually none of this behavior. This can be frustrating to the paleontologist, Gould states: the point where new species are coming into existence are the same places where the fossil record is poorest. Gould councils against frustration, however, and instead reiterates the theme that this dichotomy is a clue to the process of evolution itself.

Many have questioned whether the fossil record really shows the abrupt transitions that Gould and others claim they see. One of the counterexamples is a species of rodent in the genus *Ischyromys*, which is remarkably common in one temporal segment of the Oligocene strata. This rodent appears to show a gradual and continuous growth in size over this extended period. Gould references a recent study performed by one of his graduate students, Tim Heaton. Using statistical analysis, Heaton showed that there were actually two species of *Ischyronys* present, one smaller and one larger. Both remained essentially unchanged over the period in question; but the smaller one decreased in quantity over time, finally vanishing completely. If one measured the "average" size of the fossils together, one does see the growth trend; separately, however, it disappears. Heaton also looked for similar fossils in the preceding (earlier) band of strata, where the fossil record was much sparser. The few fossils he did find comprised not two species, but several, along with several members of a related genus. This brings the apparent paradox into focus, and helps identify one of the difficulties in grasping the fact of evolution. On the one hand, most of the well-represented organisms on the planet are not experiencing "evolution" on a year-to-year basis; on the other hand, there is no way to explain these organisms without calling on evolution.

Gould then turns to argue by analogy that human nature and history face the same paradox. Most people go for days, even years, without significant conflict. Yet most of our history is the result of those more unusual times when conflict dominates. If we only consider the events that make history, we get a rather violent picture of human nature. On the other hand, on a day-to-day, hour-to-hour basis, humans are remarkably congenial relative to other animals. How do we come to terms with the fact that most of the time we are not "making history," yet our lives are built on the foundations of those rare periods of violence? Human nature includes both the ability to be social and the ability to be violent [a position he introduced in ESD 32]. Statistically speaking, one behavior is far more common that the other. However, one act of violence may carry the same ability to make history as ten thousand acts of kindness. Gould refers to this phenomenon as the asymmetry of effects, or the Great Asymmetry. [He discussed this concept in BFB 24 and BFB 35, and returns to it in IHL 28-31 in his short works on September 11.]

ELP 20. The Declining Empire of Apes

Gould begins this essay with a simple question that tacitly assumes this false view of evolution: "If humans evolved from apes, then why do apes still exist?" The false assumption is that the evolutionary process transitions, or "morphs" apes into hominids and then man (the technical term is anagenesis). This is the "ladder of progress" metaphor of life's history that Gould rejects in many of the essays in this series [beginning with ESD 6]. The better metaphor is the bush or tree of life, in which new species arise by branching from existing populations, often coexisting with them for an extended period. Life's little joke, as Gould calls it in the essay of that title [BFB 11], is that the ladder of progress model only works on groups such as horses and apes that are *unsuccessful*, in the biological sense that the number of living species is very low. If apes and hominids were as diverse as, say, antelope (or monkeys), no one would think to "rank" them via the ladder metaphor; the branching of the bush would be obvious.

Gould was motivated to write this essay after reading a paragraph about primate evolution in a popular science book written by a famous astrophysicist, Robert Jastrow (1925 – 2008). In *The Enchanted Loom: Mind in the Universe* (1981), Jastrow writes:

> "The monkey did not change very much from the time of his appearance, 30 million years ago, to the present day. His story was complete. But the evolution of the ape continued. He grew large and heavy, and descended from the trees."

In addition to the bush versus ladder error (identifiable in part by the use of the terms "*the* monkey and "*the* ape"), this paragraph contains some additional enlightening misperceptions. The first is simply that the evolution of monkeys has not stopped, and will not be "complete" until every member is extinct. (What he suspects Jastrow is referring to is that the average brain size of monkeys has not increased significantly, another bias about "progressive" nature of evolution that Gould argues against in other essays.) Second – a small but not trivial point – all living apes still spend at least part of their lives in trees. Third, the old-world monkeys, or cercopithecoids, have diversified enormously since the branching of their group from the ape-hominid group some 20 million years ago in the early Miocene; this is the mark of a biologically successful lineage. Interestingly, our own lineage has not fared as well. Fossils of Miocene apes are rare, but (as of 1987, when he wrote this), known fossils include some "three to five genera, and perhaps twice as many species." This is more species than the apes of today, and also more than the number cercopithecoid monkey species at that time. The Miocene apes were also significantly more biologically diverse than today's apes.

How poorly have the apes faired since the Miocene? Gould describes a week he spent in the field with the famous hominid paleontologist Richard Leakey in East Africa in 1986. At the time, Leakey and his team were looking through early Miocene fossil beds for evidence of the first, broad flowering of apes. As noted, the fossil record is notoriously poor; Gould notes that we do not know which species of Miocene ape gave rise to hominids – or chimpanzees or gorillas. If the number of Miocene ape species currently known represent the complete set, Gould writes, then the change in diversity would suggest a modest decrease. If the number of Miocene species is larger, however – which would indicate that most species have not yet been discovered – then the magnitude of the die-off increases. Since we cannot know what fossils we do not have, he argues, we must use statistical arguments. If most new fossils can be identified as belonging to species we already know, then we may infer that we have most of what there is. On the other hand, if most new finds represent species we have *not* seen before, it suggests that we likely have many more to discover. Leakey found two ape skulls that season, Gould tells us, and both were new species. This suggests that the ape line is significantly less diverse than it was in the past.

ELP 21. The Wheel of Fortune and the Wedge of Progress

Darwin and Gould shared a deep appreciation for the power of metaphor to convey a complex idea. One of the most difficult ideas that Darwin struggled with, in his theory of evolution, was the concept of *progress* and predictability in the history of life. Natural selection, as he understood and defined it, was a process that led only to better adaptation to the local environment; it was not, in and of itself, progressive. [He noted that parasites, which are usually simplified descendents of free-living ancestors, are as much a product of natural selection as (say) mammals.] Nonetheless, he recognized that the first forms of life had to be much simpler than the animals and plants we see today. As a Victorian, Gould argues, Darwin believed in the concept of progress, and believed that evolutionary change had to be progressive. In response to this perceived requirement, Darwin developed a second principle, which he illustrated using one of Gould's favorite metaphors: the wedge of progress (referring to the metal tool used to split wood). In an unpublished draft of *Origin of Species*, 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.

So, natural selection itself is not progressive; however, as the wedging process replaces individual species by better adapted species over eons of time, the eventual result is an average improvement in *all* wedges. Darwin argued that this long-term trend – in the form of more complex (or in some other way more advanced) organisms – can be interpreted as "progress."

This argument is clever and sounds reasonable; but does the evidence support it? In a few cases, Gould believes it does. In particular, he references work by biologist Geerat Vermcij that shows that, among other things, a geologically extended "arms race" existed between stronger crab claws and knobbier, spinier shells on those snails that are the crabs' source of food. This is a valid example of "progress by wedging," as Gould refers to it. However, he believes this is the exception rather than the rule. He offers four other examples of major changes in earth's ecosystems over time. The first is one group of reef-building corals replacing another. The second is the reduction of four major types of crinoids to one. The third is the extinction of the ammonites, but the survival of the similar but apparently simpler nautilids. The fourth is the replacement of dinosaurs as the large terrestrial animals by mammals.

These four events seem to occur relatively abruptly, after a much longer period of apparently stable, if not peaceful, coexistence; "changing of the guard," in Gould's terminology. Further, these events all occur at well-known geological boundaries associated with the term "mass extinction." [This term predates Darwin, and in fact dates back to the days of Cuvier – see HTHT 7.] The first two are associated with the Permian extinction that marks the transition from the Paleozoic to the Mesozoic, and the third and fourth are from the Cretaceous extinction that forms the boundary between the Mesozoic and the Tertiary. If these events are the product of a progressive wedging process like crab claws and snail shells, two types of evidence should appear in the fossil record. The first is that the replacement of one group by another should take place over an extended period. (Since the groups in each example coexisted for an extended period, we should see evidence for a long war of attrition rather than a sudden winner-take-all event.) The second is that it would be, at the least, *reassuring* if the survivors were better designed in some unambiguous way (making it apparent that the "better" or more advanced group won). Yet neither of these criteria appear to be present [see HTHT 27]. The history of life shows change, but it does not generally show trends toward more advanced organisms. In an essay written five years earlier [TFS 15], Gould wrote: "I regard this failure to find a clear 'vector of progress' in life's history as the most puzzling fact of the fossil record." The fact that so many of the major changes in the fossil record appear to coincide with extinction events undermines the concept of predictability in natural history.

Gould writes: "[The apparent phenomenon of] mass extinction is a specter haunting the metaphor of the wedge, but the ghostbusters of denial and accommodation have held the fort – until recently." Darwin, he continues, drew on "denial"; he argued that the mass extinctions were not as abrupt as they appeared, and were likely the result of gaps and imperfections in the geological record. He expressed optimism that future discoveries would show that the transitions were actually much slower and more ordinary than the current, limited evidence suggested. This argument has fallen apart with the discovery of better geological evidence, almost all of which points toward abruptness. More recently, Gould continues, others have drawn on "accommodation." In this view, mass extinction is real, but involves no additional processes; when times get tough, the wedging gets tougher and faster. That is, Gould writes, "mass extinction only 'turns up the gain' on business as usual."

This view suffered a severe setback in 1980, when evidence came to light that a large comet or asteroid had struck the earth at the end of the Cretaceous period [HTHT 25], bringing the Mesozoic to a close and probably eliminating the dinosaurs, the ammonites, and a vast array of other groups. The study of mass extinction went from a small sideline to a booming field. Gould writes:

> These events, with their catastrophic causes, are *more frequent, more sudden, more profound in their extent* [groups eliminated], and *more different* (from normal times) *in their results* than we had imagined [his italics]. Mass extinction does not just turn up the gain on competition . . . mass extinction entrains new causes that impart a distinctive stamp to evolutionary results. And if the history of life owes its shape more to the differential success of groups in surviving mass extinction than to accumulated victories by wedging in normal times, then a major component of Darwin's worldview – and the only sensible argument that he could supply for our deepest, culturally bound hope of progress – has been compromised or even overturned.

What are the "new causes" regarding mass extinction and the history of life that Gould refers to in the preceding paragraph? He offers two. The first is the *random* model, in which species live or die totally by chance. If Raup is correct in his estimate that 96% of species were eliminated in the Permian extinction [HTHT 26], then it seems likely that some of those that survived did so only because they were in the right place at the right time. He second, which he believes is the more common of the two, is the *different rules* model. Here, species survive for identifiable characteristics or behavior, but these attributes were developed for reasons entirely unrelated to surviving an impending catastrophe. (Gould reminds us that one of the fundamental tenants of natural selection is that it cannot select for features that are of no utility today, but might be of some use in the future. "Be prepared," he says, is a great motto for boy scouts, but natural selection cannot follow it.) For example, mammals might have survived the asteroid impact at the end of the Cretaceous when dinosaurs did not because of their small size. Mammals did not "know" the impact was coming, and they did not out-compete the dinosaurs during their extended mutual existence. But when the catastrophe occurred and "different rules" abruptly determined who would live and who would die in a radically changed environment, the mammals had a leg up. Mass extinction, he argues – the "wheel of fortune" of the essay's title – may play a greater role in shaping the tree of life than the wedge of progress. Mass extinctions, he writes, "create, by their imposition of different rules, a new regime of oddly mixed survivors imbued with opportunities that would never have come their way in a world of purposeful wedging." [With dinosaurs gone and the "large terrestrial animal" niches open, rhino-sized mammals appeared within ten million years.]

As with Darwin's wedge of progress, the wheel of fortune mechanism may be plausible; but again, is there any evidence? Gould believes there is. By way of background, he explains that the most pronounced extinction in the fossil record at the end of the Cretaceous was not the dinosaurs, but rather the far more copious (and better preserved) photosynthetic plankton in the ocean. Most types were devastated, almost certainly leading to a collapse of the food chain in the ocean, but one group – the diatoms – suffered far less than most. Many scientists had argued that the actual lethality mechanism of the impact was not global tsunamis or forest fires (which surely were devastating where they occurred), but instead the result of an impact-induced dust cloud that blocked sunlight for several weeks. Since virtually all photosynthesizing plankton only live for a few days, this would explain their demise – but then, how did the diatoms survive? Gould references two papers that seem to point to the answer. One, by Kitchell et al., involved the study of ocean cores of late Cretaceous sediments. They found that many types of diatoms then, as now, have the ability to build "resting spores" or cysts out of silica, and essentially hibernate during certain periods. Kitchell identified two triggering conditions: extended darkness, associated with arctic winters where the sun does not shine for up to six months, and low levels of dissolved nutrients. The second paper, by Griffis and Chapman, demonstrated via a very low-cost experiment (encasing flasks of water containing plankton and nutrients in light-blocking aluminum foil) that those plankton that could form cysts could be revived weeks later, while those that could not all died. From this evidence, Gould continues, it appears that dust-induced darkness was responsible for the *global* aspects of the asteroid impact. We can also infer, he continues, that diatoms survived relatively unscathed because they could form resting spores. But the diatoms did not know a catastrophe was imminent; they evolved cysts (presumably via a wedging process) for unrelated reasons. The fact that the cyst-building capability allowed the diatoms to survive when most plankton did not is, he argues, an example of the wheel of fortune at work, creating a time of "other rules." The survival of certain types of plankton but not others, the evidence therefore suggests, is due to the wheel of fortune and not the predictable progress of wedging.

Gould is reminded of the myth of Sisyphus, who was punished in Hades by having to push a boulder up a mountain. When near the top, the boulder always tumbles to the bottom, and he must start again. He relates the slow, painful pushing of the boulder up the mountain to the wedge of progress, and the sudden roll to the bottom to the wheel of fortune. But the analogy is limited, he adds; in nature, the boulder does not roll all the way to the bottom, but travels some quirky path in a partially sideways direction.

ELP 22. Tires to Sandals

Gould owns three pairs of sandals that have been hand-crafted from old automobile tires, all bought in open air markets on different continents. He uses these as a metaphor for a structure that was designed for one purpose and is later adapted to a completely different purpose [see "exaptation" in BFB 9]. Natural selection gets the chance to turn metaphorical tires into metaphorical sandals only when the "wheel of fortune" [from the previous essay] creates an opportunity by opening a metaphorical hole in the existing supply of inexpensive shoes (that is, an ecological niche); but this can only happen if the tires already exist. Gould's vital points are that the tires were not created as raw material for sandals, but for some other purpose; and that sandals made from tires would not succeed in the marketplace if the niche were already occupied. Large segments of the macroevolutionary history of life, he will argue in this essay, can be – must be – explained in terms of this metaphor, rather than the more familiar one of linear advancement via the wedge of progress toward today's world.

In the previous essay [these two were also published sequentially in *Natural History* magazine], Gould describes how Darwin argued for "predictable progress" in natural history via his metaphor of the wedge. Gould countered that mass extinction – the wheel of fortune – can and does prevent wedging from establishing long-term progressive trends. He argued that mass extinctions are "real": intense, geologically sudden, and – most importantly – of a different *character* [see Jablonski's work, referenced in TFS 15]. To survive in the "different rules" scenario produced by the wheel of fortune, organisms can only employ what they already have, albeit possibly in new ways; there is no time for natural selection to develop anything new. Afterwards, an odd array of survivors can then proceed to adapt – perhaps via natural selection and progressive wedging – to a new world with many ecological vacancies. In this paradigm, he argued, the "winners" did not out-compete the losers; natural history instead can be seen as a "changing of the guard" [see his reference to the technical paper he co-authored on clams replacing brachiopods in TFS 30].

However, Gould continues, this still grants only half a loaf to the wheel of fortune. It allows the wheel the role of rare but devastating destroyer, but not that of creator of new forms of life; for this, proponents of the wedge could argue, the conventional mechanism is still required. Ironically, this is exactly the argument that opponents of natural selection used against Darwin. [Natural selection surely exists, they argued, but it is only the executor of the unfit; some other force must be responsible for creating new forms. One of the fundamental contentions of the modern evolutionary synthesis was that natural selection was a creative as well as a destructive force.] Gould could, he states, use the same line of reasoning: if natural selection can be a creative force, mass extinction can as well. Instead [and apparently in part because he has become skeptical of these arguments], Gould will take the opposite tack. He writes: “I claim that the wheel of quirky and unpredictable functional shift (the tires-to-sandals principle) is the major source of what we call progress at all scales. Advance in complexity, improvement in design, may be mediated by the wedge up to a certain and limited point, but long-term success requires feinting and lateral motion, with each zig permitting another increment of advance, and progress crucially dependent upon the availability of new channels.”

[Here, he is expanding his definition of the wheel of fortune from “just” mass extinction to all changes in the history of life that draw on exaptations or the tires-to-sandals principle; that is, cases in which a structure that addresses one function is, millions of years after its first appearance, pressed into service for a completely different function. This is almost the opposite of “predictable progress.” Further, Gould claims, most of the major transitions in the history of life are the result of quirky functional changes that, only afterwards, were honed by natural selection and the wedge of progress. That is, he will conclude, “predictable progress” in the history of life is an illusion.]

Gould offers three examples of what are generally considered milestones of progress in the history of life, and reinterprets them in terms of the tires-to-sandals metaphor. In order, these are: origin of the genetic flexibility, allowing a major advance in complexity; the evolution of complex (eukaryotic) cells, required for multicellularity; and the development of the defining features of human consciousness.

His first example is the origin of genetic complexity – more specifically, the appearance of multiple copies of genes in eukaryotes and multicellular organisms, which does not seem to occur in the simpler prokaryotes. First recognized in the 1960’s, this phenomenon is now recognized as a primary source of new genes, and therefore of new capabilities [HTHT 13]. (Only one copy of an essential gene may be required, leaving the duplicate available for modification. This is far easier than constructing the gene from scratch.) New, additional genes allow for an increase in the organism’s complexity, which in turn may give it some competitive advantages. However, multiple copies of the same gene probably do not, in and of themselves, offer the host any competitive advantage; modification of these genes for useful purposes lies in the distant future. The increase in genome size must have occurred, Gould argues, for other reasons; in this essay, he adds these non-adaptive, non-progressive reasons, whatever they might be, to the wheel-of-fortune category. [He discusses this, and the concept of “selfish DNA” as a possible explanation, in HTHT 13.] Once in existence, the tires to sandals principle can slowly capitalize on them to increase the complexity of descendent organisms.

His second example is related to the first: the creation and/or incorporation of organelles within these more genetically complex cells to form eukaryotes. Chloroplasts and mitochondria, in particular, appear to be the descendents of free-living prokaryotes that joined with what would become the eukaryote in some sort of symbiotic relationship. All multicellular organisms are exclusively comprised of eukaryotic cells. If one makes the assumption that multicellularity offers evolutionary advantages, then one may argue that eukaryotic cells were favored by selection because they alone could lead to this result. But again, there is a gap: complex cells could not have evolved "for" multicellularity, since the latter did not appear until several hundred million years after the former. Again, factors other than natural selection and the wedge of progress must have been at work.

His third example is the growth over time of the primate brain, presumably required to create human consciousness. He grants for the sake of argument that there was a selection-based reason for this brain growth. However, he states, we must still conclude that most of the key attributes that make us human – language, civilization, and religion, to name three – are mere side effects of this process. Humans evolved their current brain size tens or hundreds of thousands of years before inventing agriculture, so one cannot argue that the evolution of the human brain and mind was a result of the selective advantages of civilization. Language, according to Noam Chomsky, is also a highly quirky thing that appears most likely to be a tires-to-sandals phenomenon. Third, he references Freud's hypothesis on the origin of religion as a response to the recognition of (and fear of) eventual certain death. Yes, humans have large brains and, as a result, human consciousness; however, he argues, only after it came into existence did we press it into service for these functions.

These are all examples of the tires-to-sandals aspect of the wheel of fortune, rather than the more-or-less predictable outcome of hundreds of millions of years of competitive, progressive wedging. Gould adds one additional argument:

> If I have upset your equanimity by attributing the genuine complexity of human cognition to fortuity piled upon fortuity (with a little yardage for predictability after each spin of the wheel), then I must apologize for one further disturbance in conclusion. . . . I do not deny that, through time, the most "advanced" organism has tended to increase in complexity. . . . [However,] life shows no trend to complexity in the usual sense – only an asymmetrical expansion of diversity around a starting point constrained to be simple.

He proceeds to explain [see TFS 14, and his 1996 book *Full House*] that what we inappropriately associate with progress is really an increase in the *diversity* of life. In his view, the *median* (most common; where the "peak" is) level of biological complexity has not changed since early Precambrian times; it was, and is, the prokaryote. The *mean* (average) complexity has increased, but not because all of biology is gradually moving in that direction; rather, it is because the *variance* of complexity has increased. It does so asymmetrically, favoring the more complex over the less complex; this is because eukaryotes and multicellularity are possible, but since prokaryotes are so simple, it is difficult to become simpler [interestingly, he does not mention viruses as an example of simpler forms of reproducing structures that must have evolved after prokaryotes]. If we focus on the upper edge of the complexity distribution, rather than the median, we can be led to believe that life *as a whole* is "making progress" when it is merely diversifying.

Gould acknowledges that many people find these perspectives troubling. Our cumulative unwillingness to abandon the view that life is progressive (and driven toward "us") has little to do with the search for truth, he states, but instead lies in our need for solace. He writes in closing:

> Our chances of understanding nature would improve so immensely if we would only shift our search for solace elsewhere. (Solace will always be a desperate need in this vale of tears, but why should the facts of our belated evolution be pressed into such inappropriate, if noble, service?) Perhaps I am just a hopeless rationalist, but isn't fascination as comforting as solace?

ELP 23. Defending the Heretical and the Superfluous

The first part of this essay discusses the partial resolution of one of the most frustrating paleontological problems of early multi-cellular life: the nature of the "small shelly fauna" or SSF. The SSF represent the first "hard parts" to be preserved in the fossil record; they appear at the very beginning of the Cambrian (before the official Cambrian explosion), and are gone by the middle of that period. Physically, the SSF include a wide variety of plates, caps, cups, and spines that vary in size from less than a millimeter to about a centimeter. Biologically, they have been a mystery. They are clearly organic in origin, and too large to belong to a single-celled organism, but does each plate associated with a single creature, or did each organism possess many SSFs? The latter always seemed more probable, but since the "pieces" do not fit together (and undoubtedly represent the scrambled parts from many different species), how does one learn what the SSF animals "were?"

The only hope was to wait for the discovery of a fossil that preserves the soft parts of intact SSF creatures, with the hard parts still in place. This finally happened in the late 1980's – one animal in China, and a different one in Greenland. The Chinese organism, discovered in the famous Chengjiang formation (and several tens of millions of years older than the Burgess Shale), is a soft-bodied "worm" called *Microdictyon* that has small, curved plates made of hollow hexagons located on the body above each leg. The organism is about 8 centimeters long. The plates, which are identical to one type of SSF, are widely spaced on the body. The Greenland creature, *Halkieria*, was discovered in 1989 and is about the same age as the *Microdictyon* fossil. It is a flattened worm-like organism up to 7 centimeters long. The dorsal (top) side appears to be completely covered with several different kinds of SSFs, including two larger "shells" (about 1 centimeter in diameter), one near each end. Thus, the mystery appears to be solved: the SSF are, in fact, partial coverings of early soft-bodied organisms of various types, two of which have now been identified.

The second part of the essay is a challenge, to professionals and interested laypersons alike, to "not be disappointed that the SSF's are *only* worms." First, Gould notes, "worm" is only a morphological term: elongated, bilaterally symmetrical, which a mouth and sense organs near one end and an anus near the other. In the huge diversity of life on earth, most multicellular organisms fall into that category. To say that these creatures are "just worms," Gould states, is to argue that the burning of the complete works of Sophocles in the Library of Alexandria was not a big deal, because some survived elsewhere. He recapitulates some of the themes from his book *Wonderful Life*: that the Cambrian explosion led to a large number of very diverse body types, the survivors of which are the phyla of today. But there were many that did not survive, and the only record we have of these "other forms of life" is in rare fossil beds such as the ones in China and Greenland, and the Burgess Shale. *Microdictyon*, he states, probably belongs to an existing phylum, the Onychophora (the star of the next essay, ELP 24), that today includes only a few dozen species of "velvet worms." *Halkieria*, on the other hand, is too unique to be obviously a member of any phylum living today. He returns to his metaphor of the Library of Alexandria. One story of the destruction, almost certainly false, is that it occurred in 640 AD when the Muslims conquered the city. When asked what to do with the works stored in the library, legend has it that the caliph Omar replied that the books were either contrary to the Koran, in which case they were heretical, or they were consistent with the Koran, in which case they were superfluous (hence the essay's title). In this analogy, *Halkieria* is heretical, and *Microdictyon* is superfluous, so in this view, both are intellectually dispensable "worms." Gould vociferously champions them, stating that both are wonderful and fully worthy of our interest.

ELP 24. The Reversal of *Hallucigenia*

The animal kingdom includes about a dozen phyla that contain a thousand or more living species; others are much smaller. Biological taxonomists have struggled over the years with how to categorize members of these smaller groups; most dislike creating an entire phylum for just a handful of living species. Historically, Gould tells us, three approaches have been employed with these problematica. He refers to the first as the "shoehorn"; examine the group for the largest number of similarities with a major phylum, and place them there as outliers. The second, which he calls the "straightening rod," places the small phylum "in between" two larger phyla that are known to have shared a common ancestor. This acknowledges the uniqueness of their body plan, but does not grant them equal status with the most diverse lineages. The third, which he champions, is to define phyla only in terms of body plan, regardless of the number of living species. [This is consistent with his view of life as a bush, with some branches growing thick – representing diversity – while others do not. The *formation* of the branch, whether it is large or small today, is what gives us insight into the history of life and the nature of evolution; and in his view, all are of equal value in this regard.]

The specific examples of this essay are the "velvet worms," the phylum Onychophora (literally "claw bearer," for the claws on the ends of their fleshy legs). They superficially resemble caterpillars, but their bodies are not segmented (like arthropods and annelids) and their legs are not jointed (like arthropods). There are only about eighty species world-wide. The man who first described members of this phylum "shoehorned" them in with mollusks, as he believed they looked like slugs with legs. Others have tried to link them with Uniramia, a dominant arthropod group. Proponents of the straightening rod, Gould continues, identify Onychophora as relics of the separation between annelids and arthropods. He counters that if there were 80,000 living species today instead of 80, the uniqueness of the body plan would easily grant the Onychophora "phylum" status; that is, the problem is with the number of species, not the design. (He does, however, include an extended parenthetical note recognizing the common ancestry of Onychophora with these other groups. He writes: ". . . I am not making an untenable claim for total separation without any relationship to other phyla. Very few taxonomists doubt that onychophorans, along with other potentially distinct groups known as tardigrades and pentastomes [see DIH 9], have their evolutionary linkages close to annelids and arthropods. But this third view of life places onychophorans as a separate branch of life's tree . . . .")

One way to at least qualitatively explore the legitimacy of this third view is to study the diversity of this group in the distant past. If we can establish, Gould argues, that the Onychophorans used to be as diverse as the phyla that are considered "major" today, this would support granting them taxonomic equality. Referencing the work of Harry Whittington in reinterpreting the Cambrian period's Burgess Shale fauna, he notes that one species, *Aysheaia*, has been identified as an Onychophoran. But there is more; it turns out that there is not just one, but several species (or rather, genera) of these velvet worms in the Cambrian period. Another creature, *Xenusion*, was found in Europe in the 1920's. More recently, it turns out that at least some of the mysterious "small shelly fauna" (SSF) turn out to be the hard parts of previously unknown, partially armored Onychophora [see the previous essay]. Then, in 1991 (the time of this writing), an article appearing in the British journal *Nature* suggested that one of the more exotic fossils from the Burgess Shale, *Hallucigenia*, had been misinterpreted; it was also most likely another Onychophora. Thus, this group was apparently relatively well-represented in the past, and may have been more diverse at that time than many of the larger groups today.

[As many fans of Stephen Jay Gould know, there is something else going on in this essay. The reinterpreted organism, *Hallucigenia*, was made famous in Gould's bestselling 1989 book, *Wonderful Life*. In this book (and in these essays), Gould argues that the Cambrian explosion was "real," in the sense that it represented a genuinely unusual period in the history of life; many professionals oppose this view in favor of a more gradual, largely "business as usual" transition. Even more controversially, he argued – following Whittington – that, not only did all modern phyla come into existence during this relatively brief period, but so did many others that died out before the Cambrian was over. His view, as discussed in ELP 21, is that many of the survivors of the decimation did so not because they were better designed or better adapted, but because they were "lucky" (favored by the wheel of fortune). He states that if "the tape of life" were rewound, erased, and played again, a different set of survivors might dominate the planet today – and perhaps not the chordates, our own group. Of all the "weird wonders" that did not survive this period, *Hallucigenia* (as interpreted by Simon Conway Morris, a student of Whittington's, in 1977 and referenced by Gould) was among the weirdest; it had spines for legs and a series of tubes on its back. The 1991 reinterpretation, which came while Gould's book was still selling well and therefore made news, turned the animal upside down (hence the essay's title). The revised perspective argued that the "tubes" were actually one pair of legs (with the other buried; this had misled Conway Morris), while the spines were – just spines, presumably for protection. (Further discoveries showed that other Onychophora-associated SSF's had similar long spines.) Those opposed to Gould's views on the significance of the Cambrian explosion and the following decimation argued that this "reversal" (Gould's pun) undercut his thesis, suggesting that there were not so many unusual phyla during the Cambrian after all. In his own defense – this is the only place where he does so in these essays – he notes that he only spent a few pages of *Wonderful Life* on *Hallucigenia*, and actually "bets against" Conway Morris's interpretation (after expressing fascination with it). Further, the reversal does not challenge any of the arguments Gould makes in the book; to reference the previous essay, it switches one organism from "heretical" to "superfluous," but there are still plenty of oddballs left. In this essay, Gould does not come across as flustered or defensive by this turn of events. His defense here is no defense at all; he stands by all of his *Wonderful Life* inferences. These sorts of detailed corrections happen all the time in science, he continues, which is why it works as well as it does. He notes that he assisted in this effort, by making a key Burgess Shale fossil with several *Hallucigenia* specimens from Harvard's collection available to those challenging the Conway Morris interpretation.]

ELP 25. What the Immaculate Pigeon Teaches the Burdened Mind

After the publication of *Origin of Species* in 1859, but before the formalization of the modern evolutionary synthesis in the 1930's and 40's, the biological community was in an uncomfortable position. Almost all scientists accepted the empirical fact that lineages evolved over time (Louis Agassiz [BFB 21, ELP 29] being the last major holdout); but there was no general consensus on the mechanism driving it. In the first decade of the 1900's, there were four major contenders vying for acceptance. The first was *natural selection*, the mechanism proposed by Darwin and Wallace in 1859, which argued that deterministic selection of partially random variations (within certain biological channels) was sufficient to explain all evolutionary change when geologic time was considered. The *existence* of natural selection was readily accepted, but only a minority considered this mechanism to be powerful enough to do more than tweak changes that had arisen in some other way. A second mechanism, drawing on the recently rediscovered genetics of Mendel was *mutationism* [referenced in TPT 18]; proponents argued that random mutations in individual genes might directly produce new species. [Early fruit fly studies showed that this was not the case.] A third was *Lamarckism* [TPT 7, LSM 6], colloquially known by the phrase "the inheritance of acquired characteristics"; it argued that the organism itself had some control over a process that would modify its offspring in a beneficial way, by some undetermined means. The fourth, *orthogenesis* [ESD 9, HTHT 30], again argued for a separate (and undetermined) force that drove change in a particular direction over many generations, but argued that the organism itself had no control over it. Most supporters of this model believed that evolution had a direction but not a purpose, and could even act in ways that were harmful in the long run to the lineage.

Within this context, Gould presents a short biography of Charles Otis Whitman (1842 – 1910), a great if forgotten American scientist who did early work in the field of embryology, founded the Marine Biological Laboratory at Wood's Hole, and generally helped America catch up with Europe in the field of biology. He was an evolutionist, even though he had studied under Louis Agassiz. Like Darwin, he raised and studied pigeons. Pigeons had been bred into many different varieties, yet could all be traced back to a common ancestor species of *Columbia livia* via centuries of breeding documentation. Darwin had used pigeons to argue that, if "artificial selection" over a few centuries could produce such diversity, that the natural analog of the same process ("natural selection") could, over geologic time, produce the variety of life that we see today. In 1904, Whitman presented a series of public lectures arguing that Darwin's view was incorrect. (He meant to write a book on this, but died before he could complete it. Some of his work was published posthumously, ten years later; Gould draws on this, and his 1904 presentation, for the essay.) Whitman believed in the orthogenesis paradigm, and presented evidence that he believed showed that at least one aspect of pigeon morphology – coloration pattern – showed a clear multigenerational direction, in direct conflict with the predictions of Darwin and of natural selection. He noted that he could breed the common pattern of two color "bars" on an otherwise gray pigeon from those with a more complex "checkered" pattern on their upper wings, but not vice versa; he argued that this reflected a genuine trend, produced by an undetermined but empirically apparent mechanism that overpowered selection. He extended this view to argue that the original pigeon was even more highly checkered, and that the end of the trend was the light, completely uniform ("immaculate") coloration of the dove (also a type of pigeon).

While disagreeing with his conclusions (long since decided in favor of Darwin, he points out), Gould defends several aspects of Whitman's work. First, he notes, Whitman – and most orthogenesists generally – were not trying to reintroduce vital forces or divine intervention, as their opponents often charged. Most were confirmed mechanists, and were trying to identify and study evolutionary mechanisms that they believed were present via a scientific methodology. Second, he notes that Whitman collected extensive amounts of data over several decades – again, in contrast to charges by some critics. Third, Gould continues, his analysis of the breeding, comparative anatomy, and ontogeny (the development of individual birds from egg to adult) shows some interesting results. For example, Whitman was correct in his observations of how the coloration of individual birds changed as the embryo and young bird developed along a pathway generally toward uniformity. One of his mistakes was in generalizing the ontogeny of an individual bird to the phylogeny (evolutionary history) of the lineage – but this was a widely accepted, if incorrect, working paradigm of the day [TPT 24]. Further, to Whitman's credit, he recognized that both development and evolution tend to work along certain channels [HTHT 14, ELP 27], and that these channels are at least sometimes related to each other. (One aspect of the orthogenesis paradigm that led to its undoing is its claim that, while trends can be modified in terms of length and strength, the *sequence of events* must occur in a defined, causal order: no skips, reversals, or transpositions allowed. Today we know that these evolutionary variations can move in either direction along these channels, not just one way as orthogenesis requires.) [Gould's first book, 1977's *Ontogeny and Phylogeny* – aimed at a technical audience – discusses this subject in detail.]

Part of Gould's admiration for Whitman's work appears to stem from its challenge to the purely adaptationist paradigm. If, Gould argues, adaptationists are correct and natural selection works to optimize every feature of every organism, then why do so many of us suffer from bad backs, and why are humans so bad at certain types of mental functions and operations, such as understanding probability? The latter question leads to the second part of the essay's title.

ELP 26. The Great Seal Principle

One of the fundamental puzzles of Darwin's theory of evolution, Gould begins, involves the inception or initiation of new morphological structures. Once an organism has developed, say, a crude wing that supports flight poorly, it makes sense that natural selection would favor descendents with better wings, since they offer the hosts a selective advantage. But how does the proto-wing, which is incapable of supporting flight – a process that requires many generations – first develop? Darwin's solution was to suggest that the proto-structures served some other purpose at first, such as thermal regulation, and were only co-opted for flight when they achieved a certain size and capability. [Gould discusses this specific example in BFB 9, and elaborates on his view of the importance of this concept in ELP 22.] However, this does not completely resolve the inception problem, for even if the very first appearance offers an advantage, it cannot arise *because* of this advantage. Natural selection cannot predict the future; the feature must arise *before* it can be selected.

Darwin himself recognized this puzzle. Gould argues that the solution he offers is "interesting, probably correct, and largely unappreciated": an accident. The feature first appears for other adaptive reasons, or for no reason. Any one of a million things could have happened, within the constraints of the organism's developmental process; thousands no doubt did happen, but most were disadvantageous, if not directly fatal, to the host. But some were advantageous, or at least relatively benign, offering natural selection a handle to work with. [This reflects one of Gould's favorite themes: the contingency of history. He no doubt took great pleasure in being able to trace this idea back to Darwin himself.] Gould chooses to refer to this concept as "the great seal principle," referencing the Latin expression on the Great Seal of the United States, which appears on the back of the one dollar bill (along with the pyramid with the eye on top): *annuit coeptis*. The creators of the seal intended this to be translated as "He [God] smiles on our beginnings." Gould borrows the phrase and translates it as "She [meaning 'Lady Luck'] smiles on the initiations."

This is an interesting conjecture, but is there any evidence to support it? Gould offers two lines of contemporary research that investigate aspects of this origin-by-accident worldview. Both involve the mechanism of sexual selection rather than natural selection.

The first paper involves a species of fish with a swordtail (an extended tail ray), and a closely related species that does not have a sword. The author implanted an artificial "sword" in the tail of the male of the swordless species, and finds that the swordless female is more attracted to this fish than the control fish. This demonstrates that the female of the swordless species exhibits a preference (for unknown reasons) for swords, even though her species does not grow one. Therefore, one can argue that, if some males of this species did "accidentally" develop an oversized tail ray, it could instantly offer a breeding advantage. This is evidence that the first species (with the natural sword) at least could have produced the initial structure by a contingent, non-adaptive process. What if the sword had grown from the pectoral fin instead of the tail fin? Perhaps the result would have been the same, or perhaps not. Evolution, in Gould's view, is what *did* happen, which is only a small subset of what *could have* happened.

The second example involves frog calls. In this case, a species that croaks span two frequency ranges is found attractive by a female of a similar species only croaks in one; but both species develop a hearing organ that is sensitive to the same overall sonic range. In one case, the males "evolved" to exploit it, and in the other they did not. This is again suggestive that, at least on occasion, the accidental formation of a novel structure (and, in this case, a behavior) can meet with unexpected (and, as far as we can tell, non-predictable) success. Lady luck smiles on the initiations, at least sometimes.

ELP 27. A Dog's Life in Galton's Polyhedron

This is one of Gould's defining essays on two of his favorite themes: the limits of adaptation via natural selection, and the role of internal constraints on evolution. A debate that began well before Darwin involved the following question: could plant and animal breeders produce *any* desired feature via selective breeding? The range of variation in dogs, pigeons, and domesticated crops and livestock is indeed amazing. Surely, Darwin argued, if humans can produce such features in the timescale of years to a few millennia, nature herself can do far more with the eons of time available to her. He argued in *Origin of Species* that natural selection was an optimizing force, constantly tweaking organisms to be better adapted to their local environments. On the other side, it was well-known to breeders, naturalists, and to Darwin that there were limits to what they could achieve. On small scales, breeders never succeeded in producing a chicken that could consistently lay more than one egg per day, despite concerted efforts. At a higher level, while domesticated animals do come in a wide variety of forms, Charles Lyell noted in 1832 that only a handful of animals (and plants) had been domesticated at all. [This is also one of the key themes in Jared Diamond's 1997 best-seller, *Guns, Germs, and Steel*.] (Gould notes that Darwin did consider the limits of selection in *Variation in Animals and Plants Under Domestication*, published in 1868.)

Francis Galton (1822-1911), Darwin's "brilliant but eccentric" cousin [Gould's phrase], created a metaphor that many have used to describe the terms of this debate. In his 1869 book *Hereditary Genius*, which also happens to be the founding document of eugenics [see Gould's 1981 book *The Mismeasure of Man*], Galton envisioned a billiards table with a ball on it. The ball represented the morphology (physical form) of a species, and the table represented the possible forms that the species could take. Those who believed that organic matter was a perfectly plastic substance that natural selection could shape any way it pleased envisioned the ball as a perfect sphere, one that could be moved anywhere on the table by the external force of a metaphorical pool cue. Galton, however, argued that the ball was actually (well, metaphorically) a polygon, covered with numerous facets of different sizes. This implies that the ball itself includes some internal factors that constrain what the ball will do under external pressure. The first is that, if the pressure is relatively small, it will resist changing, or "push back" against the external force. The second is that, if it does move, it will not be in any possible direction, but only along a smaller number of possible channels, corresponding to coming to rest on another facet. In some directions, the facets are small and closely spaced; in others, they are larger and farther apart. The ball will thus move farther and more easily along certain "pathways" than others.

[Gould's views on the existence of internal constraints on the evolutionary process, and his debates with the adaptationist community on this topic, date back to his early career. At one point in this essay he uses the word "Panglossian," a reference to his famous 1979 paper (with Richard Lewontin) *The Spandrels of San Marco and the Panglossian Paradigm*; this was a critique of what he argued was the professional community's acceptance of the perfecting power of natural selection, with the implication that no other mechanisms were required to produce the history of life. Here, Gould explicitly refers to this view as in conflict with "the primary message of history – the lesson of the panda's thumb and the flamingo's smile: The quirky hold of history lies recorded in oddities and imperfections that reveal pathways of descent.]

Gould interprets the limitations of breeding and the ability to domesticate an animal at all (discussed above) in terms of Galton's polyhedron. In the previous 1832 reference, Charles Lyell also noted that no animal that did not have a certain type of hierarchical, social structure in its natural state had ever been successfully domesticated; wolves, dogs, cows, and pigs have such a structure, while hippos, zebras, seals, and in fact most mammals do not. In this metaphor, the social behavior of the first group corresponds to a facet on the polyhedron, allowing the breeders to shift the host to a stable state of domestication. Viewing animal breeding in this way sheds light on the well-established rule that domesticated animals tend to have more "juvenile" proportions than their wild relatives. Most were not bred for these characteristics, but rather for tame and playful behavior – but many trends tend to hang together during development. Gould writes, "If ordinary variation in growth provides the main source for breeders, then a wild species' own juvenile stages are the primary storehouse of available change." This is referred to as an ontogenetic trajectory, and it corresponds to a finely-stepped channel along which Galton's polyhedron can roll.

Gould then becomes more specific. He explores the nature of limits in the breeding of dogs, and in particular the shapes of their skulls, drawing on the work of Robert K. Wayne. By way of background, Gould discusses some of the underlying trends associated with growth in mammals. Different parts of animals scale differently as the animal increases in size. Some of this is tied directly to geometry: the thickness of the legs, for example, has to grow faster than the height of the animal [see ESD 21]. But there are many other "scaling laws" as well that effect non-proportional growth in everything from deer antlers [ESD 9] to vertebrate brains [ESD 23] with respect to body mass. Collectively, these scaling laws go by the term *allometry*, and there are two principle categories. The first, ontogeny, addresses how one part of an animal scales with another part of the same animal as it grows from embryo to infant to adult. The second, interspecific scaling, addresses differences in shapes of different-sized adult animals within the same group. The former addresses how the shape of one dog's skull changes from puppy to adult, while the latter addresses differences in the skull shapes of, say, adult foxes and adult wolves. Wayne (and Gould) are less interested in the scaling laws themselves in this research as he is with the variation around those laws. He examined natural canid (fox, wolf, and so on) skulls, and found that there was very little variation of skull *length* with respect to overall size across species. However, there was a significantly larger amount of variation in skull *width*. This same trend held within species, as the animal grew. Importantly, Wayne found that these same trends in variation held in virtually all breeds of domesticated dogs; skull width could vary over a large range, but the length showed almost no variation with respect to the nominal "law." Thus, we may infer, the raw material of variation in the original species (the wolf *Canus lupus*, in the case of dogs) *constrains* what breeders can do with their descendents via selective breeding. Animals are not perfectly plastic, he concludes; species are polygons in this metaphor, not spheres. [Gould discusses some examples of constrained microevolutionary change in "the wild" over short timescales in LSM 22.]

ELP 28. Betting on Chance – and No Fair Peeking

This essay discusses the "neutral theory of molecular evolution," a concept first introduced by the Japanese geneticist Motoo Kimura in 1968, and the subject of his 1983 book of the same title. Kimura proposed his model in response to two unexpected discoveries in the field of genetics in the 1960's. The first of these, Gould begins, was the discovery that the *rates of change* in the strings of amino acids that make up all proteins are remarkably uniform over the span of tens of millions of years. [This is based on measuring differences in proteins in modern organisms that the fossil record indicates shared a common ancestor at a certain time.] The second is that the *degree of variation* in the genome within a fairly uniform population was much larger than expected. The modern evolutionary synthesis of the 1940's, which fused natural selection and Mendel's genetics (among other things), predicted a close correlation between both overall variation and rates of changes in the genome with the organisms they form. Specifically, this paradigm predicted that those features that are evolving rapidly within a species should correspond to a rapid change in that part of the genome as well, while those parts that were not "evolving" should show little genetic change over time. The discovery that large parts of the genome were in flux while the overall organism appeared to be relatively static seemed contradictory. Secondly, it challenged the mechanism of natural selection acting on genes, for the following reason: If two genomes are almost identical, then any difference between the two organisms that result can be favored or disfavored by natural selection – which only works on organisms. By selectively choosing the stronger gene over the weaker gene over many generations, the weaker gene is eventually eliminated from the population. However, if two offspring of the same parents have genomes that differ in dozens, hundreds, or even thousands of places, natural selection may be overwhelmed – because it can only select the final result, not the contribution of each gene individually. How are we to resolve this puzzle?

Kimura's proposed solution is relatively simple: he suggested that most (but not all) genetic changes are neither favored nor disfavored by natural selection – that is, they are *neutral*. By far the easiest way this can occur is if most genetic material does not actually do anything, such as code for the strings of amino acids that form all proteins. [This is, in fact, the case – at least for eukaryotic cells – and was another great and surprising discovery in 20th century genetics.] In this case, one would expect to see rapid, random changes in the parts of the genome that serve no biological function, and much slower rates of change in those parts that do – since most such changes would be disadvantageous, if not directly fatal, to the resulting organism. In this case, natural selection acts as a "watchdog" (Gould's term) to *inhibit* the genetic change that would normally occur at a more rapid rate.

In the twenty years between Kimura's first paper and the time Gould wrote this essay, three types of supporting evidence for the neutralist model have been established. The first, "synonymous substitutions," capitalizes on the observation that there are 64 possible combinations of three-letter DNA sequences, but only 22 kinds of amino acids synthesized in life on earth. Thus, there is some redundancy in the DNA code, usually in the "third letter"; it has been established that this letter changes much more rapidly than the other two over time. The second involves "introns," which are sections of DNA within a longer genetic sequence that are "snipped out" before the protein is synthesized; the remaining, functional part is called an "exon". Changes in introns take place much more frequently than changes in exons. Third, "pseudogenes" are defined as descendents of genes that produced proteins in the past, but due to a mutation, no longer do. Pseudogenes mutate at rates on the order of a hundred times higher than functional genes.

Importantly, Kimura observed that the relatively uniform way that the pseudogenes and other elements change is well-suited to statistical models that assume random change. Gould discusses the technical, as opposed to the colloquial, meaning of the term "random": it is a good thing in science, because while one cannot say much about what a single random event will produce, the results of the *average* of many random events are highly predictable. (This statistical randomness leads directly to the concept of a "molecular clock"; in practice, it has proven to be less accurate than first hoped, but still widely used as a tool to measure the amount of time since two modern organisms shared a common ancestor.) Since the essence of science is to produce *testable* hypotheses, randomness is welcome – because it offers quantitative predictions that can be tested. If the resulting model is supported by data, it can then be developed into a tool that can be used to explore further. By way of example, Gould offers the Near Eastern mole rat, *Spalax ehrenbergi*. This animal, which lives its entire life underground, is completely blind; thick skin grows over the rudimentary eyeball, and flashing lights produce no neurological response. [This creature appears to be the source of the second part of the essay's title.] But is it possible that the structure itself still serves some purpose, directly or indirectly? Kimura's neutral theory offers a way to address this question. A team led by W. Hendricks, Gould reports, recently published a paper that examines one of the proteins in the rudimentary eye, and compares it to related species that are known to have shared a common ancestor some 40 million years ago. If the protein is a mere remnant that no longer serves any function, the model predicts a specific (large) amount of difference from the seeing relative. If, on the other hand, the protein is still serving some unknown function, we would expect to see a much smaller (but still quantifiably predictable) variance. Interestingly, Gould states, the answer in this case is decidedly in between these two extremes.

Kimura initially overreached, Gould tells us – in his original 1968 paper he argued that most, if not virtually all, evolutionary change was due to non-adaptive, largely random molecular processes such as genetic drift. The Darwinist community, on the other hand (Gould continues), at first argued in response that a few genetic changes might be neutral, but most were not. Both sides agreed that both processes occurred; the question became the relative amount of each. The results, as of the time Gould wrote this, suggest an answer squarely in the middle; he adds that the debate has been highly fruitful. [Gould presents an example of actual, 20-million-year-old DNA that supports this model in DIH 31.]

[Gould omits a point that plays a role in his larger, evolving worldview. Not mentioned is the probability or possibility that real, morphological changes in the organism may also be effectively neutral. The concept that the speciation process might produce multiple, differing lines of descent, each leading to more than one daughter-species that share a range but do not interbreed – neither "better adapted" than the other, at least in terms of their initial existence via a punctuation of natural selection – becomes a key part of the hierarchical view of evolution that he expresses in 2002's *The Structure of Evolutionary Theory*. He does imply that the separation between evolution at the genetic level and at the organism level (also see HTHT 13) may hint that there are other, higher levels at which evolution works also.]

ELP 29. Shields of Expectation – and Actuality

The "shields" of the title refer to the bony head structures that encased the front portion of the ancient and extinct group of armored fish of the genus *Cephalaspis* (literally, "head shield"). This was the first genus discovered of what would become the class of fish known as ostracoderms ("shell-skinned"), which are themselves a subset of Agnatha, or jawless fishes. There are no living Ostracoderms today (nor have there been since the Devonian Period), but there are a few living agnathans. The ostracoderms are an important group in our own natural history, as they are not only the first true fish, but also the first true vertebrates (earlier chordates had a non-bony notochord) and thus ancestors to all other vertebrates, including us. However, since no modern fish has this bony encasement today, and since most fossils preserved only the mysterious and not-very-fishlike head shield, early paleontologists did not know what to make of them. They were originally classified as arthropods, due to the superficial similarity of their head shields of trilobites, eurypterids, and other related groups found in strata of the same age.

Gould uses the changing interpretations of these head shields over time to discuss a larger philosophical question: "Is science truly progressive, or does it simply reflect the changing biases of human culture?" The vast majority of scientists would state that *of course* science makes true progress, in the sense that we learn more unquestionably true facts about nature as we apply the scientific method to our study of the world around us. However, there are some, Gould tells us (without identifying anyone other than "those suspicious of science," but implying fans of the humanities rather than creationists), some who argue that what we call science is really just a form of intellectual fashion like art and music. Gould states that he does believe that science is truly progressive; but he also states that, as a human intellectual construct, science is built upon the *interpretation* of external facts. In this rather convoluted essay, he discusses the changing interpretations of the *Cephalaspis* head shields over time in terms of two fictitious groups. The first is the "cardboard realists," who argue that science is pure truth and nothing but. The second is the "cardboard relativists," who argue that science makes no absolute progress at all, and that our so-called theories are merely the organized biases of each generation regarding our current perception of the outside world. The essay is further complicated by the fact that he acknowledges that neither side truly thinks this way, but in many cases, each is convinced that the other side does.

Cephalaspis shields were first identified at the beginning of the 19th century, and as mentioned above, were initially grouped with arthropods. It was the great Swiss (and later American) naturalist, Louis Agassiz (1807-1873), who first identified *Cephalaspis* as a vertebrate and a fish. Agassiz is famous for several things: he was the "discoverer" of earth's ice ages; he came to America and founded the Museum of Comparative Anatomy at Harvard (where Gould was curator); and he was the last major holdout against evolution. He is also famous for his monograph *Fossil Fish*, published in five volumes between 1833 and 1843. In researching this work, he obtained some well-preserved *Cephalaspis* fossils. They clearly showed the body of a fish attached to the enigmatic head shield; he was able to report that *Cephalaspis* was a vertebrate and not an arthropod. He was unable to expose the underside, however, and thus did not learn of its jawless nature. He knew from the strata in which it was found that the organism was old, but he was not able to establish its relationship as ancestral to other fish or other vertebrates.

Agassiz's *Fossil Fish*, Gould tells us, was more than a series of descriptions; it was also a presentation of his biological worldview. Agassiz believed in a form of creationism. He believed in an ancient Earth with an extended history in which species periodically came into existence and later went extinct, but in his view each was formed "as is" by an external creator. This was a mainstream view in the scientific community at the time, but it was not the only one. Some, for example, argued that older creatures might transform or evolve into younger ones, by some undetermined mechanism. Agassiz strongly opposed these views, and used his treatise to express his version of creationism. He was fascinated by embryology, and in particular, by *differentiation*: the development of a small group of essentially identical cells into a much larger number of specialized ones. In his view, the natural history of life reflected an analogous path. In Earth's early history, he believed, there were only a small number of similar organisms; over time, God produced a larger number of more differentiated and specialized ones. He followed the taxonomic structure of his mentor, Georges Cuvier, and recognized four basic groups: vertebrates; articulates (arthropods and annelids), mollusks, and radiates (radially symmetrical organisms, such as corals and echinoderms). He used *Cephalaspis* to buttress this theory in three ways. First, it addressed the perceived problem that vertebrates (that is, "normal" fish) appeared to arise well after the other three groups. (This was both philosophically distasteful to him, and used by others as evidence that they "evolved.") *Cephalaspis* was older than other fish, however, thus pushing the origin of vertebrates at least closer to that of the other three groups. Second, the head shield itself contained no sutures, as modern skulls do. He took this as evidence that structures such as skulls became more differentiated over time, following his preferred analogy with embryology. Third, he used the superficial resemblance to trilobite shields to argue that all four groups, while always separate, were less differentiated in the distant past; this is again supportive of his views relating natural history to embryology.

The decades passed, and several others took up the study of ostracoderms. New finds clearly showed that *Cephalaspis* had a mouth but no jaw. [The development of jaws from gill arches is mentioned in ELP 6]. More types of armored fish fossils were discovered, and it was determined that they formed a coherent group rather than a collection of unrelated oddballs. Evolution became widely accepted within a few years of the publication of Darwin's *Origin of Species* in 1859, and the new interpretation of ostracoderms was that all other fish, and all other vertebrates, descended from this group. But it became apparent that fish, even armored fish, were still not as ancient as other groups. Who were their ancestors? [The epilogue of Gould's 1989 book *Wonderful Life* reports the tentative identification of *Pikaia*, a soft-bodied chordate discovered in the Burgess shale, as a closely-related ancestor; but this discovery was decades away. Also see IHL 18.] Gould's next detailed interpretation of *Cephalaspis* comes from William Patten, who argued that vertebrates evolved from arthropods, with the ostracoderms as the intermediate link.

That vertebrates might have evolved from arthropods was not actually a new idea; it was first proposed in the early 18th century. The reasoning was that, since vertebrates had to have some ancestor older than fish (according to any of the evolutionary theories of the time), arthropods seemed to be a good choice. Some of the largest and most complex invertebrates were arthropods; and it was well-known even then that there were more arthropod species than all others combined. Some had proposed that a crustacean, such as a lobster, had evolved into a simple fish. William Patten argued in his major work *The Grand Strategy of Evolution* (1920) that the transition occurred between a species of eurypterid with a distinctive head shield and *Cephalaspis*, the armored fish. This was based on a certain visual similarity, to the fact that they were occasionally found in the same strata, and to Patten's mistaken identification of arthropod jaw components in the *Cephalaspis* fossils. (Gould begins this essay by noting the beauty of the eurypterid fossils that Patten collected, which – as curator of Harvard's museum – were displayed in the corner of his office.) Of all the anatomical changes that would be required to convert an arthropod into a vertebrate, the one (and apparently only) major problem that concerned the proponents was the relationship of the primary nerve to the digestive tract. In vertebrates, the nerve runs along the ventral (top) side, while the digestive tract runs along the dorsal (bottom) side; in arthropods, the reverse is true. Proponents of this school of vertebrate origins argued that, at some point in natural history, an arthropod rolled over on its back, which became its front, and became a vertebrate. Much effort was expended trying to determine a plausible series of evolutionary events by which this occurred, and how the old mouth might have disappeared while a new one on the other side formed. None were ever successful enough to convince skeptics, but Patten's work was a published attempt. [Gould discusses the "inversion" theory in detail in LMC 17.]

Patten also turned out to have an ulterior motive, in the form of a biological worldview he was trying to support. He believed that evolution was a progressive phenomenon, moving organisms not only toward higher complexity, but higher levels of morality and social behavior as well. There was no doubt some simple one-celled organism at the beginning of this "great highway," and man was (of course) at the other end. He faced two problems, in his mind. The first, as mentioned, was that the vertebrate path did not seem reach back to the origin. The second was that the arthropod group was simply too large not to have the great highway pass through it somehow. His solution to both of these problems was *Cephalaspis*: in his view, it resembled an arthropod because it was an intermediate form (contrary to Agassiz), a "missing link" between the two groups. This may sound crazy; but as Gould points out, just because a theory sounds crazy does not mean it is wrong. How do we know that *Cephalaspis* is not part fish and part eurypterid?

The answer to this question comes from the remarkable work of a Swedish scientist named Erik Andersson Stensiö, who published his results in 1927. Stensiö also acquired some well-preserved *Cephalaspis* head shields, but his had an additional unusual feature; they had more fossilized bone than usual. He guessed, correctly, that in these particular fish the bone not only grew around the outside of the head, but filled in all the space around the soft tissue within. With remarkable effort, Stensiö was able to develop a highly detailed, three-dimensional model of the ancient fish head, including the brain, nerves, and blood vessels. Based on the details, he was able to unambiguously show that *Cephalaspis* was pure vertebrate. He also showed that *Cephalaspis* was closely related to modern jawless fishes, such as lampreys and hagfish. This resolved a debate as to whether the jawless nature of these fish was original and ancient (true), or the result of jawed fish losing this feature (false). His worldview is the one we have today: *Cephalaspis* was an early vertebrate and the first true fish, and all other fish and vertebrates are its evolutionary descendents.

Throughout the essay, Gould discusses how the cardboard realists and cardboard relativists might interpret each event. Realists, he believes, would argue that the changing interpretations of the *Cephalaspis* are almost entirely the result of increased knowledge. Agassiz learned that it was a fish, although he did not have the data to understand its relationship to other vertebrates. Patten came along after we had learned that evolution was true, but before we understood vertebrate origins. Stensiö learned, by studying the data, that *Cephalaspis* is closely related to modern jawless fishes, and not to arthropods. Their worldviews differed, but only because each had more facts to deal with.

Cardboard relativists, on the other hand, would see things differently. Agassiz looked at *Cephalaspis* and saw a form of divine creationism analogous embryological development. Patten looked at the same object and saw a link in a progressive evolutionary chain connecting simpler arthropods to more complex, and more virtuous, vertebrates. Stensiö viewed the fossil and saw it as the root of an evolutionary limb that "branched" into all modern vertebrates. Today, the relativists would argue, scientists believe that Stensiö was "right"; but what makes them think that his worldview will not be lumped in with those of Agassiz and Patten in a few decades, replaced by something else?

Gould's point is that each of these extremes contains a fundamental truth. Yes, our understanding of nature really does improve as we learn more facts. And yes, the process by which we organize the facts we have, and how we prioritize their importance, is heavily dependent on the creativity and biases of individual humans. These two aspects can work with each other, not just against each other. Agassiz may have been predisposed to emphasize the ancientness of vertebrates for his own reasons, but that does not diminish its importance. Patten may have been dead wrong about Cephalaspis being part arthropod, but the result was to motivate Stensiö to gather new data to disprove it. In science, data and theory are forever intertwined.

ELP 30. A Tale of Three Pictures

This essay is essentially a continuation of the previous one; the two appeared in *Natural History* magazine in consecutive months. It considers the same object (the head shield fossils of the armored fish *Cephalaspis*), and the interpretations of this object by the same three scientists (Louis Agassiz, William Patten, and Erik Stensiö). This time the focus is on the pictures or images that each of these three men created to express *Cephalaspis* within their worldview. We are visual creatures, Gould states, and the linear construct of written text does not convey thoughts in the conceptual way that images do. When drawing a concrete object, context is often given by the shading and background. In the case of theoretical concepts, such as the relationships between groups of animals to each other, an image can often tell us much more about the author's thoughts than his writing. [Gould also discusses the relationship of image and worldview in LMC 3, and in his 1987 book *Time's Arrow, Time's Cycle*.]

The picture from Agassiz shows four major groups of fishes as vertical lines. The vertical axis represents time, with the beginning and ending of the lines representing creation and extinction respectively. The horizontal axis represents similarity; lines that are closer together represent genus of fish that resemble each other anatomically more closely. Further, the thickness of the lines corresponds to the diversity of that group at the time; this nomenclature is still used as the basis of "spindle diagrams," used in every evolutionary biology text today. Importantly, the number of lines grows through time, while becoming more widely separated; this reflects his view of "life as differentiation," with its analogy to embryology. Just as importantly, Gould notes, the lines do not join at the origin. Agassiz was a creationist, and the joining of the lines at earlier times would suggest that one organism gave rise to others, which is an inherently evolutionistic viewpoint. *Cephalaspis* is shown as a short-lived side branch on the oldest group, indicating that Agassiz considered it an early but brief thought in the mind of God.

Gould chooses Patten's drawing of all animal life. It is unusual in that time is not the vertical axis, but rather a series of balloon-shaped contour lines that intersect the horizontal axis. He makes this choice so that the vertical axis is free to represent "progress," which is a concept at the heart of his evolutionary worldview. Sponges and mollusks exist in the present just as humans do, but they are off to the side while man sits at the top of the image. Patten's drawing highlights the "great highway of progress," running from single-celled animals through arthropods, through the transitional organism of *Cephalaspis* and the ostracoderms to vertebrates, and on up through amphibians and reptiles to mammals and man. Gould makes the point that Patten's drawing is not an updated version of Agassiz's drawing that includes evolution; the two are fundamentally incompatible. First and foremost, Agassiz considers *Cephalaspis* to be a fish and vertebrate, while Patten considers it to be an intermediate group between vertebrates and arthropods.

The third image is a simple line sketch by Stensiö, showing only the relationship of ostracoderms to each other. At first glance, it seems similar to the drawing by Agassiz, only with the lines connected; but it differs in a very important way. The Agassiz drawing shows the lines converging towards certain common points; this reflected the embryological "divergence" view of life. Stensiö's image shows a repeated branching pattern; lines branch off, and then other lines branch off from them. The lines do not converge toward a single point. This hierarchical model represents the "speciation" worldview that holds today.

Gould closes by reiterating a point that he has expressed before: that we do a disservice to any thinker by only stating those parts of his or her model that conform to today's viewpoints. It is important to give the context of their worldviews; we learn more about their times and ours when we do so.

ELP 31. A Foot Soldier for Evolution

Near the end of this essay, Gould announces that it closely follows one of his early professional papers from 1968. Looking back almost two decades later, he states that he "got part of the story right," but missed the larger point. That point involves the interaction of fact and theory, and the actual (versus the idealized) nature of scientific progress: that a single fact cannot overthrow an entire theory, any more than a single foot soldier can win a war (leading to the essay's title).

The work of dating earth's geological strata began in the 18th century [HTHT 7], when it was determined that fossils could be used to date sedimentary rocks separated by large distances. The best fossils to use were those that were common, widespread, and lived for a relatively brief amount of geologic time. The working-level assumption of this field was that the organisms in question lived during the same period everywhere they were found. One such "guide fossil" was a genus of clam called *Trigonia*, which lived during the Mesozoic era and vanished at the end of the Cretaceous period (along with the dinosaurs and much of the rest of life on earth). Then, in 1802, the shell of a recently deceased *Trigonia* washed up in Australia; twenty-five years later, a living one was dredged from the sea floor off the Australian coast. These discoveries caused quite a stir in scientific and naturalist circles; what did it mean? Had the genus died out and then been recreated, or re-evolved? Or had a small pocket survived during the entire Cenozoic era? (The missing 65 million years of fossil evidence for it became known as the "Cenozoic gap.") There were some differences between the fossil and modern shells, the most obvious being that the fossil *Trigonia* had both concentric and radial ridges, while the modern one had only radial ridges. Was this the significance of these differences? Some of the most prominent scientists of the 19th century weighed in, and Gould proceeds to discuss four of them. His first point will be that each of these scientists fitted the "fact" of a living *Trigonia* into each of their (very different) theories of life on earth. Rather than being a deciding factor among differing worldviews, each player focused on the details that supported their theory and played down those that did not.

The first professional paper on *Trigonia*, published in 1804, was written by the famous non-Darwinian evolutionist J. B. Lamarck [TPT 7, LSM 6]. At this time, Lamarck was curator of the Museum of Natural History in Paris, and it fell to him to formally describe the organism. He assumed that the modern *Trigonia* was a direct descendent of the Mesozoic one, modified by the evolutionary process of "the inheritance of acquired characteristics." The environment had changed, he argued, and the clam had changed with it. He offered no reason why the clam would struggle to improve itself by shedding the shell's concentric ridges, only implying that it must have had one. He also used the existence of the fossil to challenge not only the reality of Cenozoic gap, but of extinction generally (while acknowledging Cuvier's earlier argument that it could occur on occasion – see HTHT 7 again). No doubt many other organisms known only from fossil beds would also be eventually found in the depths of the sea, he believed.

Another soon-to-be evolutionist, Charles Darwin, wrote about *Trigonia* a generation later. In his private 1844 essay that would eventually be expanded into 1859's *Origin of Species*, his emphasis was not that the organism evolved, but rather that its extinction, and by extension its "creation," were geologically extended processes. That is, he used *Trigonia* to support his gradualist view of life's history. He also dismissed the Cenozoic gap as an artifact of the poor quality of the fossil record, explicitly stating his view that once extinct (the concept that had become universally accepted in the intervening years), an organism would not reappear.

Stepping back in time to 1811, Gould next discusses a three-volume work entitled *Organic Remains of a Former World* by the naturalist James Parkinson. Parkinson was a mainstream creationist of his day, and as such believed that creation was an ongoing process, with a limited number of major creation and extinction events. For him, the Cenozoic gap was the important feature: *Trigonia* had become extinct, and then been re-created in a slightly different form in the recent past. The differences in the character of the fossils were details. He struggled with these details, however, because his view of creationism was *progressive*; he believed that each successive round of creation produced better and better organisms. What argument could he make that the absence of concentric ribs constituted progress? Like Lamarck, he could only argue that it must do so, or else it would not have happened.

Louis Agassiz [ELP 29] also weighed in on *Trigonia*, publishing an entire volume on them in 1840. Agassiz was also a believer in sequential creationism, and started out as a progressivist like Parkinson. Later, however, he concluded that all of God's creations were of equal excellence [see LSM 9 for a discussion of the similar views of Richard Owen] – in large part, Gould states, because of his opposition to all evolutionary theories, which invariably drew on progress in one way or another. Thus, he was unconcerned with the differences in the shells, and enthusiastic about the Cenozoic gap. In his 1840 volume, he wrote that the existence of this gap, if upheld, would disprove all theories of evolution.

Gould concluded his 1968 paper by discussing the first discovery of a fossil *Trigonia* shell in Cenozoic strata, also in Australia. The results were reported in a paper by H. M. Jenkins in 1865, just a few years after the publication of *Origin of Species* and when Darwin's theory was in need of just such a find. The Cenozoic gap was not real, but instead an indicator of the poor quality of the fossil record; evolution wins, creationism loses.

What Gould failed to notice at the time, he states in the essay, is that this discovery had virtually no impact. The paper appeared in an obscure journal, and Jenkins himself was not even the discoverer – that honor fell to the notable Australian naturalist Frederick McCoy, who had not bothered to publish at all. Darwin never mentioned the discovery, although *Origin of Species* had several editions yet to run. No one else mentioned it either. Why not? It turns out, Gould continues, that the 1865 discovery did not really disprove creationism; Agassiz had left himself an "out," stating that any later discoveries of Cenozoic *Trigonia* fossils could simply mean that God created the genus multiple times, not just twice. As to the evolutionist side, Gould writes: "*Trigonia* didn't hurt, but a multitude of fish were frying, and one extra clam, however clean and pretty, didn't bring the meal to perfection." Theories as overarching as evolution host thousands of facts, not all with complete comfort. One more fact, he argues, like a single foot soldier, does not decide the outcome of a major battle.