Hen’s Teeth and Horse’s Toes

HTHT 1. Big Fish, Little Fish

Male mammals are usually larger than their female counterparts. However, in most of the rest of the animal kingdom, the opposite is true. After a discussion of the misplaced importance that humans have associated with physical size – variants of “bigger is better” – Gould asks why males are not universally much smaller than females. It is females, after all, who produce nutrient-rich eggs, and who far more often provide the majority of care and resources for the offspring. Male sperm, on the other hand, are little more than clumps of DNA with flagella (“tails”); in most species, the males provide no support to offspring at all (emperor penguins and humans being two popular exceptions).

The standard answer to this conundrum, which Gould presents here, is that natural selection acts on individuals, rather than on groups or species. [This is the same argument as in TPT 6, which involved the ratio of male to female offspring.] If natural selection worked on species, it would make "sense" from an energy and resource perspective for males grow just large enough to be able to deliver their genetic material. In nature, however, males often compete for females – either directly via competition, or indirectly via sexual selection by the female. Both cases tend to favor larger, more robust males. That is, males are "large" because Darwin's theory of evolution, based on natural selection acting on individuals, favors size.

This hypothesis is plausible, but can we test it? A standard tactic in this situation is to look for exceptions that prove (meaning "test") the rule. If we examine environments in which males cannot compete with each other, and females cannot choose between mates, do we find small males? Gould offers two examples in which this is the case. The first is a parasite in the mollusk phylum that lives within sea cucumbers, which are relatives of starfish and sea urchins. The relatively large female parasite establishes a tube to the sea cucumber's esophagus; this tube is large enough to pass the much smaller male, if one is "swallowed" from the surrounding water. The male parasite is admitted through the tube into the female's body, where it is supplied with nutrients, and in return provides genetic material. The tube between the parasite and the host atrophies after a single male is incorporated, so the first male to arrive on the scene "wins." The example indicates that the large female - dwarf male strategy can be found, at least sometimes, in ecological niches where males do not compete. The male can "afford" to be small.

The second example comes from the vertebrates. It involves a species of anglerfish that lives at great depths, where again both food and other anglerfish are scarce. In 1922, a female specimen was captured that appeared to have two smaller fish physically attached to it (the small fish's mouth to the large fish's flank). They were so integrated, in fact, that tissue from the large fish had grown inside the smaller fish, fusing them together. In fact, the circulatory systems of the two were merged – handy for the smaller fish, since it no longer had a mouth to feed with. It was later discovered that the attached fish were sexually mature males. (Gould notes that in this species, more than one male is often found attached to the female; this indicates a less-than-optimal selective advantage for any particular male, complicating the theoretical argument.) In an aside, Gould warns that there are many other species of deep-sea anglerfish that do not merge in this way, or do so only temporarily; one cannot speak in terms of "the" anglerfish. Nonetheless, the large difference in size is consistent across the group. [He returns to the topic of gender and body size in TFS 3.]

HTHT 2. Nonmoral Nature

What can or should humans learn from nature regarding morality? Philosophers, theologians, and scientists have proposed a wide range of answers over the centuries. Gould now adds his: "Nothing." His conclusion is that nature is neither moral nor immoral; these are human concepts that do not apply to the natural world. Nature says nothing, positive or negative, about how humans should live or treat each other. Before presenting this conclusion, however, he summarizes some fascinating (and often morbid) 19^{th} and 20^{th} century arguments that attempted to show otherwise.

One popular 19th century school of thought that attempted to make the case that morality could be found in nature was *natural theology* [ELP 9, LMC 15]. Some of the ideas date back to antiquity, but the seminal document is William Paley's 1802 book of this title. Natural theology, as opposed to revealed theology, was in part an attempt to reconcile the early flowering and findings of science with scripture. It included two central tenants. The first was that God's *existence* could be deduced from the structure of the natural world, which shows "design." Paley argued that, if design exists, then there must be a designer – and this would be God. [This argument still exists in non-scientific circles today as "intelligent design."] The second tenant, which is the more relevant to this essay, is that the Designer's *goodness* can also be proven by observing his Creation: the world is beautiful, and nature is in balance. But if God is benevolent and the Creation displays His goodness, then why is the animal world full of pain, suffering, and apparently senseless cruelty? Addressing this question became one of the key areas of activity in the field.

Upon his death in 1829, the Earl of Bridgewater provided funds for the creation of a series of volumes on Natural Theology, each on a different branch of science. These became collectively known as "The Bridgewater Treaties on the Power, Wisdom, and Goodness of God as Manifested in the Creation." One of these was authored by William Buckland [TFS 7, LSM 9], England's first official academic geologist and later dean of Westminster. Buckland approached this challenge by focusing on carnivores hunting prey, which (he argued) reduces "overall suffering" by allowing the prey a quick death, instead of a lingering old age and prolonged illness, injury, or starvation. "Perhaps," Gould states, but notes that this is nowhere near the most difficult case that natural theologians must explain. This falls with remarkable regularity to the "ichneumon fly," a term that actually applies to several thousand species of wasp. These wasps use caterpillars, or in some cases aphids or spiders, as sources of food for their larvae. The detail that makes this particular case so difficult to explain in terms of a benevolent Creator is that the hosts are kept alive and apparently "awake" during the extended feeding process, with the wasp larvae carefully consuming the non-vital parts of the host first.

Buckland sidestepped the issue of finding a good and "moral" understanding of ichneumon flies in nature by simply avoiding them. However, many other writers of the period did not. Gould spends the major portion of the essay describing and quoting examples of 19th and 20th century naturalists, theologians, and other writers who discuss the ichneumon's behavior. He identifies two recurring themes in this literature, both of which he dislikes: the agony of the prey, and the power and efficiency of the wasps and their larvae. (Gould himself is rather non-sympathetic to what he argues is "perceived suffering" of the prey, and discusses the process in unusually gruesome detail.) Charles Lyell, the famous geologist, simply argued that whatever it took to keep caterpillars from ravaging human's food supply was good. The Reverend William Kirby, leading entomologist and author of another of the Bridgewater Treaties, chose to ignore the plight of the prey and instead discusses the maternal virtue of the wasp in providing sustenance for offspring she will never see. He also writes about the virtuous frugality of the larvae in husbanding their resources to prevent "spoilage" by not killing the host immediately. St. George Mivart, an important Darwin critic, wrote that the physical suffering of animals was "incommensurate" with morality, since beasts are not moral agents. He goes on to add that animals feel little if any pain, since (he argues) the ability to feel pain is dependent on the mental capabilities of the creature in question. (Gould notes that the same arguments were being used to justify the imperialistic and often brutal occupation of human-populated territories by Britain at this time, as well as American treatment of slaves and Indians.)

The acceptance of Darwin's theory in the 1860's effectively ended the reign of natural theology [LMC 15]. Gould states that there are two ways we can proceed from the loss of belief that every act of nature reflects God's goodness. The first is to retain the view that nature does hold a moral message, but to presume instead that it is something bad; and that we, as civilized beings, must rise above it. Thomas Henry Huxley advocated this position in his 1893 essay "Evolution and Ethics," and supporters tend to see nature as "red in tooth and claw" [Tennyson's phrase; see DIH 6]. The other approach, radical at the time and still controversial today, is to accept a view of nature that is nonmoral; this is certainly Gould's view [LMC 14]. In this perspective, the ichneumon's behavior is simply an adaptive strategy for survival and reproduction, with no lessons to teach us about good and evil, right and wrong, or our own underlying moral and ethical condition. Darwin himself seemed to partially accept this; he wrote to a friend that he could not believe that God would deliberately have designed cats to play with mice – or have created ichneumons to behave as they do. Still the Victorian, however, he expressed a hope that nature's laws might still reflect some higher purpose, but concluded that such relationships would likely be too profound for the human intellect to grasp. He added: "Let each man hope and believe what he can."

HTHT 3. The Guano Ring

On a visit to the Galapagos Islands, Gould observed the odd nesting and reproductive behavior of two species of booby. Boobies and Gannets are seabirds that nest near the ocean and hunt fish. Some species make nests in trees, but these boobies lay their eggs directly on exposed rock outcroppings. (The absence of predators on the Galapagos allows this reproductive strategy to work.) The blue-footed boobies produce circular, nest-shaped areas of "turf" on these rocks by excreting rings of guano (bird poop). Each bird will sit on its egg or eggs and feed its chicks inside this ring, ignoring the others – unless another bird (or, in Gould's case, an inadvertent toe) approaches the center too closely. In the case of encroachment, the bird responds with hostile cries and displays, including pecking. The particular event that riveted Gould's attention was the apparent extension of the overly simple algorithm of "if inside, nurture; if outside, ignore or reject" to the bird's own chicks. Gould watched with some distress as a mother booby ignored the plaintive cries of its own hatchling, which had ended up outside the guano ring, effectively leaving it to die. Upon researching this behavior afterwards, he found that this was a common event in the lives of blue-footed boobies – because an older chick (which emerged from an egg laid a few days earlier) will often deliberately push the younger chick outside the nest/ring. This behavior seems to be correlated with the supply of food; in good times, two or three chicks can be raised to maturity, but when times are hard, the "soft siblicide" occurs. Gould concludes that the mechanism behind the parent bird's behavior is, for lack of a better word, stupidity. The booby, he believes, simply thinks of anything outside the ring – even her own chick – as "not mine," and ignores it. Whether the underlying mechanism is accurate or not, the behavior itself has been well-documented. Gould adds that the male has to make a ritualistic display to enter the ring occupied by the female, presumably to overrule this algorithm, even to feed their chick.

Another species of Galapagos-dwelling booby, the white or masked booby, is even more peculiar. The masked booby's food source is usually farther out to sea, so more time is required to make each trip, and therefore fewer overall food-gathering trips can be made in a given period of time. In almost all cases, the mother lays two eggs, typically a few days apart. When the younger one hatches, the older one invariably kills it, either by pushing it out of the nest or by directly stomping it to death. How does an evolutionary biologist explain the behavior of the mother boobies in terms of Darwin's theory?

The standard approach, with which Gould concurs, is to show these behaviors are adaptations that actually do offer a selective reproductive advantage. In the case of the blue-footed boobies, the behavior works to insure that in times of stress, at least one chick can make it to maturity. If the mother tried to raise two or three chicks when there was really only enough food for one, all would likely perish. As for the masked booby, Gould references research that suggests that the second egg acts as an insurance policy. The odds of an individual of this species raising two chicks to maturity is small; if two eggs are laid, but only one requires feeding, the odds of one chick reaching maturity are greatly increased.

Gould could end the essay here: curious, seemingly non-Darwinian behaviors that really can be explained in terms of natural selection. However, as he argues elsewhere, although "adaptationism" is an important mechanism in evolution, it is not the only one. He proceeds to discuss two others that may have played a role in producing the boobies' unusual behavior. The first is the constraint that natural history has placed on the size of the bird's brain and neural circuitry. "Inside, nurture; outside, ignore" is a simple algorithm; it may be, he argues, that more complex decision-making algorithms that might produce the same result with less "cruelty" are simply not supportable in bird-sized brains. A third factor that may play a role is that a strategy that was shaped by natural selection in the past (and is, or was, "adaptive") led indirectly to the current behavior in a new environment – the Galapagos Islands – simply by "being available to work with." The ritualistic behavior that the booby's mate must exhibit to enter the guano ring is almost certainly to be a relic of mating and nest-building behavior of their ancestors; this, in turn, impacts the current behavior, since the chicks cannot perform these rituals. [Gould refers to this mechanism elsewhere as *exaptation* – see BFB 9]. He reiterates that such features are some of the best evidence we have that evolution occurs.

HTHT 4. Quick Lives and Quirky Changes

Gould begins this multifaceted essay with the presentation of a "curious organism." *Histiostoma murchiei* is a mite that parasitizes earthworm cocoons, and both the males and females go through several developmental stages between egg and adult. The first unusual feature of this organism is that the female has an additional pre-adult developmental stage that the male does not have, called the hypopus; females spend the vast majority of their lives in this phase. The manifest result is that the females live many, many times longer than the males. A closer examination shows more unusual behavior. Referencing the work of James H. Oliver, Gould tells us that when the hypopus does, finally, complete her transition to an adult (while inside an earthworm cocoon), she lays two rounds of eggs. The first round develops without being fertilized, and produces two to nine males, but no females. These offspring then mate with their mother, and die shortly afterwards. The second round of egg-laying produces about 500 offspring – all females, this time. How are we to understand such behavior in terms of Darwin's theory?

The first step, Gould explains, is to recognize that *H. murchiei* is "haplodiploid." Most animals are diploid, meaning that they have two copies of each chromosome – one from each of their parents. In some animals, however, the females are diploid, but the males have only one set of chromosomes (from their mother). This makes them "haploid," meaning that they only have half of the usual number of chromosomes. Species in which the males are haploid and the females are diploid are thus referred to as haplodiploid. Haplodiploid species can control – at least to a larger extent than diploid animals – the sex of their offspring [see TPT 6 for another example]. Fertilized eggs develop into females in all cases; the unfertilized eggs can also develop, but in all cases they become males. Thus, the mother can "determine" the sex of her offspring by providing or denying access to sperm.

Gould introduced haplodiploidy in ESD 33 as part of an explanation for the remarkable social behavior of many species of the order Hymenoptera, which include ants, bees, and wasps. One of the problems that evolutionary biologists faced in trying to explain social behavior in, say, an ant colony is that there is an entire class of sterile "workers" that spend their lives taking care of the offspring of another ant – the queen. Since Darwin's theory argues that organisms compete against the environment or each other to survive and reproduce, how can we explain this apparently "altruistic" behavior of the worker ants? The answer that Gould discussed in ESD 33 drew on the haplodiploid nature of all social insects (except termites, which are diploid); in such cases, the queen's other offspring – which are the worker's sisters – actually have a higher genetic component of the worker's genome than their own offspring would have, if they were not sterile. Thus, if one thinks of reproductive success in terms of maximizing one's own genes into the next generation, then this social, apparently altruistic behavior is actually "selfish," and thus consistent with Darwin's theory. The biological community refers to this as "kin selection." It also provides an explanation as to why the workers are female in all cases (excepting termites, again; their workers are of both sexes).

The recognition of this correlation between haplodiploidy and social behavior was so exciting, Gould reports, that many scientists came to feel that the two evolved together; that haplodiploidy developed "for," or at least in the context of, large-scale social cooperation in ants and bees. But this almost certainly cannot be true, Gould counters, for two reasons. First, *all* hymenoptera are haplodiploid, and only a small fraction of these are social. Most members of this order are solitary wasps. Second, haplodiploidy occasionally appears in other orders of insects, and again on occasion in other phyla, including rotifers, nematodes, and of relevance to this essay, mites. This leads us to conclude that haplodiploidy arose multiple times, independently. [In the terminology of TPT 24, it is an analogy, rather than a homology, at least at levels above the order of Hymenoptera.] Since none of these other cases produce the type of social behavior seen in ants and bees, it appears that something else produces this mode in nature.

Looking across the broad array of species that exhibit this genetic characteristic, including *H. murchiei*, Gould identifies a trend: they are all "colonizers." He uses this term to refer to organisms that rely on food sources that are hard to find, but super-abundant when present. [Gould discussed this behavior in gall midges in ESD 10, although they are apparently not haplodiploid.] *H. murchiei* uses the earthworm's cocoon as its food source; when this is gone, hundreds or thousands break out to search for new ones. Most fail and die. When a roaming hypopus does stumble onto a pristine earthworm cocoon, it works to capitalize on its luck as fast as possible. It enters the adult phase; then, rather than having to wait for a male to find its way to the same cocoon, the female produces several of its own (without fertilization, since the males are haploid). The males rapidly mature and mate with the mother, providing sperm that she can use to create females; then they die. The mother then produces hundreds of fertilized eggs, each of which grows into a (female) hypopus that can either reproduce further or break out and search for the next ephemeral food source. The genetic tactic of haplodiploidy not only allows a single mite to colonize a new food source; by controlling the timing and ratio of male and female offspring, the colony's founder can achieve maximum population in minimum time.

This colonizing lifestyle, Gould argues, is probably the original selective advantage responsible for the evolution of haplodiploid species from purely diploid ancestors. The social behavior of ants and bees is most likely, he continues, a co-optation [see BFB 9] of this feature, employing it for a very different purpose. The fact that the critical "searching" segment of the colonist's lifestyle, performed entirely alone, is essentially the opposite of anthill and beehive social behavior is an illustration of the power of this evolutionary mechanism. It is this "quirky change" in the functional utility of haplodiploidy that the essay's title refers to. But even so, he concludes, haplodiploidy cannot arise just anywhere in the animal kingdom. Since human females have two X-chromosomes, a diploid human would have to be a (sterile) female; a Y-chromosome is required to produce a male in our (and most) species. Some diploids, however, have a so-called XX-XO system of sex determination; two X's make a female, while one X (the "O" is really a zero), with all other chromosomes fully diploid, makes a male. If all haplodiploids evolved from XX-XO diploids – there may be others – this would place an additional constraint on their formation. That is, another mechanism is involved in the evolution of all such species: historical contingency, another of his recurring themes.

HTHT 5. The Titular Bishop of Titiopolis

Nicolaus Steno (1638-1686) is considered to be one of the founders of geology, along with Thomas Hutton [next essay] and Charles Lyell [ESD 18, LSM 7]. He was born Niels Stensen in Denmark, and published under the Latinized version of his name, Nicolai Stenonis; this was commonly shortened to Steno. His journey to geology was indirect, and his stay relatively brief. He was one of the eminent research anatomists of his day, making several important discoveries that brought him some fame in his time, and others that were only appreciated decades after his death. He traveled widely, and spent some critical years in Florence under the sponsorship of the Medici's. It was in Florence that he spent two years working on the puzzle of the origin and formation of geologic strata. This effort resulted in a book, published in 1669, entitled *De solido intra solidum naturaliter contento dissertatationis prodromus*, or *Prodromus* ("abstract") *to a dissertation on a solid body naturally contained within a solid*. This abstract – he never wrote the full dissertation – is the principle source of his fame today. Also during this period, he converted from the Lutheranism of his native Denmark to Catholicism. He would shortly change careers again, and join the clergy. He eventually becoming a bishop, assigned to minister to the few Catholics who remained in northern Germany, Denmark, and Norway. He could not formally reside in this bishopric, since it was in the hands of the infidel Protestants. Since a bishop must have a bishopric, he was given title to the titular ("placeholder") bishopric of Titiopolis, a region currently located in modern Turkey; hence the essay's curious title.

One of the turning points in his life came when he was given the honor of dissecting the head of a great white shark, dragged ashore and killed (in that order) in a nearby town, in front of an interested crowd in Florence that included the grand duke. Steno recognized the teeth as being very similar to objects called *glossipetrae*, or tongue stones. These existed by the thousands in collections of unusual natural objects throughout Europe, and were commercially mined in Malta due to their supposed medicinal properties [see LSM 3]. There were many theories for the origin of tongue stones, including that they fell from the sky during thunderstorms (since they were often found on level ground, washed out of nearby sediments, after such storms). Others knew that this could not be true, as they dug them out of the ground in various places. One widespread theory, which had been around since the time of Aristotle and the Greeks, was that the *glossipetrae* were, in fact, actual shark teeth – or, in some cases, their mineralized remains. In fact, some very convincing work had been done to establish this in the previous decades. Steno came to this conclusion as well, but this theory faced some challenging problems. The first and foremost of which was how shark's teeth ended up on land, often miles from the sea. Another was the "young earth" problem; how could so many have been produced in the few thousand years that biblical scholars allowed since creation, if the *glossipetrae* had not been present from the beginning? (Aristotle believed in an eternal earth.) A third problem was how these objects came to end up, in many cases, inside of solid rock.

An alternative paradigm of the time, which appeared to resolve many of these problems, was that the *glossipetrae* and other "fossil" objects such as shells and crystals were formed and grew inside the rocks [see LSM 1-3]. It was clear that many interesting objects did form inside geological cavities, such as agates; in an age in which belief in spontaneous generation flourished, it did not seem impossible *a priori* that whatever process formed a seashell in the ocean could have an analog in the mineral world. All sorts of interesting shapes could be found in the earth; examples of each letter of the alphabet, along with images of saints and the crucifixion, could be "found" in agate patterns and veins of rock. Many believed that rays from the sun formed deposits of gold inside the earth; who was to say that nature could not produce *glossipetrae* inside rocks, as well as inside the mouths of sharks?

Steno's essential contribution to the founding of geology, Gould states, began with his recognition that *glossipetrae* were only a specific example of the more general category of objects – including shells and "letters" – found inside rock. This, then, explains the title of his book on the subject of solids within solids. Although the mechanism he proposed turned out to be incorrect, Steno was quite right that in certain rocks, some parts formed before others. Using what came to be known as "Steno's principle of molding," he could determine the order in which the subcomponents had solidified. He established two subclasses. The first was those in which the included object – shark tooth, shell, or pebble – solidified first; this left an impression on the younger material as it solidified around it. The second were those cases in which the rock "matrix" formed first, leaving a void, or later cracking and leaving a gap. In these cases, the space was filled in by younger material, which then took the shape of the "mold." Importantly, he was able to place tongue stones and shells, and basically everything that we consider a "fossil" today, into the former category. Patterns resembling letters of the alphabet and images reminiscent of Christ all fell into the latter. Gould states that this revised taxonomic structure – first grouping all "solids within solids" into a coherent category, and then making the important subdivision – was revolutionary. He writes, "[Taxonomies] both reflect and direct our thinking . . . . Historical changes in classification are the fossilized indicators of conceptual revolutions."

Steno added a second principle, that of "sufficient similarity." Here, he argued that all objects that upon detailed inspection appear to share identical form must have been produced in the same way. That is, *glossipetrae* are produced in only one environment – the mouths of sharks. Similarly, sea shells found inside rocks from strata found on mountains were once parts of living creatures that lived in rivers, lakes, or the ocean. He offered no explanation for how the shells came to their present location, and this absence of a credible mechanism resulted in few new converts to this perspective. [Perhaps this is how it should be – see ESD 20 and TPT 19.] Also, in contrast to the spirit of the age, he offered no "purpose" as to why such structures should form [see the next essay].

Importantly, Steno extended the application of the principles of molding and sufficient similarity beyond shells and crystals to sedimentary layers in general. He argued that the strata of sedimentary rock – no matter what their present elevation – are also the remnants of depositional processes seen in rivers, lakes, and oceans today. As a result, he argued, we must conclude that earth has a *history*. Sedimentary rocks were not formed during genesis, but rather during the period of time since then. (Steno never doubted that the Earth was on the order of six thousand years old, but his approach laid the groundwork for others.) Again, there were Greeks and Romans who considered this, but they assumed an infinite past, and concluded that the strata reflected quasi-infinite chaos. Steno was the first to advocate that, using these principles (and assuming a finite period of time since the earth's formation) that earth's history was – at least in principle – something that humans could come to understand. He concluded *De Solido* by applying the principles to the geology around Tuscany, and produced a notional history. It has proven to be incorrect in its particulars – that part of Italy has a very complex geological structure – but it provided a useful working example for his approach.

[Steno presents three additional laws, often unfortunately also called "principles," in his book, each of which follows from the two principles discussed above. The first is the *principle of superposition*: younger strata (those deposited more recently) lie on top of older strata. The *principle of original horizontality* states that the geological strata, being at one point the floor of the ocean, were formed horizontally, even if they are tilted today. The third, the *principle of lateral continuity*, states that when formed, strata filled their basin, so that "bared edges of strata" indicate that something disrupted the continuity after formation, and that more of the formation should be found elsewhere. While scientific and theological debate continued for decades, those with hands-on responsibility to identify and map mineral deposits within their states or nations relied on Steno's three principles continuously from their first publication.]

Gould argues that Steno's breakthrough stemmed from the way he ordered and grouped things; a change in *taxonomy*. The results, which Steno is known for today, came not from better observation (as Gould implies most textbooks advocate), but are corollaries that arise from this new way of organizing the information available.

HTHT 6. Hutton's Purpose

Scientists, like their predecessors, the natural philosophers, are fascinated by the question of why the physical "world" (including stars and planets) is the way it is. Yet, perhaps ironically, the question "why" plays almost no role in what has become known as the scientific method. Science, as a technique for understanding the nature of things, focuses on the observable, the measurable, the calculable, and the testable. Kepler found that the planets follow elliptical paths around the sun; Newton showed that this could be derived from the assumption that the force of gravity between the two masses decreased with the square of the distance between them. One may conclude that Newton's laws explain "why" planets travel in elliptical orbits, but Kepler found his result without it. And Newton's law of universal gravitation makes no attempt to explain "why" gravity behaves this way and not some other way; it is essentially an empirical, quantitative (and, after Einstein, apparently only approximate) expression in the category of "what." The "why" questions may motivate the scientist to explore new directions, but the scientific method itself has no use for it. The "why questions" are left for philosophers and theologians (and the rest of us, including scientists, "after hours").

[Applying this craftsman-like approach as the *exclusive* operational technique to understanding nature is new, historically speaking. Although Kepler and Newton helped create this new paradigm, they were not raised within it, and neither would likely feel at home in a modern scientific community. This view is, in general, completely accepted in the physical sciences today. It is not accepted in fields involving human activity, such as anthropology or psychology; here the "why" or "to what purpose" questions still play an essential role. In the area of study in between – that of biology and evolution – there exists considerable debate as to the appropriate role of "why" questions. This debate manifests itself in Gould's essays in discussions of adaptationism versus structuralism, and the relative importance of contingency in the history of life. Geology, the subject of this essay, is in almost all cases grouped with the physical sciences in this triage today (but see BFB 34). Gould's point will be that James Hutton, one of the men most responsible for this modern perspective in geology, did consider the *purpose* of his mechanism, the "why questions," to be essential. That is, Hutton was not a "modern" scientific thinker, although he laid essential groundwork for others.]

The concept of "purpose" in the study of nature precedes Aristotle, but he is famous for formalizing it as one of the four essential "causes" for all things in his *Organon*. Gould begins with Aristotle's own example, the construction of a house, which he tells us has been in continuous use for two thousand years. According to Aristotle, a house has a *material* cause, which are the bricks, boards, and nails that go into its construction. A house is based on a design or form, perhaps specified by a blueprint; this is the *formal* cause. While materials and blueprints are still essential for the production of a house, these are not considered "causes" today. The *effective* cause, in reference to an effector (a carpenter, plumber, electrician, etc.) corresponds most closely with what we consider a cause – the "how" or the "mechanism" – in the modern physical sense. Lastly, there is the *final* cause, which involves the motivation for the event or action in the first place – in this example, to provide shelter for its inhabitants. The final cause is associated with purpose, and thus addresses the question "why." Most of the Greeks, and apparently most human cultures throughout time, have associated formal causes (or something like them) to the inanimate world around them. Stones fall when released from a hand "because" they seek their proper place (Plato); lightening creates thunder not only as the physical result of "quenching" lightening, but also in order to threaten the souls in Tartarus (Pythagoras). This paradigm carried through well into the modern era. Louis Agassiz [TFS 7, BFB 21, and others], who discovered the existence of ice ages in the 1860's, offered both an efficient cause (the buildup and movement of glaciers in the northern regions) and a purpose or formal cause (to fertilize the soil in Europe and North America). A few decades earlier, William Buckland [HTHT 2, TFS 7] stated that the distribution of coal within the earth – with veins of these ancient sediments reaching the surface in some places – had, as its formal cause, the purpose of allowing their discovery and exploitation by God's favorite creation, man.

[One of the great "pedestal-smashing revolutions" in human thought has been the recognition that physical processes such as ice ages and plate tectonics (the latter now recognized as the "cause" of surface seams of coal) were not done "for" man's benefit. In DIH 25 and LMC 15, Gould discusses how this revolution has succeeded in the inanimate world, but has not conquered an important implication of Darwin's theory: that the origin of humans, and in particular of human consciousness is, itself, "purposeless" in the Aristotelian sense (although what humans have done with consciousness is not). In LMC 15, he discusses how this perspective led to the development of natural theology – also discussed in HTHT 2 and ELP 9 – which continues in part today in the guise of "intelligent design."]

Background complete, Gould now turns to James Hutton (1726 – 1797), who was born in Edinburgh, Scotland, and spent many years working as a "modern" farmer. He published the first version of his fundamental work in 1788, and expanded it into a book entitled *Theory of the Earth* in 1795. His theory, in keeping with the endlessly orbiting planets of Isaac Newton and the steam engines of his personal friend James Watt, was based on the view that earth was a perfect, cyclical machine. Each cycle of Hutton's planetary machine takes far longer than the 6000 years allocated by the recognized paradigm of the day to complete, and (he argued) there have been many cycles. Thus, he concluded, the earth must be very old indeed; this conclusion is often credited as the point at which the ancientness of the Earth, or "deep time," is formally discovered. Hutton ends his 1788 treatise, referring to the earth, with the famous sentence: "The result, therefore, of our present inquiry is, that we find no vestige of a beginning, – no prospect of an end." Unlike Aristotle, Hutton believed that the world *did* have a beginning and an end, but that these were non-natural events performed by God. His argument was that all the geological record showed was cyclical evidence of the functioning of "the machine" during the period in between these two events, with no apparent "winding down." [Gould discusses the metaphors of linear and cyclical geologic time through history, including Hutton's work, in his 1987 book *Time's Arrow, Time's Cycle*. He discusses the common and important misunderstanding that Hutton was claiming an eternal earth – with implications about the necessity of God – in BFB 30.]

Like Watt's steam engines, Hutton's Earth has four phases: 1. Erosion, in which mountains are worn down and sediment carried to the sea; 2. Deposition, in which these sediments are deposited in layers; 3. Compaction, in which the layers are cemented into strata of solid rock; and then, completing the cycle, 4. Restoration, in which these strata are uplifted to form mountains. None of these concepts were new [see the previous essay]; but the fourth one was where the difficulty lay. What had inhibited this view previously was that no practical restoring force had been identified. This, in turn, made the concept of an ancient earth untenable; without a restoring force the earth could not be very old, as it still has mountains. Hutton argued that the source of the restoring force was heat ("internal fire") within the earth, which manifested itself not only in the form of volcanism, but in raising great areas of land as well. He argued, correctly, that granite and basalt were not sedimentary rocks (as many thought at the time), and used both their widespread presence and ability to punch through sedimentary strata to form "dykes" or igneous intrusions in support of his theory. An essential piece of evidence in support of his view that a restoring force exists is the "angular unconformity" (Gould reproduces the key figure from Hutton's 1795 treatise). In geology, an angular unconformity is a location where strata abut at an angle; in the key figure, strata that have been tilted nearly vertically are overlaid with horizontal strata. The mere visibility of these distorted strata show that a restoring (or uplifting) force must exist, and the unconformity demonstrates that the process has happened at least twice, and (Hutton argued) is therefore cyclical. (Today it is recognized that the "restoring force" is not, in most cases, based on a subterranean upwelling of magma, but instead due to heat-driven plate tectonics – see ESD 20). Once the existence of a restoring process – whatever its true nature – was established, Hutton's argument that the earth was much older than 6000 years (perhaps even millions of years old!), "deep time" became not only reasonable but essential to explain the geologic facts as they were now understood.

Gould then poses the question, did Hutton base his restoring mechanism on direct observation and modern scientific techniques? The common textbook answer is "yes," but Gould tells us that the reality is different. While Hutton did engage in a lot of fieldwork, Gould (referencing G. L. Davies) concludes that this was not the source of his theory. He bases this on Hutton's own writings, and from the fact that Hutton did not discover the key angular unconformity depicted in his treatise, nor incontrovertible examples of igneous intrusion, until well after he had publicly presented his theory! So how did he formulate his model? Hutton tells us himself, in his discussion of the "paradox of the soil." Soil, Hutton notes (again correctly), is derived from sand, which has in turn been eroded from mountains. Soil is necessary for supporting agriculture, and thus God's favorite creation (us). But without a restoring force, the soil along with the mountains would eventually all end up in the sea, extinguishing human life. God would not do such a thing, Hutton argues, so he concludes – based on this argument, rather than empirical evidence – that a restoring force *must exist* so that human life can be maintained. Returning to the restoring force, Gould quotes Hutton: "The end of nature in placing an internal fire or power of heat, and a force of irresistible expansion, in the body of this earth, is . . . to form thereof a mass of permanent land above the level of the ocean, for the purpose of maintaining plants and animals [and thus humans]." That is, Hutton proposed a mechanism based on a final cause (a purpose), not an effective cause, and then sought evidence in support of it. The fact that he found it makes this a "fruitful error," in Gould's terminology. Gould does not defend Hutton's approach, even with its fruitful error, and in fact places Hutton in the pre-scientific camp of the "world makers" [ESD 18 & 19, and BFB 25] that Charles Lyell would later cast out. [He does note in BFB 30, however, that Hutton – unlike the other world makers – recognized that the study of the earth's *origin* was outside the scope of any testable hypothesis that he could propose.] He reiterates his oft-stated argument that it is important to understand scientists in the context of their times and knowledge base, as opposed to holding them up as (false) examples of early modern thinking.

HTHT 7. The Stinkstones of Oeningen

This is a biographical sketch of Georges Cuvier (1769 – 1832), a key player in the history of science who falls in between the generations of Hutton and of Darwin. He is known as the father of both paleontology and comparative anatomy, and is credited with proving that extinctions do, in fact, occur in natural history. Despite these accomplishments, Gould notes that Cuvier is not known widely today, despite the same breadth of knowledge and fame in his own day as Darwin. Those who have heard of him, usually from textbooks, know him mostly for being on the "wrong side" of two of the great debates of his era. First, in geology, he believed that catastrophes [which he called "revolutions"] played a major part in earth's natural history (which he helped prove was very long), losing the intellectual battle to Charles Lyell and his "uniformitarianism" [see ESD 18]. Second, in biology, he believed in "the fixity of species," rather than their evolution from one into another. As a result, he has often been associated with the "religious right" of his day, supporting Noah's flood over empirical data. The implied moral lesson, Gould states, is that Cuvier "failed" because he allowed prejudice to cloud objective truth. In fact, Gould continues, quite the opposite was true – Cuvier was a true empiricist, and was led to his views based on what he observed. He opposed "system builders" or "world-makers," of whom he considered Hutton to be one (accurately; see the previous essay), and searched for empirical tools to study earth's history. [He also placed his senior colleague Lamarck into this category; see LSM 6.] Further, Gould tells us, he used the doctrines of creationism and catastrophism as fruitful research strategies, not as pre-ordained conclusions. [One of Gould's recurring themes in these essays is that science does not, contrary to popular belief, advance in a straight line.] This essay is Gould's attempt at restoring Cuvier's reputation as a true and great scientist, with many lasting contributions.

Fascinated with geology and natural history, Cuvier addressed the problem of determining the relative ages of strata on a global scale. Steno [HTHT 5] showed that lower strata were older and higher strata were younger, but how does one compare the relative ages of strata in, say, England and Switzerland? The rocks themselves are only of limited utility here, since one band of shale or limestone looks pretty much like another. The debate on the origin of fossils (in the modern sense of the word) had been settled in favor of the remains of formerly living organisms for a century or more. Cuvier's thought was to use the unique fossils that appeared to exist in each layer of sedimentary strata for this purpose; this is exactly how the process works today. But this approach required a fundamental assumption: that the creatures leaving the fossils lived for only a finite period of time. Only if this were true could the fossils be used to correlate the deposition of one strata with another some extended distance away. But this, in turn, required two additional assumptions. First, new species had to come into existence at different times, as opposed to "all at once, at the beginning." Second, each of these species had to become extinct at some later time. These were highly controversial points within scientific circles at the time, not to mention in society at large. If new species continually arose, what was their origin? And if extinctions occurred, what did that say about the perfection of God's Creation?

Cuvier essentially proved both the reality, if not the mechanisms, of ongoing species formation and extinction, by employing a two-pronged approach. First, he carefully noted the stratigraphic location of the fossils he collected, and urged others to do so as well (prior to this no one had thought to bother). He identified virtually all of the essential questions: Do different fossils always appear in the same chronological order? Do certain types of fossils disappear and then reappear later? Which species overlap in time with each other? This line of questioning, and the answers he helped discover, laid the foundation for the science of paleontology.

His second line of attack was to address the problem of the fragmentary nature of the fossil record. Often, especially in the case of vertebrates (his specialty), only a few teeth or bone fragments were found. His ambitious solution was to study modern vertebrates – unambiguously complete – in such detail that he and his colleagues could eventually recognize and identify a species of (say) antelope from a single bone. This involved studying many examples of each animal, in order to understand what was within the range of variation for each species and what was outside of it. This led to the foundation of the science of comparative anatomy, a widely-used and powerful tool today. (Cuvier hoped to find "laws" or "principles" by which to predict what missing parts of an unknown animal must have looked like from known parts, but did not succeed. Today, other than in the most general sense – grinding teeth are associated with herbivores, and so are unlikely to be associated with features of carnivores – it is accepted that such laws do not exist. But as a "match to type" empirical approach, it works well.)

With the foundation based on living vertebrates in place, Cuvier applied his techniques to fossils. In an famous early example, he showed not only that Indian elephants and African elephants were different species, but that the similar-looking jawbones found in Europe belonged to neither living group, and therefore were not (as had been argued) remains of the elephants that Hannibal had taken across the Alps. (These animals are today recognized as mastodons.) This careful attention to detail also showed that many other fossils of Europe (and, later, North America), including the famous Irish Elk [ESD 9], were different from any living animals, thus effectively proving that extinction was a fact. [Interestingly, there is no reference to the dodo, known to be extinct on the only island it was ever found on more than a century earlier – see LMC 12.] He also carefully examined multi-thousand-year-old mummified ibises brought back by Napoleon from Egypt, and found them to be effectively identical to modern ibises. [His motivation was to demonstrate that evolution did not occur. While ultimately unsuccessful in this goal, his work did demonstrate in a more quantitative way than Hutton the existence of "deep time." If species remained unchanged for thousands of years, and the fossil record held thousands of such changes, then the earth must indeed be ancient.] His great four-volume work, *Recherches sur les ossemens fossiles* (*Studies on fossil bones*), published in 1812, is a long argument that fossils represent lost worlds of extinct species. With the concept of extinction validated, fossils could be used to date the relative ages of strata worldwide, allowing terms such as "Cambrian" and "Jurassic" to have global meaning. Cuvier's approach quickly showed that, the farther back in time one looks, the more different from today the organisms appears to be; life has a history and a direction.

Cuvier apparently considered and rejected the concept of evolution as the source of new species, based both on an absence of intermediate species (an area of concern to Darwin as well, and one he spent much effort discussing in *Origin of Species*), and on his observation that each component of a skeleton was inderdependent on the others. He concluded that changing one bone would disrupt the functions of the others, and found it implausible that all of the bones in a species could evolve coherently simultaneously. Gould notes that, while incorrect, he was actually being more of an empiricist than Darwin; evolution, after all, requires a certain kind of faith, since we cannot observe the process directly. Cuvier certainly believed in an ancient earth, and he did not claim to know the mechanism (divine or secular) by which newly created species were formed.

The second "blemish" on Cuvier's reputation came from his belief that catastrophic events had played the primary role in the formation and extinction of species, and in the geological record. Again, a quick glance at (say) the Grand Canyon shows distinct bands of strata, rather than a more gradual "morphing" of one type of rock into another. Based on the empirical evidence available of the time, a succession of large-scale if not global catastrophes seem apparent. The problem Cuvier experienced, in the form of Charles Lyell's uniformitarianism, is that there were dozens of "kooky" catastrophic models receiving lots of attention in the scientific and popular media of the day [see, for example, BFB 25, and ESD 17-20]. (Uniformitarianism allows for earthquakes and volcanoes, but not, say, sudden changes in earth's axis of rotation.) Cuvier does argue for the reality and global nature of Noah's flood as the most recent of many "revolutions," but bases this on stories from many cultures (not just the Bible), and from deposits that his student, Louis Agassiz [next essay], would later prove to be the result of ice age glacial activity. Cuvier was (unfairly, according to Gould) lumped in with the "world-maker" crowd, along with anyone else who argued for major earth-transforming events that no human had ever observed. [Gould argues elsewhere that Lyell's victory was so complete that there was no serious role for large-scale disruptive events in geology until evidence arose in the 1980's that an asteroid impact had wiped out much of life on earth, including the dinosaurs. However, he also acknowledges that some of the inference that Lyell and Darwin draw on is necessary, and sides with them in most cases.]

Gould's closing argument that Cuvier was not a dogmatic, unobservant reactionary, but rather a forward-looking, modern man of science who ended up on the wrong side of two debates, is as follows. He always looks to the closing paragraphs of important works to assess the purpose of the author. Authors writing in what Gould calls "the pontifical mode" close with words about "what it all means" for man and morality. In contrast to this, Cuvier closes with a ten-page list of areas for future study in the field of fossils in strata, drawing on his empirical experiences. One of these is the determination of the actual location of the Oeningen stinkstone shale, which he had heard contained numerous vertebrate fossils, thus giving the essay its title. [Oeningen, pronounced "Wengen," is on the Rhine on the German-Swiss border.]

HTHT 8. Agassiz in the Galapagos

Louis Agassiz (1807-1873) was a Swiss-born zoologist and geologist (studying under Cuvier, among others) who became the greatest American naturalist of the 19th century. His contributions were broad indeed, from fossil fish, echinoderms, and mollusks, to discovering the existence of ice ages in earth's history. He was as adept at fundraising as he was at lecturing to both students and the public, and Gould tells us that this essay was written in the museum that he had built, Harvard's famous Museum of Comparative Zoology. He is widely credited as establishing natural history as a professional discipline in the United States. Still, for all of this, he is remembered as much for being the last great intellectual holdout to Darwin's theory of evolution, and to evolution in general. Agassiz believed that "the history of life reflects a preordained, divine plan, and that species are the (created) incarnations of ideas in God's mind" (Gould's words) to the end of his days.

Thus, Gould tells us how surprised he was to learn that, late in life, Agassiz retraced much of Darwin's *Beagle* voyage, complete with a week's stay in the Galapagos Islands. (Gould tells us this while recalling his own visit there, and the essay contains several interesting "travelogue" moments.) Gould reiterates the significance of the Galapagos Islands – first and foremost, they are geologically very young (the oldest being about 5 million years). Yet not only are they home to species that live nowhere else, but their nearest relatives live in South America. This is in turn critical because, even though the latitude is the same, the climates are very different. Despite its equatorial location, the Galapagos Island climate is effectively temperate, due to the prevailing cool ocean currents. South America, on the other hand, is anything but. Yet the plants and animals are clearly related. If creation occurs, whether due to divine or secular mechanisms, then why are the Galapagos flora and fauna so similar to their continental cousins? Why are they not more optimized for their environment? Agassiz apparently never published any writings about his voyage, although he did publish on several other topics between the time of his return and his death. To learn more about what he thought of the trip, Gould went to the Houghton Library at Harvard (containing Agassiz's papers and letters) to read the great man's actual words.

In an unpublished letter to Benjamin Peirce, his colleague who helped set up the voyage on the small scientific vessel *Hassler*, Gould finds that Agassiz's motivation was specifically to retrace Darwin's steps, with the (admittedly difficult, by then) goal of disproving his conclusions. Consistent with the views he held his entire life, he wrote "If there is, as I believe to be the case, a plan according to which . . . the order of [animals'] succession in time were determined from the beginning, . . . if this world of ours is the work of intelligence. . . then the human mind . . . should so chime with it." That is, Agassiz was not having doubts in his old age. Despite the poor accommodations for him and his wife, who joined him on the voyage, and being ill much of the trip, Agassiz clearly had a most enjoyable time examining the evidence for large-scale glaciations in southern South America. As to the Galapagos, however, Gould tells us that he wrote very little of it, despite visiting five of the volcanic islands (Darwin himself visited only four). The only record Gould could find of the visit itself comes from a letter written while still at sea. Gould quotes the entire passage, which takes less than a page. In it, Agassiz marvels at the geologic youth of the islands, and the unique animals that live there, even commenting on how recent these new species must be to the earth. The sole argument presented in this letter is that the islands are too young for evolution, as it was then understood, to have created these new species. (Gould counters that Agassiz was referring to the youngest islands, while the creatures in question lived on older ones. He also notes that Agassiz seems to have missed Darwin's point that the animals most closely resembled South American fauna, with a very different climate and geology.) In the end, Gould remains puzzled by Agassiz's silence on his time in the Galapagos. He concludes that Agassiz wrote little about the place because it did not really make an impression on him; his mind was closed to the subject, so he did not see the same nuances that Darwin was more receptive to. [In TFS 23, Gould does point out that Darwin himself missed most of the significance of the Galapagos while there; it was not until he returned to England and showed his specimens to experts that the true significance became apparent to him.]

Gould closes by noting that we have lost something with the passing of Agassiz's world view, with its comfort in the belief that "there is a plan" with humans playing the central role, even if we cannot understand it. (Gould quotes Agassiz: "If it had been otherwise, there would be nothing but despair.") What we have gained in its place, he writes, is a satisfactory and general theory of life's history. Gould feels that the trade to be worth it, at least to him. [Gould returns to Agassiz's view of life in BFB 21.]

HTHT 9. Worm for a Century, and All Seasons

This essay first appeared in the April 1982 issue of *Natural History*, approximately on the 100th anniversary of Charles Darwin's death. It represents Gould's personal tribute to the man, he tells us. Rather than discuss what he is best known for, Gould instead discusses one of Darwin's least known works, and offers his thoughts on its true significance.

Besides writing on "big picture" topics such as the origin of species and the decent of man, Darwin wrote books on what appear to be narrow, highly specialized topics: coral reefs, barnacles, and orchids to name three. His final book was on earthworms, and is entitled *The Formation of Vegetable Mould, Through the Action of Worms, With Observations on Their Habits* (1881). (The term "vegetable mould" in this case refers to the top few inches of topsoil.) In the past, Gould tells us, some critics of Darwin have used these books – or at least their titles – to argue that Darwin was not really a great thinker, but instead a rather dim-witted dilettante who stumbled across something that was already in the air. The actual text of these books, however, tells a different story, if one reads carefully.

In his worm book, Darwin argues that the slow and steady action of earthworms, acting over millennia, is responsible for the existence of soil as we know it. Their actions also shape the landscape into the low, rolling hills that tend to exist wherever worms are found in quantity. The topic is closer to geology than it is to evolution; Darwin, Gould tells us, is essentially applying Lyell's geological uniformitarianism to a biological system: slow but continuous effort over vast stretches of time can yield spectacular results, without having to call on unprecedented or supernatural forces. Darwin goes into great detail in discussing two major functions that worms perform, relative to soil and landscape. The first is that, by passing coarse soil through their digestive tract, the rocky components are ground into ever finer particles, which are more easily moved downhill (thus smoothing the terrain). When combined with decaying organic material, the result is the formation of soil ("vegetable mold"). The second stems from the fact that the processing of soil is an ongoing, repetitive process. The "topsoil" in an area does not get thicker over the centuries, but instead constantly "churns," slowly leveling the landscape further. Darwin presents detailed evidence to show that the quantity of worms in soil is sufficient to perform this task. Next, in support of his soil-churning argument, he shows how large stones "sink" into the ground over long but measurable amounts of time (about 2.5 inches over three decades, in the case of one of his own fields).

At one level, Gould tells us, Darwin's last book is just what it appears to be – a discussion of the behavior and geological impact of a moderately complex invertebrate. But it is also something else; it is a practical example of how to do science in a field in which a chronological sequence of events – that is, history – matters. Physics and chemistry can advance by doing controlled, repeatable experiments. But the “historical” sciences – evolutionary biology, geology, and cosmology, to name three – cannot do this. How are workers in these fields, on a day-in, day-out basis, to advance our understanding of “what happened” using scientific principles? The answer is to find ways to analytically study small but measurable details in nature, and to compare the results to a larger model. What Darwin was actually doing in this book, Gould claims, was presenting a long but specific example of one such technique. Further, he argues, his other “specialty” books offer other approaches, suitable for differing amounts of available information. Darwin’s worm book illustrates an approach to use when the process of interest – in this case, rocks sinking into worm-churned soil – are directly observable on a human timescale. (Obviously, one component is patience!) With careful observation and measurement, one can determine the rate at which the process occurs; one can then extrapolate directly, if with some uncertainty, to geological time scales. This is essentially what Charles Lyell did with his uniformitarian view of geology.

But what if the processes are so slow that they cannot be directly observed in a human lifetime? If the process is gradual but continuous, and occurs repeatedly with different start times, then a productive approach is to recognize that the present contains examples of the process at different points in the cycle. If one can develop an underlying model of the entire process, then one can arrange the “snapshots” in the correct order. Astronomers do this for stars; they recognize their formation, their various stages along the “main sequence,” and their deaths as supernovae or as something less spectacular. Interestingly, Gould notes, Darwin’s very first book – on coral reefs – also followed this approach. Published in 1842, he argued that fringing reefs that abut an island, barrier reefs that are separated from an island by a lagoon, and atolls, in which a reef structure encloses nothing but ocean, are three consecutive stages of the same thing: a volcanic island that slowly sinks into earth’s mantle under its own weight, while the coral continues to grow vertically to the surface. (This is recognized as true today.)

How does a scientist determine “what happened” if the process is slow, the intermediate stages are difficult to find, and the subject itself does not appear to change in any coherent direction? This was the problem Darwin faced with evolution itself, and he addressed it in a most clever way – by looking for what he called “contrivances.” These are structures that are not optimally designed for their present function, but were “jury-rigged” or pressed into service – often not very well – because they were the only parts available. Darwin also wrote a book (besides *Origin of Species*) using this technique: his 1862 treatise on the fertilization of orchids by insects. Orchids modify flower parts to resemble the bodies of distinct species of insects, in ways that no good designer would ever do if he could start from scratch. This, Darwin offers, is evidence that evolution occurred. (Gould uses this approach in several of his own essays, including *The Panda’s Thumb* [TPT 1]. In this essay, he references HTHT 1, 4, and 11 from this collection as additional examples.)

Did Darwin actually appreciate what he was doing with these books, Gould asks, or was he simply working intuitively, as many men of genius do? Gould uses the closing paragraphs of Darwin’s book on worms to suggest that he did explicitly recognize that he was working on general techniques to support the practical advancement of historical sciences.

HTHT 10. A Hearing for Vavilov

Nikolai Vavilov was one of the Soviet Union's leading Mendelian geneticist in the 1920's and 30's, and became the director of the prestigious All-Union Lenin Academy of Agricultural Sciences in Leningrad. Agriculture was a top priority in Stalin's state, as food was badly needed. Vavilov traveled all over Europe and Asia collecting species and varieties of wheat and other cereal crops, and worked in a professional scientific capacity to understand the genetic and manifest nature of these crops. He found what he believed to be an underlying principle in the nature of variations across species, which he called *the law of homologous series within variation*. It was first published in the Soviet Union in 1920 (and revised in 1937); he also published a paper in English in the prestigious *Journal of Genetics* in 1922. But in the Soviet Union, even science became highly politicized. Vavilov came under attack from the infamous Trofim Lysenko in 1936. Lysenko, also a scientist, attacked Vavilov on the grounds that his law was neither "dialectal" nor "materialistic" – effectively a charge of heresy in Stalin's world. Vavilov's wide travels and English-language publication also allowed him to be tarred as a spy. He was arrested in 1940 and sent to a gulag, where he died in 1943. Lysenko's career continued under Stalin, where he promoted a quasi-Lamarckian, quasi-Marxist (and unsuccessful) agricultural theory that assumed plants could be "trained" to provide higher yields. While Vavilov became a scientific martyr in the West, intellectually he did not fare much better there; his work was quietly ignored.

Gould next proceeds to tell us what Vavilov's law of homologous series was about. In examining different species of cereal in Russia, Iran, and Afghanistan, he discovered that certain very specific variations popped up in each, such as colors of the seeds, forms of the ears (bearded or unbearded, smooth or hairy), and season of maturation. In the West, where the modern evolutionary synthesis was taking shape, these results would have been interpreted in terms of the power of natural selection to shape different sets of genes to form virtually identical structures or behaviors. That is, the similarity of variations in different species would have been interpreted as analogies, or examples of convergence [TPT 24]. Vavilov, however, proposed similar but nonetheless distinct interpretation. In his view, only certain genes changed as (say) wheat and rye descended from a common ancestor, while most – including those that coded for the recurring variations across species and genuses – remained the same. Thus, he argued, the variations appeared the same because the genes themselves were, for the most part, the same. The variations in question represented *homologies* in Vavilov's theory, rather than analogies; hence the name of his "law." This perspective is consistent with Darwin's theory, since natural selection is still responsible for controlling which variations appeared in which environments. However, it violates the spirit of the "strict Darwinism" associated with the modern synthesis, which argues that natural selection is, at least in practice, the dominant if not exclusive creative mechanism in evolution. In Vavilov's model, the underlying (and unchanging) genes place constraints on the evolutionary pathways that control, and even dominate, the macroscopic forms and behaviors that result.

Excited by his idea, Gould continues, Vavilov overreached. He essentially concluded that there were only a moderate number of genes in existence, that they did not change readily, and that different species largely represented different combinations of the same set. His view was that these genes were analogous to chemical elements, and he professed the hope that genetics could be reduced to something akin to chemistry or crystallography. He backed away from this extreme as it became apparent that genes were both numerous and highly variable, and that many of the variants he used as examples did not have identical genes after all. (In other words, some of Vavilov's homologies turned out to be analogies.) Gould quotes a passage from his 1937 paper in which he acknowledges that natural selection plays a larger role than he had previously allowed. Nonetheless, he defended a milder version of his law of homologous series until his arrest. This included an argument that species can and sometimes do differentiate genetically *before* they differentiate in outward appearance or behavior, which again differs from the modern synthesis view. [Gould discusses "chromosomal speciation" again in HTHT 26.]

Gould is not finished. In a revealing coda to this tale, he writes: "Yet I feel that in his imperfect way Vavilov had glimpsed something important. . . . I have found [his] views very helpful in reorienting my own thinking in directions I regard as more fruitful than my previous unquestioned conviction that selection manufactures almost every evolutionary change." For the first time in these essays, Gould introduces his argument that the modern synthesis itself has overreached, in its neglect of non-adaptive mechanisms in evolution. [He and Richard Lewontin had injected these views into the professional community in 1979, with their presentation entitled "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme."] He discusses two examples here. The first involves a scaling law that empirically shows that brain mass grows at one-fifth to two-fifths the rate of body mass for a certain subset of mammals. [Gould discusses the more general mouse-to-elephant curve in TPT 22.] It had always been assumed, he states, that this law represented some optimal state that was controlled by natural selection. He then discusses recent studies in which mice were bred for body size alone; despite the absence of selection for brain size, the scaling law held. This suggests that the law is *not* adaptive, but rather a "hardwired" trait of mammalian development; if true, it would loosely represent a homologous series in Vavilov's sense. The second example involves his own area of research, land snails in the genus *Cerion*. Over and over, he would find that the shells of those snails that lived on steep terrain near rough seas were strongly ribbed, and also had a number of other distinct characteristics. Those living on gentle slopes near bays or lagoons, on the other hand, almost always had smooth shells, and a different unique set of characteristics. At first he assumed that all ribbed snails were descended from one group and the smooth snails another; but differences in many other details quickly showed that this was not the case. Instead, it appeared that the same sets of adaptations had arisen again and again in different lineages. Gould apparently tried but failed to convince himself that natural selection alone produced the same set of distinctive adaptations over and over. It was far more likely, he concluded, that all of the snails were constrained by the inherited pathways of their history (as manifested in their genes) to respond to their local environments, in most cases, with only the distinct set of variations that were available to them. [HTHT 28 presents another example.] Gould closes by stating his position that external (adaptive) and internal (largely non-adaptive) constraint forces both play essential roles in directing evolutionary change. [Gould continues this theme in the next several essays, in BFB 7-9, and elsewhere.]

HTHT 11. Hyena Myths and Realities

This essay is about the genitalia of the spotted, or laughing, hyena, one of three species in the genus. Hyenas have been described in disdainful terms by naturalists for millennia, for a variety reasons (most undeserved). Gould discusses some of the more prominent criticisms, along with a few defenses. Some of the recurring charges against the spotted hyena are that it is hermaphroditic. This is false, but the claims stem from the apparent similarity of the male and female sex organs. The female spotted hyena's clitoris is as large as the male's penis, and there is a well-developed scrotum (albeit without testicles) as well; illustrations are presented. The adaptationist-oriented biologist asks, what purpose is served by this unusual structure? The implicit assumption is that it must provide the individuals with some evolutionary advantage. Gould references the work of Hans Kruuck and his book, *The Spotted Hyena* (1982). Kruuck discusses many aspects of the animal, dispelling many of the myths, and then states his case that the cause of the female's unusual anatomy is the hyena's "meeting ritual." When spotted hyenas of the same tribe – male or female – are hunting or traveling alone but run into one another, they exhibit a unique formalized behavior. Standing parallel but facing opposite directions, each raises a leg (the less dominant one first) and they expose their genitals to the other's mouth – and teeth. After some sniffing and licking, the hyenas proceed on their way. Kruuck argues that the female's ability to participate equally in this meeting ritual might offer the appropriate advantage to the force of natural selection, which would amplify it over hundreds of generations.

Kruuck, like most biologists (Gould states), is willing to leave cause and effect at that: the male-like appearance of the female's genitalia is an adaptation to the hyena's meeting ritual. But Gould cannot [see the previous essay]. He counters: is "why" really the right question to ask? Should we not investigate the question of "how is it produced" a bit more first, to see if something can be gleaned there? In fact there is. He references the work of Racey and Skinner, who found that the female spotted hyenas (but not brown or striped hyenas) have a higher level of male hormones present in their bloodstream at all stages of life, including as an embryo. Gould informs us that in mammal embryos, it is several weeks before the proto-sex organs differentiate into male or female. Male hormones, if present in quantity at this developmental stage, cause the embryonic genitalia to become male; without them, female sex organs develop. The above-average level of male hormone in female spotted hyenas can, by itself, lead directly to the observed result; the clitoris grows to resemble a penis, while the labia majora descend, fuse, and form a quasi-scrotum. Gould suspects that Kruuck may be confusing cause and effect. It is certainly possible that the meeting-ritual-induced behavior led to the selection of female spotted hyenas with higher male hormone levels. However, he thinks it is more likely that higher hormone levels, probably produced by a small change in a regulatory gene, led directly to the oversized female genitalia. The hypothetical hormone change could have been an adaptation to something other than producing male-like sex organs in the female, or it could have been the result of chance. In either of these cases, the unusual genitalia would be a non-adaptive "side effect" that was later co-opted for the meeting ritual.

HTHT 12. Kingdoms without Wheels

The invention of the wheel is often used as the prototypical example of progress in human history. In a reversal, Gould discusses a period in which wheeled carts were replaced by pack animals. The time was the centuries following the fall of Rome, and the animal was the camel; he references *The Camel and the Wheel* by Richard W. Bulliet, 1975. The reasons are all quite sensible, considering the local conditions: the roads are in disrepair, camels cross water well, one man can control more camels than draft animals, and so on. Gould uses Bulliet's observations to illustrate one of Darwin's key points about his theory: evolution is not about "progress," but about adaptation to the local environment.

Nonetheless, camels aside, wheels are clearly "better" than legs in many situations. Why, then, do we not find wheels in nature? The problem, of course, is not with the wheel, but with the living organisms that would have to implement it. Wheels by their nature must be able to turn freely about an axle without having to "rewind." This precludes passing blood vessels, nerves, muscles, and connective tissue that we generally associate with life to rotating extremities or organs. Gould's point is that natural selection is not so powerful a force as to be able to create wheels out of organic components, no matter how superior they would be; evolution is *constrained* by internal biology. This is another gentle poke at adaptationism.

Once the rule of "no wheels in nature" is established, Gould sets out to "prove" (that is, test) it by discussing an exception! He refers to two sets of researchers (Berg et al., and Larson et al.) who have studied rotational motion in *E. coli*, the famous bacteria. *E. coli's* flagellum (plural, flagella) is a stiff fiber that is attached via some interesting architecture to the cell body. The traditional understanding of how the bacterium uses its flagellum to propel it through its environment is that it whips it ("flagellates" it) back and forth, like a tadpole's tale. However, the effective viscosity of water on an object as small as *E. coli* is very high ("like asphalt"), and this approach would prove ineffective. The researchers found other features of the actual motion that could not be explained by a flagellating mechanism. They were able to determine was that the flagellum actually rotates, acting like a propeller. It can also reverse direction. This does not make it go backwards, but instead changes the orientation (and thus direction, once forward motion resumes), albeit essentially randomly. The trick that makes this possible (and hence "proves" the general nature of the rule) is that the organism is so small that nutrients can pass across the rotating interface by diffusion. This can only work at small scales, since the boundary area is proportional to the square of the dimension of the organism, while the volume requiring nutrients scales with the cube of this dimension. (This effect is also responsible for the difficulty *E. coli* has in moving through water.)

HTHT 13. What Happens to Bodies if Genes Act for Themselves?

This essay is more technical than most. This is because the overall topic is of great interest to the evolutionary community, and because the essential evidence is in the details. The underlying question is whether Darwin – and the modern evolutionary synthesis – are correct in their presumption that natural selection works only on individual organisms, or whether it can also act at the level above (groups or species) and/or below (genes). The essay was stimulated by two papers published in the journal *Nature* in 1980, one of which was co-authored by Francis Crick, the co-discoverer of the structure of DNA. These papers argue in favor of what Crick calls "selfish DNA" (not to be confused with the "selfish gene" concept of Richard Dawkins, discussed in TPT 8), which is a detailed argument for natural selection – and thus evolution – operating directly on certain types of genes. In an interesting parenthetical statement in the middle of this essay, Gould writes: "I confess to what evolutionists call a 'preadaptation' for favorable response to the selfish DNA hypothesis. I have long argued that species must be viewed as true evolutionary units and that macroevolutionary trends are often powered by a 'species selection' that is analogous to, but not identical with, natural selection acting upon bodies." [Few of his essays discuss his "hierarchical evolution" views explicitly, but see TPT 18 and DIH 26. However, it is at the heart of several of his professional papers, and in his final technical work, *The Structure of Evolutionary Theory* (2002).]

Scientists knew about the concept of "genes" since 1900, but little of the mechanism was understood until Crick and Watson determined the molecular structure of DNA in 1953 – a double helix, with matching, separable base pairs connecting them that could also code for proteins, via RNA. It was at first assumed – or at least hoped – that the genes would simply be contiguous chunks of DNA, connected together end to end on chromosomes like "beads on a string." While this view is partially applicable to many kinds of prokaryotes, the DNA in eukaryotic cells – including humans – turns out to be far more complex. For one thing, it was discovered that only one to two percent of human DNA actually makes proteins. Second, it was quickly noticed that fifteen to thirty percent of both fruit fly and human genomes were composed of "middle-repetitive DNA"; these are moderately long, virtually identical sequences that appear a few tens to a few hundreds of times, scattered apparently randomly across different chromosomes throughout the genome.

The standard adaptationist or "strict Darwinist" approach to the puzzle of so much middle-repetitive DNA is to begin by assuming that it must offer the host organism some competitive advantage, and then to look around for what that advantage might be. (Gould acknowledges that this general approach is often fruitful.) Adaptationist hypotheses generally fall into two classes, he states. The first of these, which he refers to as *retrospective significance*, argues that copies of essential genes allow natural selection to create new genes from the copies, without simultaneously destroying the essential functionality of the original. Gould agrees that this happens, and references a 1970 book by Susumu Ohno on the subject; but this is not a selective adaptation. He explains: natural selection, by definition, can only act on variations that offer an immediate advantage to the host. Natural selection may help reptiles with proto-feathers survive, but only because it offers some near-term advantage, such as thermal insulation. Darwin's mechanism cannot favor proto-feathers because, someday, they might evolve into something that can support flight; it cannot see the future. However, *once in existence*, natural selection could modify feathers to support a different function. (He references a technical paper he and a colleague wrote on the difference between an adaptation, which is immediately subject to the forces of natural selection, and what he refers to as an *exaptation*, which is a structure that arose for another reason, or for no reason at all, but becomes available for evolutionary exploitation. He discusses this further in ELP 22.) In the case of repetitive DNA, he argues, the potential for a copy of a gene to evolve in such a way as to support a new and advantageous capability *in the future* cannot serve as a selective advantage in the copying of a gene *today*. Therefore, even if the process occurs, it is not *adaptive*, and thus cannot be considered as a "reason" for the existence of middle-repetitive DNA.

A second class of arguments, exemplified in a 1971 article by Britten and Davidson, proposes that the copies do provide some immediate advantage to the host. This could be by bring two genes which are normally separated together, leading to new and possibly advantageous interactions. It is also possible, they argue, that some of the DNA represent "regulatory genes" (a concept then in its infancy), which produce no proteins themselves, but control the timing and activation sequence of those genes that do. But the problems remain that there is *so much* repetitive DNA, and that it appears to be distributed so randomly; it seems unimaginable that these processes could explain all of the observed genetic behavior.

If conventional adaptationist arguments cannot explain the existence of so much middle-repetitive DNA, are there any unconventional arguments that can? This is where the *Nature* paper on "selfish DNA" by Leslie Orgel and Francis Crick, along with a companion paper by Doolittle and Sapienza, enter Gould's narrative. Their argument – both simple and subtly revolutionary – is that the repetitive DNA sequences offer no advantage to the host organism at all, but simply form multiple copies because they can, and because there is no "penalty" for doing so. If one considers the materialistic essence of natural selection to be that those variations that leave more copies of themselves will eventually come to dominate an ecosystem, then we can argue that the repetitive DNA sequences may be doing something analogous – but at a different "level." (Both papers discuss the limit of this – if millions or billions of copies are made, rather than tens or hundreds, there will be a negative selective effect on the organism as a whole, leading to its demise. This implies that there is some degree of interaction between the different levels, complicating things further.) If there are not too many copies of the repetitive DNA sequences, then the host simply does not "see" them (although they may be available for modification later), and thus those nuclei with extra genes are neither selected for nor against. They are effectively *neutral* at the level of the organism. [The neutralist theory of molecular evolution was first proposed by Kimura in the 1960's; see ELP 28.] Gould states his dislike for the term "selfish" in this case, as it implies a bias for the adaptationist perspective that all DNA "ought" to be doing something to support the overall organism. He offers the less-pejorative "self-centered DNA," in an attempt to suggest that genes have the same "right" to try to multiply themselves as individuals.

Another reason that Gould dislikes the term "selfish DNA" is because it is so readily confused with "the selfish gene" concept, presented by Richard Dawkins in his 1976 book of the same name. This is an entirely different, and in many ways opposite, concept that Gould unfavorably critiqued in TPT 8. Dawkins, Gould states, is the ultimate strict Darwinist. Rather than believing that natural selection can work at multiple levels, he believes (like other strict Darwinists) that there is only one level at which it can act; but he goes further than most by proposing that this level is the gene *rather than* the individual. This, Gould tells us, is based on Dawkins' reductionist views that genes, or collections of genes, map linearly to individual features in the organism, and that these can be individually and separately optimized by natural selection. If this were true, then (Gould agrees) the individual is nothing but the genome made manifest, and selection at the genetic level becomes *synonymous* to selection at the organism level; thus, a step can be skipped by going to the genetic level directly. Gould reiterates his support for the belief that natural selection – or something analogous to it – is functioning at multiple levels. He emphasizes his continued support for the conventional role of natural selection at the level of the individual.

HTHT 14. Hen's Teeth and Horse's Toes

One of the early victories in the struggle for the acceptance of evolution in the 1860's was the discovery of fossil horse bones that indicated a transition, over millions of years, from four-toed browsers to the single-toed grazers we know today. [Oddly, this turned out to be a largely false impression; see BFB 11 and LMC 7]. Nonetheless, throughout recorded history, there have been horses born with more than one toe on each foot; Gould discusses a case involving Julius Caesar. In the new, evolutionary interpretation, such animals were identified as *atavisms*, a word literally meaning ancestor; the interpretation was that these horses were "throwbacks" to an earlier state. The Victorian view of atavisms was rather negative, Gould tells us. In part, this stemmed from the (false) view that evolution implies progress; atavisms were regarded as less advanced. In the metaphysical sense, their very existence suggested that an organism's primitive past lurked right below the surface, "holding it back" either metaphorically or literally. In this essay, Gould argues – based on where the field of genetics stood as of the date it was written – that atavisms should be used as examples of the potential that organisms can draw on for *future* evolution. He uses atavisms to put forth the case that macroevolution need not proceed exclusively via a series of infinitesimal microevolutionary steps; sometimes, slight changes in the timing of certain genetically-controlled developmental processes can produce significantly different – that is, *discontinuous* – macroscopic structures, which can then be tweaked further over many generations by the more conventional selective process [see the next essay, and TFS 24].

Genes, Gould reminds us, do not code directly for body parts such as toes. Some genes are used as templates to make proteins. However, as had been discovered in the decade or so prior to this essay, there are apparently genes that do not make anything themselves, but appear to regulate the timing and other attributes of the functional genes. Further, there appears to be a hierarchy of these regulatory genes. There are some subtle but important implications of this revised perspective on the connection between genetics and evolution. The first is that an organism's genome almost certainly contains more information than is actually expressed in the "production" of that organism. In the case of horses, Gould argues that at least some of the genetic information to produce multiple toes remains in the horse genome, even though it is not used. This is quite different than the earlier perspective that the genome is "optimized" to produce that particular design, with natural selection actively weeding out non-advantageous genes. Second, this perspective implies that a change in a *single* higher-order regulatory gene can lead to a noticeably different, but still functional (at least in some cases) adult. This, again, differs from the earlier assumption that evolution requires *multiple* genes to change *simultaneously* (and thus slowly, over many generations) to produce a functioning macroscopic change such a modern horse with multiple toes. Gould continues that these sorts of genetic changes are not limited to producing features that are reminiscent of ancestors, but can also produce structures never seen before. In other words, the genetic mechanism behind an atavism is a potential source of macroscopic evolutionary change.

Gould was motivated to write this essay after reading a 1980 article in which the team of Kollar and Fisher managed to produce something close to "hen's teeth" via a manually-modified embryonic process. Archaeopteryx had teeth, but no bird has had any for at least sixty million years. The process of producing teeth is rather complex; it involves combining two layers of cells, and the proteins that each layer produces are required to stimulate the other. (That is, genes are not sufficient to produce teeth by themselves; there are further "downstream" interactions between the genetically-produced components that must also occur.) By combining one layer of cells from a chick embryo with another from a mouse embryo, the researchers were able to produce –in a few cases – rudimentary teeth. Since this process requires the chick layer of cells to produce certain proteins that have no utility in toothless chickens, the conclusion is that chickens contain at least some of the genes required to produce teeth, even though no ancestor of the chicken has done so for eons. This is another example of Gould's point that there is much more information in an organism's genome than was previously appreciated.

There is another important point in this discussion, one that Gould illustrates with a final example that also involves chickens. In 1959, French embryologist Armand Hampé used some lower-tech approaches to produce an atavistic bird leg. In humans and many other animals, the two bones of the lower leg – the thicker tibia and the thinner fibula – are of approximately the same length. This condition also holds in archaeopteryx. However, in all modern birds, the fibula has been reduced to a mere splint (like all but one of the modern horse's toes), and the tibia grows to fuse with both of the two main ankle bones during embryonic development. By physically preventing the tibia in the chick embryo from absorbing material from the fibula, Hampé was able to get the latter to grow to its full length. Further, the resulting fibula then formed a joint with the corresponding ankle bone, while the associated tibia formed a joint with its "own" ankle bone (rather than fusing with both of them). This clearly shows that genes do not control the entire developmental process; an ankle bone can change when a developing fibula interacts with it, with no change to the genome at all. This has important implications for how evolutionary change may actually occur.

HTHT 15. Helpful Monsters

A technique that can be used to gain insight into how genes "produce" an organism is to study the developmental consequences of damaging or destroying individual genes. This process has been performed on the fruit fly – which is noted for its relatively small genome (only four chromosomes), as well as its rapid rate of reproduction – since the 1930's. In this essay, Gould discusses some of the key "monstrous" manifestations that result from damage to two specific fruit fly gene complexes, and what it implies about regulatory genes in embryology. He generalizes to discuss the implications for macroevolution.

Fruit flies in particular, and insects (in fact, all arthropods) in general, start their embryological development as a series of repeated, largely similar segments. Each of these segments is capable of producing a pair of legs; a few are also capable of additionally producing a pair of wings. The first five segments fuse to form the fly's head; the "legs" are modified to produce antennae on the first segment, and mouth parts on the last three segments. We know this, Gould tells us, because damage to one particular part of the gene complex known as ANT-C will result in legs growing on the fly's head where antenna should be! (Mutations in which a structure is "replaced" during development by a related, more "basic" form of the same structure are called homeotic mutations. They differ from the atavisms discussed in the previous essay in the sense that no ancestral fruit fly ever had legs for antennae.) These legs are not functional; nerves and muscles do not form along with the leg structure. However, the fact that the deletion of single gene can result in an entire series of morphological changes in a developing organism provides important clues about how certain genes work. ANT-C is apparently, Gould tells us, a regulatory gene complex (composed of seven or more individual genes, each of which may be a slightly mutated copy of a single original gene). It does not "code" for proteins or other structures itself, but influences changes in other genes that do; in this case, when working properly, it directs (by unknown means) the basic "leg" structure to undergo the modifications required to make it an antenna instead, or a mouth part.

Gould discusses another regulatory gene complex, BX-C, which influences the thorax and abdomen of the insect (ANT-C also affects the thorax). Complete deletion of the BX-C complex results in no abdomen, but instead a "thorax" composed of many segments (not the normal three), each with a pair of legs. (This mutation is fatal to the insect; it dies in development.) Thus, again, the BX-C gene complex appears to modify a repetitive, default behavior into something that produces a unique structure; in this case, an abdomen comprised of ten fused segments, all without legs. Another, more specific modification yields a fruit fly with four wings – because the third thoracic segment, without wings, develops "as" a wing-producing second segment. Another important implication is that there must be another level of regulation above ANT-C and BX-C, to turn their effects on and off under the appropriate circumstances.

Homeotic mutations, Gould concludes, provide an important window for geneticists and embryologists to study the overlap of these two fields. But can they tell us anything about evolution? Possibly, he concludes, at a general level. Homeotic mutations suggest that the major transitions in evolutionary history may begin as small changes in a regulatory gene, rather than as gradual and coordinated changes to many genes simultaneously. However, he cautions, these mutations should not be considered as the "hopeful monsters" of the followers of Richard Goldschmidt. Goldschmidt argued [or was at least accused of arguing; see TPT 18] that new species could arise in more-or-less complete form in just a few generations. Gould points out that most homeotic mutations are fatal, and that even in the "successful" cases they could only function as instigators of macroscopic changes; the more conventional natural selection process would almost certainly have to refine the new organism for hundreds or thousands of generations before a stable, practical species resulted. Nonetheless, these findings do suggest that insects followed an evolutionary pathway from an organism with a larger number of more similar segments. This touches on Gould's argument that evolution is constrained by internal design to proceed along certain pathways. [He discusses the possible macroevolutionary impacts of small genetic changes in HTHT 11 and TFS 24.]

HTHT 16. The Piltdown Conspiracy

In TPT 10, "Piltdown Revisited," Gould tells the story of three men who "found" fossil evidence of a human ancestor in two quarries in Piltdown, England, between 1908 and 1915. The fossils turned out to be fraudulent. More embarrassing for the scientific community was that the hoax was not exposed until 1953, although some suspected from the start. Gould's earlier essay focused on how such obvious fakes could have fooled the majority of the scientific community for so long. In this essay, he turns to the "whodunit" question, and specifically to whether Pierre Teilhard de Chardin was a co-conspirator. Teilhard was one of the three men who "discovered" the fraudulent material, and he went on to later fame as a Jesuit priest, scientist, and author of several speculative books on Man's place in the universe [see HTHT 18]. He also participated in the legitimate and important discovery of Peking Man [now recognized as *Homo erectus*]. The leading figure of the three "discoverers" was a lawyer and amateur anthropologist named Charles Dawson; research by the discoverers of the fraud, K. P. Oakley and J. S. Weiner, concluded that Dawson (who had died) was almost certainly guilty. [Dawson turned out to have dozens of fakes in his personal collection, some of which were modified in the same way as the Piltdown material.] The third man was Arthur Smith Woodward, a curator at the London museum; all investigators (including Gould) believe him to be an innocent dupe. Gould mentions a few other names as potential co-conspirators, but thinks all of them unlikely. [He does not mention Martin Hinton, who worked at the London Museum during this period. A trunk belonging to Hinton was found in the museum in 1970 – more than ten years before Gould wrote this essay – which contained animal bones filed and stained in the same manner as the Piltdown material.]

The essay focuses on whether Teilhard was an active participant in the hoax, or whether he was also merely duped by Dawson. Gould's interest in this subject, he tells us, dates back to his reading in the newspaper – at age twelve – of the announcement of the fraud, and his fascination with the subject ever since. The announcement caused an uproar in the paleontological and anthropological communities, and Gould references several people that he looked up to (including Louis Leakey) who expressed their suspicions of Teilhard. Gould takes up the case in this essay, effectively acting as a prosecutor arguing to a jury (his readership) for Teilhard's guilt. The evidence is circumstantial, but Gould goes into great detail; he discusses a number of unpublished letters between Teilhard and Dawson that, depending on one's suspicions, suggest either guilt or exoneration.

Gould offers two major arguments, and a number of smaller ones. The first major argument is that, when asked about Dawson's role in the fraud some 40 years later by Oakley, Teilhard's responses included a number of inconsistencies. Gould argues that these reflect a guilty man not being able to keep his story straight; he acknowledges other, more innocent interpretations, but believes that none are plausible. His second line of attack is Teilhard's silence on the Piltdown material during his professional career. He wrote extensively about the Peking Man material and much else on the history of man. Gould also notes that Piltdown Man, if valid, would buttress his personal views of man's evolution moving in multiple, parallel lineages [HTHT 18]. Yet he writes almost nothing about it, ever. Gould again interprets this as a sign of guilt, although in the next essay he recognizes (but rejects) the hypothesis that Teilhard discovered Dawson's fraud, refused to participate, but kept his silence on the matter.

As to motivation, Gould acknowledges that he is at a loss; the best he can offer, he says, is that Teilhard's participation in the hoax started out as a practical joke that got out of hand. While he believes his case is solid, albeit circumstantial, Gould says that he is not out to "destroy" Teilhard. As he summarizes in the following essay, "I think he was a complex and fascinating man . . . . I really do forgive him if he did what I suspect. He was young; he did not act for profit, either monetary or personal; he suffered; he maintained steadfast and admirable loyalty to all involved; he made no excuses."

HTHT 17. A Reply to Critics

This essay is a significantly-edited version of Gould's June 1981 column in *Natural History*. The original column printed several of the many letters Gould received regarding the previous essay, and in particular the role of Teilhard's participation in the Piltdown hoax, along with Gould's replies. The harshest letters, he tells us, come from supporters of Teilhard's later writings. Some were merely expressing anger, but others raise important points and are worth responding to. These criticisms, Gould continues, come in two categories: those that interpret the existing evidence in a different light, and those that offer new evidence. In the first category are charges that Gould misinterpreted the meaning of some of the statements in Teilhard's letters that he claims are inconsistencies indicating guilt. He presents his counter-counterarguments. Next is the presentation of a previously unpublished letter from Dawson to Smith Woodward by none other than J. S. Weiner, one of the discoverers of the fraud and author of a 1955 book on the subject, at a meeting in 1981. Gould reproduces the contents of the letter in their entirety. Weiner himself argues that the letter undercuts Gould's argument regarding Teilhard's inconsistencies. The letter is short and fairly general, and Gould states that it does not undercut his argument at all. Others suggest that Teilhard's life as a Jesuit student in England, which included extensive oversight, would not have allowed him the opportunity to enter into a conspiracy of this magnitude. Gould offers suggestive counterevidence. Still others submit that letters from Teilhard to Dawson indicate a student-teacher type of relationship, in addition to no explicit discussion of fraud or conspiracy. Gould counters that neither the nature of the relationship, nor the absence of a "confession," proves that a conspiracy between the two did not exist.

In the end, Gould acknowledges that a personal friend said that he had presented enough evidence for an indictment, but not enough for a conviction. He notes that Kenneth Oakley, the original discoverer of the fraud, wrote a letter published shortly after his death that Teilhard should probably be given the benefit of the doubt (although in a personal conversation with him some months earlier, Gould says that Oakley agreed that Teilhard was probably involved; HTHT 16). Gould closes by expressing his disappointment that, despite all the turmoil his earlier essay generated, no definitive evidence has surfaced one way or the other regarding Teilhard's role in the matter.

HTHT 18. Our Natural Place

This essay returns to the subject of man's place in nature. In TPT 12, he discussed two forms of what he calls the "picket fence" view of man, by which he means that we – because of our brain, mind, and/or soul – are a fundamentally different kind of being than animals. The first, *transcendence*, argues that man's consciousness is due to processes that have not been seen on earth before. The second, *preparation*, offers that natural history is a prelude to man's arrival; that man is the culmination of an inevitable process, either divine or secular. In this essay, Gould considers two perspectives in which man is not separated from the rest of nature by a picket fence; in these views, we are "simply" animals, mind and all. He expresses his dislike for most versions of these as well. He states that the problem of "finding" our natural place may actually be our need to try to create all-encompassing models to explain the complexity of the world around us, and to explain human consciousness in particular. Nonetheless, he will conclude, it is worth it to continue trying.

Gould refers to one type of this "continuity" perspective as *zoocentric*. He acknowledges his personal preference for a mild version of zoocentricism, but says that this view is easily taken too far. The particular example he presents is that of sociobiology [which he critiqued in ESD 32]. Rather than a general view that genetics, biology, and evolution influence behavior in humans as well as animals, sociobiologists believe (he states) that each human behavior (infidelity, xenophobia, homosexuality, and so on) is directed by a specific set of genes that have been shaped by natural selection for the lifestyle of a hunter-gatherer. Gould strenuously objects; a male duck "forcing himself" on a female duck is not a genetically-driven homolog of human rape, he says, any more than a female spider eating its mate is homologous to homicide in humans. He reiterates his view [ESD 32] that human behavior can and does differ from that of animals because of our large brain and its inherent flexibility. Nothing as complex and diverse as human culture exists in the animal kingdom; we are animals, but with differences that cannot be ignored. Further, he claims, zoocentric systems are almost never what they pretend to be; they are invariably attempts to rationalize certain human behaviors by "finding" them in nature.

On the other end of the continuity-with-animals spectrum is what he calls *anthropocentricism*. This perspective, he tells us, is that evolution has a direction, usually toward complexity, and also a goal, the production of mankind. [This is similar in many ways to the "preparation" version of the picket fence view of man discussed in TPT 12.] The specific example he offers is from a book, published in 1955 and popular in the 1960's, called *The Phenomenon of Man* by Pierre Teilhard de Chardin. [This is the same paleontologist and Jesuit priest discussed in the previous two essays.] Teilhard's view of evolution is that it moves directionally toward greater *spirituality*. His view of man is that he is not a culmination, but a midpoint; in man, the spiritual part of substance exceeds the material part for the first time, resulting in our consciousness. Eventually, he continues, the spiritual world will be all that exists. This is definitely not a mainstream anthropocentric argument. Gould acknowledges that it is an extreme case; "the anthropocentric vision with a vengeance." He also notes that Teilhard's technical work in paleontology was sound. [Gould argues that the appearance of increasing complexity in natural history – i.e., the appearance of complex animals after a long period of nothing but single-celled organisms – is misleading in his 1996 book *Full House*.]

HTHT 19. Evolution as Fact and Theory

This essay is not one of his regular monthly columns; it was originally published in *Discover Magazine* in May 1981, some six months after social conservatives helped elect Ronald Reagan President of the United States. In the face of a powerfully revived creationist movement, Gould discusses how we know that evolution occurred. He also makes the case that the movement to teach scientific creationism in schools is political in nature, rather than scientific or religious. He offers specific examples of how the creationist community distorts arguments, including a discussion of how his own work involving punctuated equilibrium was offered (incorrectly!) as evidence that the scientific community itself no longer believes in evolution. [Gould will go on to play a prominent role in the legal case on the constitutionality of teaching scientific creationism in schools. This case would eventually go to the Supreme Court.]

The concept that life evolves over time implies that populations of organisms can change from one species into another. This is in contrast to the view that each species was separately created, either all at once or at different times, and have not changed appreciably since then. So, what is the evidence that has convinced biologists that evolution actually occurs? Gould offers three lines of reasoning. The first is that small changes in organisms – microevolution – has been observed in human lifetimes and over human history; examples include the breeding of dogs, and of changes in the color of moths as light-colored trees in 19th-century Britain were darkened by soot. (Creationists acknowledge that this occurs, Gould says; "How could they not?" But they argue that this differs completely from macroscopic evolution.) The second argument is the existence of homologies in biological structures. "Evolution" states the reason that the front limbs of wolves, whales, and bats are all composed of different versions of the same bones is that they are all descended from a common ancestor. Within this line of reasoning, the most convincing examples are the imperfections, or poorly-designed contrivances, that indicate the adaptation of an ancestral structure. [Gould has written several essays on this topic, most notably TPT 1.]

It has been long noted, by many people – including Gould and his colleague Niles Eldredge in their punctuated equilibrium presentations, as well as by Darwin himself – that "intermediate forms" between one species and another are almost never found in the fossil record. Creationists have, of course, used this as an argument that evolution does not actually occur. Gould turns this around; his third line of evidence in support of evolution is that intermediate forms *are* found in the fossil record, but at taxonomic levels above that of species. He offers the example of two bones found in the jaw in reptiles that "migrate," over millions of years, to form two of the inner ear bones in mammals. [He discusses this in detail in ELP 6. He later will take joy in discussing discoveries in the 1980's and 1990's of early whale fossils during their transition from land to sea (DIH 28), effectively demolishing one of the creationist's most widely used examples.]

What are the creationist's arguments? Gould discusses two of the tactics in their arsenal. The first is to capitalize on the different meanings of the word "theory" in scientific and conventional circles. In everyday life, the term is synonymous with hypothesis or speculation, as in: "I have a theory about why my stock portfolio is doing poorly." In this vein, creationists often state that "Evolution is just a theory." The implication is that a theory is something that, if it turns out to be correct, would be upgraded to "fact." However, to a scientist, theories and facts fall into different categories. A fact is a piece of data (which may, upon further inspection, turn out to be incorrect or reinterpreted; see HTHT 30). A theory, on the other hand, is a model that attempts to organize and provide a coherent understanding of data. Thus, Gould states, "evolution" is both a fact (see above) *and* a theory. When scientists talk about the theory of evolution, they are referring to the *mechanism* by which the evolutionary process occurs. In most cases today, this refers to Darwin's theory of evolution, which postulates that the dominant mechanism by which new species arise is natural selection acting on random variation; but there have been several others. Changes in the perceived mechanism by which evolution occurs do not alter the fact that it does occur. Gould offers the analogy of the theory of gravity: Newton developed one, and later Einstein developed a different one; but apples fall "down" in any case.

Even within what is called "Darwin's" theory of evolution, there are several areas of debate. Gould himself was, at this time, involved in two of them. The first, involving punctuated equilibrium, was about whether evolution occurs gradually and continuously, or only during geologically short periods followed by longer periods of stasis. The second was about the relative importance of non-adaptive mechanisms in speciation, *in addition to* natural selection. These internal debates are a sign of health and vigor in the scientific community, he tells us. One of the philosophical "rules" is, for a theory to be considered scientific, it has to make predictions that, by experiment or by other forms of data gathering, can be proven false. Much scientific debate centers on trying to do exactly this to a competing model. Gould states that the second common tactic in the creationist's arsenal is to enter this fray under false pretenses. Creationists will offer "evidence" – often dubious – that they claim falsifies one version of the model or another. Sometimes their arguments are variants (often distorted) of those made by scientists themselves. Using guilt by association, they imply that a problem with one version of the evolutionary model is a problem for all of them; the next step is usually to draw on the first tactic and imply that the problem is not with the theory, but with the fact of evolution.

Gould discusses personal experience with these tactics. After he and Eldredge published their first paper on punctuated equilibrium, a creationist pamphlet appeared entitled "Harvard Scientists Agree Evolution is a Hoax"; it referenced their work, and him personally. He names Duane Gish and Luther Sunderland as two of the more notable perpetrators. Even if their motives were sincere and their arguments valid, Gould point out, their approach does not qualify creationism to be considered scientific. This is because they fail to meet the test of falsifiability themselves; there is no data, no objective "facts" that would ever convince a confirmed creationist that creationism is wrong. (The whole point, after all, is that it is really a matter of faith.) However, Gould continues, the worst part is that the leaders of this movement know this. They are not sincere when they state that they believe creationism to be as scientifically valid a way of looking at the world as evolution. These leaders are deliberately playing on the unhappiness and fears of a segment of the population, he charges, not for sincere scientific (or religious) reasons, but purely for money and political power.

Their efforts are detrimental to society, he states. They cast a chill over textbook publishers [see HTHT 21] and high school teachers regarding the teaching of one of a half-dozen "great ideas" developed by science, the one that ties the entire field of biology together. It also casts a pall over the scientific community, many members of which argue that a unified, even dogmatic support of some version of Darwin's theory may be better than debating the subject further, for fear of giving ammunition to the creationists. Finally, it emphasizes dogma over reason in the communal and intellectual parts of American life, which Gould considers to be both reprehensible and a tragedy.

HTHT 20. A Visit to Dayton

This essay discusses the famous Scopes "Monkey Trial" of 1925. It is also a bit of a travelogue about Dayton, Tennessee, where the trial took place. Gould visited Dayton in June of 1981, and ended up posing for a photograph with the president of the fundamentalist Bryan College (named for the prosecuting lawyer in that case) and the (now middle-aged) son of "Doc" Robinson, the man most responsible for bringing the trial in Dayton.

Gould begins with a fascinating overview of the Scopes trial, drawing details from Ray Ginger's 1958 book *Six Days or Forever?*. In a nutshell, unless you have studied the case in detail, everything you know about it is wrong. Some of this is due to the trial's circus atmosphere, and some of it is due to the 1950's movie, *Inherit The Wind*, which was nominally about the Scopes trial but was really about McCarthyism. The canonical version of the story is: John Scopes was persecuted for teaching evolution, and Clarence Darrow beat back the forces of darkness championed by William Jennings Bryan, and demolished creationism – at least for a while.

The true story, Gould tells us, is as follows. The Butler Act, outlawing the teaching in Tennessee of anything that contradicts the Bible, was passed in March of 1925. This occurred without much debate, on the grounds that the sponsoring legislator needed some campaign fodder, and because everyone thought the governor would veto it. The governor's stated reason for not vetoing what he apparently considered to be a silly bill was that evolution was not being taught to any extent anyway. (At that time, most residents of Tennessee had no objection to the teaching of evolution. This was not because they doubted the literal interpretation of the Bible, but because they did not see "evolution" as a serious threat to anything that mattered to them. Most people never thought about it at all.) Once passed, various groups that included the ACLU hoped to have the law ruled unconstitutional. But before this could be done, someone had to be convicted of violating it.

Enter the people of Dayton, who thought that volunteering for this service would bring their small town some recognition. John Scopes willingly played along. Scopes did not actually teach evolution; he merely assigned reading from the standard textbook of the day that briefly referred to it, some months prior. He thought nothing of it at the time, and neither did anyone else. (He was, Gould tells us, a "free thinker," and later went on to become a geologist in the oil industry; but by all accounts, he felt comfortable and at home in Dayton.) Unfortunately, what was supposed to be a rapid conviction (with all fines paid by the ACLU) that would set up the desired appeal, turned into a circus that dragged on for weeks and captured national attention. (Gould discusses a few of the highlights.) When the smoke cleared, Scopes was convicted. However, the judge made the mistake of levying a $100 fine. At the time in Tennessee, any fines over $50 had to be recommended by a jury; the conviction was thrown out on this technicality. No conviction, no appeal; Scopes (or rather, the ACLU) did not have to pay the fine, but the Butler Act stayed on the books until 1967!

During that period, Gould notes, no one was ever prosecuted for it. However, although the popular view is that the Scopes trial was a huge defeat for the creationists, Gould argues that just the opposite was true. The "defeat" rallied the evangelical community, and forced creationism to the top of their agenda (where it is in no other country). Further, he continues, after the trial, textbook publishers all over the US – without having to – removed all of the *existing* references to evolution [see the next essay]. Bryan, by dying shortly thereafter, regained his mythical stature as the protector of the downtrodden, and the creationist movement had their first hero and martyr. [Gould argues elsewhere that, had it not been for Bryan, there would never have been a creationist movement in the United States as we know it. For a fascinating account of Bryan's motivations in the Scopes trial, which are also quite different than the canonical view, see BFB 28.]

Gould found the town of Dayton attractive, and the people – including the aforementioned president of Bryan College – to be courteous, pleasant, and respectful of his views. He was reminded that it is not religion – not even fundamentalism – that is the enemy of rationalism; it is intolerance. He writes, "In this case, the intolerance is perverse since is masquerades under the 'liberal' rhetoric of 'equal time.' But mistake it not. Creationists . . . . would substitute biblical authority for free scientific inquiry as a source of empirical knowledge. . . . We have nothing to fear from the vast majority of fundamentalists . . . . Rather, we must combat the few yahoos who exploit the fruits of poor education for ready cash and larger political ends." In another powerful paragraph, he writes, referring to the resurgent creationist movement in 1981: "As in 1925, creationists are not battling for religion. They have been disowned by leading churchmen of all persuasions, for they debase religion even more than they misconstrue science. They are a motley collection to be sure, but their core of practical support lies with the evangelical right, and creationism is a mere stalking horse or subsidiary issue in a political program that would ban abortion, erase the political and social gains of women by reducing the vital concept of the family to an outmoded paternalism, and reinstitute all the jingoism and distrust of learning that prepares a nation for demagoguery."

HTHT 21. Moon, Mann, and Otto

Gould begins and ends this essay by discussing a trial in Arkansas that he participated in, as an expert witness, in December 1981. Unofficially referred to at the time as "Scopes II," it involved the constitutionality of a law mandating equal time for the teaching of scientific creationism alongside of evolution in Arkansas public schools. Despite the obvious similarities to the 1925 Scopes trial, Gould notes there are differences as well. Certainly, the tone is much more serious; there is little of the circus atmosphere that pervaded the first trial. One mildly positive factor is that the creationist side was trying to get their pseudo-science back into the classroom, rather than simply kick the evolutionists out. (One thing at a time.) Gould's area of trial testimony involved geology, specifically how we know that the earth is older than 6000 years. He briefly describes the testimony of some of the high school teachers who would be affected by the new law. He was clearly moved by their courage and dedication. In a postscript, Gould states that the Arkansas law was overturned on the grounds that it taught religion in the classroom.

The majority of the essay is about how high school textbooks removed virtually all references to evolution within a few years of the Scopes trial. He attributes this to sheer cowardice on the part of the textbook publishers, in the face of some irate local school boards. Interestingly, the event that finally precipitated its reinstitution was the Soviet Union's launch of Sputnik in 1957. Gould describes coming across a copy of the very biology textbook he used in the mid-1950's in a used book store. Since all textbooks on a subject tend to have similar if not identical names (this one was *Modern Biology*), it is common to refer to textbooks by the names of their authors. This book, which was the largest seller during the period, was written by T.J. Moon, P.B. Mann, and J.H. Otto, so it is referred to as Moon, Mann, and Otto. Upon examining it as an adult, one thing in particular stood out to Gould – the word "evolution" does not appear in the book at all. There is a brief discussion in chapter 58 (of 60), that Gould notes most teachers never even get to before the school year ends, of "the hypothesis of racial development." It suggests that some scientists believe that today's species are descended from other, different species. This is quite different from the 1921 version of this textbook's predecessor, credited to Truman J. Moon alone. In this version, he tells us, evolution is a common theme throughout all sections of the book, helping the student to connect of all the otherwise separate facts of biology. The 1921 version, with none other than Charles Darwin on the cover, was published four years before the Scopes trial, and clearly makes the case for what was lost.

Most of this comparison fills Gould with a mixture of amusement and sadness, but there is a quote in the last section on "Science and Religion" that makes him angry. Moon, Mann, and Otto take a quote of Thomas Henry Huxley's out of context to suggest that he was a devout

Christian as well as an evolutionist. Many people are both of these things, Gould tells us, but Huxley – who coined the term *agnostic* – was not one of them. Huxley's youngest son had just died, and a friend wrote him a letter saying, in effect, that if he were to accept the Christian notion of an immortal soul, he would be comforted. Huxley's response, which Gould feels reflects the highest level of intellectual courage, is that all he felt that he really knew to be true came from the process of science, and he would not abandon that process no matter how comforting it might be in the short term. The specific quote involves Huxley's *analogy* between his views on science and those of devout Christians to their beliefs.

HTHT 22. Science and Jewish Immigration

In the spirit of Gould's 1981 book *The Mismeasure of Man*, and drawing on information from Allan Chase's *The Legacy of Malthus*, this essay discusses how some scientists misused their techniques and prestige to help justify racist political policies. Laws were enacted in the United States in the 1920's and 1930's to limit immigration from eastern and southern European countries. The Slavs, Greeks, Italians, and Jews were different in appearance and custom than the earlier waves of English, Germans, and Scandinavians. Societies have a need to rationalize discrimination against one ethnic group or another, and scientists "came to society's aid" with an early IQ test to show that these undesirables were stupid, thus justifying their exclusion. Much like literacy tests of blacks in the Jim Crow years, it is easy to bias the tests against those who the test givers have an interest in failing. The methods, in many cases, were reasonably sound; it was the biased implementation that led to the "problems." Nonetheless, one particular ethnic group tended to do well academically in the United States; the Jews. Rather than stick to principles (such as they were) and admit more Jews, other approaches were taken. In LSM 18, Gould discusses how low morals (caused by heritable genes), rather than low intelligence, was used to justify excluding Jews. Here, he examines ways in which the system was rigged, and how the proponents of the system convinced themselves that they were not rigging it.

Gould presents two examples: the work of H. H. Goddard in the United States, and that of Karl Pearson in Britain. Pearson's work in the field of eugenics, and his arguments regarding the threat to British society from the inevitable contamination of the gene pool, were the more aggressive. Pearson was also a leading statistician, which added to his clout. Nonetheless, the immigration laws he supported were not enacted. Goddard, on the other hand, was more successful in the United States, even though he personally had qualms about what he was doing. Laws in the US were enacted that severely limited immigration from southern and eastern European countries. Gould states that some form of these laws would have passed in any case, but emphasizes that the justification was provided by members of the scientific community. He notes that the closing of this "escape route" for the people living in those countries must be considered as a factor in the deaths of many of them in the decades that followed.

HTHT 23. The Politics of Census

This brief essay was written shortly after completion of the 1980 census in the United States. The census attracted some political controversy over the underreporting of poor people living in inner cities, who were predominantly black. The actual subject of this essay, however, is the 1840 census, which was the first to count and identify people with mental health issues ("lunatics" and the "feeble-minded," in the terminology of the day." Ironically, Gould states, blacks were over-counted in this census in these categories. Gould draws on William Stanton's book *The Leopard's Spots* for details, along with original documents.

Dr. Edward Jarvis, who would become a national authority on medical statistics, at first praised the collection of this data. One curious result, however, was the fact that the rate of insanity among blacks was about ten times higher in the North than it was in the South. In these antebellum times, political leaders in the South used this as evidence that slavery was the natural, or at least preferable, state for blacks; freedom made them crazy. Jarvis was puzzled by this data, and dug into it. What he found was a large number of inconsistencies and downright errors. In some towns, the population of insane blacks was greater than the entire black population. In another case, occupants of a particular mental institution were all classified on census data as black when they were, in fact, all white. Some of these errors were almost certainly unintentional, but it Gould suspects at least some deliberate malfeasance.

Jarvis pursued the matter for years; it caught the attention of the aging John Quincy Adams, still the leader of the antislavery forces in the House of Representatives. Adams got the House to ask the State Department, under whose jurisdiction the census fell at that time, to formally review the data. However, the Secretary of State was none other than John C. Calhoun of South Carolina, the nation's preeminent defender of slavery. Calhoun had recently used the census data in rejecting a request from Great Britain to exclude slavery from the Republic – and soon to be the State – of Texas. He evaded the official requests from the House, twice. Gould closes by stating that the checks and balances in the census process today preclude such errors from reoccurring. But he adds that, since the true motivation for the census has always been to gather data for the purposes of taxation, representation, and conscription, it is by its nature political, and will therefore always be controversial to some extent.

HTHT 24. Phyletic Size Decrease in Hershey Bars

This partially tongue-in-cheek essay did not appear in *Natural History Magazine*, but rather was published as part of a 1980 book entitled *Junk Food* by Charles J. Rubin, et al. Gould introduces himself as a paleontologist, where part of the job description is to look for consistent, recognizable patterns in the evolution of life over geologic time. As a community, paleontologists have been largely unsuccessful in this mission. However, he identifies one pattern that does spring up with relative frequency: "Cope's rule of phyletic size increase." For reasons that are at best poorly understood, he writes, the body sizes of organisms within an evolutionary lineage often tend to increase with time; they rarely decrease. Perhaps large size offers an evolutionary advantage; or perhaps small size offers the advantage, and the start of phyletic growth (from ancestral species to descendents) marks the beginning of the end for that lineage. On the other hand, within the human cultural environment – which does not have to obey the law of natural selection – phyletic size decrease is a much more common phenomenon. He references the weight versus the cost of the classic Hershey bar as an example, using data from 1965 to 1980. He identifies two trends. The first is that, for a given price (nickel, dime, and so on), the weight decreases over time as the result of inflation. When the price goes up (say, from a nickel to a dime), the mass of the bar goes up as well. However, the second trend is that the weight of the bar after each price increase itself decreases; the first 15-cent bar did not weigh as much as the first 10-cent bar, and the first 20-cent bar weighed even less. Gould humorously "extrapolates" to predict the year that the mass of a Hershey bar will drop to zero.

HTHT 25. The Belt of an Asteroid

On June 6, 1980, an earth-shaking paper (pun intended) appeared in the journal *Science*, entitled "Extraterrestrial Cause for the Cretaceous-Tertiary Extinction." The authors were Luis Alvarez, Walter Alvarez, Frank Asaro, and Helen Michel, all from the University of California at Berkeley. This is the famous paper that proposed that the extinction of the dinosaurs was the result of a large comet or asteroid hitting the earth. Many other groups perished as well; these included all of the large flying and swimming reptiles, many other marine groups such as ammonites, and most plankton. The plankton are particularly important because their fossil record is so well preserved. Gould's essay appeared in the June 1980 issue of *Natural History*, and therefore represents his thoughts on this discovery very close to the time it was made.

[Ever since Charles Lyell's uniformitarian view of geologic process prevailed in the 19th century, the realities of "catastrophic" extinctions in natural history were doubted by most geologists and paleontologists. In *Origin of Species*, Charles Darwin stated his belief that the apparent abruptness of the "mass extinctions" merely reflected poor preservation in the fossil record, and that they were far more gradual than the data seemed to show. Even in 1980, most scientists believed that dinosaurs had been in decline for several million years; the impact may have been the *coup de grâce*, but they were on their way out anyway. (See DIH 12 for a discussion of how this view was finally overturned.) Gould also expresses this position here, reflecting the mainstream opinion, and even uses this particular phrase. This is interesting because he actually advocated for "catastrophes" leading to mass extinctions in earlier essays (such as ESD 18). It is also consistent with, if not absolutely required for, his model of punctuated equilibrium (TPT 17), which he introduced some eight years earlier. It is most certainly consistent with his views on the contingency of history, and the improbability of the evolution of humans, that he has expressed in several earlier essays (for example, TPT 12) as well as many later ones (e.g., ELP 21). Despite his caution here, the discovery of the cretaceous-tertiary boundary event provided an astonishing degree of support for his entire worldview.]

Ever since dinosaurs were discovered, people have wondered about the cause or causes for their extinction. Despite the lack of evidence – or perhaps because of it – dozens of "theories" have been proposed over the years. [Michael J. Benton's 2003 book *When Life Nearly Died* presents a list of one hundred such hypotheses that have appeared in *peer-reviewed* journals. Gould discusses two classes of these in TFS 28.] These vary from viruses to climate change to sea level change to large-scale volcanic eruptions to extraterrestrial causes, including changes in solar energy output, a nearby supernova, and even a large meteor impact. The problem with all of these hypotheses is that none offered any evidence other than the extinction itself. Many of these speculations could be dismissed at face value, Gould says, based on what was known of the event. Any model that could not simultaneously explain extinctions in both terrestrial and marine environments, such as mammals eating dinosaur eggs, could be safely excluded by neutral participants. Nonetheless, this left a near-infinite number of hypothetically possible explanations.

This is where the Alvarezes come in. Walter Alvarez was a geology professor at Berkeley, and had been studying sediment samples from Gubbio in northern Italy, which just happened to span the Cretaceous-Tertiary (KT) boundary. His father, Luis Alvarez, was a Nobel Prize-winning physicist, and also a professor at Berkeley. The problem Walter was wrestling with was how to determine the sedimentation rate in geological strata, for the purpose of dating subdivisions within formations more accurately. One meter's worth of sediment could have been deposited in a year, or in ten thousand years; how does one tell? The method they proposed was to look for traces of iridium, a rare and highly non-reactive element. Iridium is not rare in the solar system, but virtually all that earth had when it formed is now at its core, since the planet was originally molten and iridium is even denser than iron. However, earth collects a certain amount of extraterrestrial meteoric dust every day, which also contains a certain amount of iridium. If this material settles to earth's surface at a regular rate, and if it is sufficiently unreactive to remain in place, then the density of iridium in strata would be an indicator of how rapidly the layer accumulated. Others had considered this type of approach, we are told, but the quantity of iridium in strata is still very low. Iridium, being so inert, is hard to detect chemically in any case, but is especially hard at such low concentrations.

But the elder Alvarez had a physics trick up his sleeve – neutron activation. [Alvarez selected iridium out of a number of possible choices because of its large neutron capture cross section.] If the sample were bombarded with neutrons, what few iridium atoms that were present would acquire an extra neutron, become radioactive, and break down; in the process, it would emit a characteristic gamma ray that could be detected. In other words, Luis Alvarez proposed to find the small amount of iridium with a nuclear, rather than chemical, technique. [No one ever seems to talk about the success of this approach in terms of what it was trying to accomplish; but the fact that it does not seem to be used today suggests that it was not generally successful.] Going sample by sample through the strata, they came across an anomaly; one particular batch had a factor of 30 times more iridium than the surrounding layers. In checking, they found that the sample in question straddled, exactly, the KT boundary. Quickly, they checked samples of the same period from another location (this one in Denmark), and found the same spike.

Much of success in science comes not from carefully laid plans, but in recognizing the one or two times in a career when an unexpected find – of which there are thousands – is important. The team did not miss; they rushed into publication with an article proposing that the source of the iridium was a metal-rich asteroid or comet that struck the earth, vaporizing on impact. This pumped vast amounts of dust into the stratosphere, as the volcano Krakatau did in 1883, which settled out globally over the course of a year or a few years. (Gould states that the Alvarezes considered the nearby-supernova model as well, but rejected it for a number of reasons.) The fact that this layer occurred at about the same time as the great Cretaceous extinction, they argued, was probably not a coincidence. The paper speculated the actual extinction mechanism was blockage of sunlight for an extended period, cooling the earth and shutting off photosynthesis thus causing the food chain to collapse. [Supporting evidence for this mechanism is briefly discussed in ELP 21.] Gould notes in a postscript that, since his essay was published, the iridium spike was found everywhere it was sought, including deep sea cores.

Gould is very pleased about the fact that, for the first time, someone has proposed an extinction mechanism that includes some actual physical evidence. He is excited by the fact that this mechanism could explain the extinctions both on land and in the ocean. He recognizes that at this early stage, it is possible and even likely that the model will not carry the day; he acknowledges the unresolved issues at the time, such as evidence that the plankton extinction and dinosaur extinctions may not have occurred exactly simultaneously, the absence (at that time) of any known crater of the right size and the right age, and – perhaps most importantly – whether such an impact would really be a global, rather than a merely a regional, disaster. [This argument is laid to rest, he will argue in DIH 13, with the observation of the effects of the Shoemaker-Levy 9 comet with Jupiter in 1994.] But he recognizes the implication of what this model would mean, should it prove to be true. He discusses what he calls his own "foolish" rejection of mass extinctions as playing a significant event in life's history early in his career. Now, he argues, he feels differently, writing: "Mass extinctions do not simply reset the clock; they reset the pattern. They wipe out groups that might have prevailed for countless millenniums to come and create ecological opportunities for others that might never have gained a footing. And they do their damage largely without regard to perfection of adaptation (the most gorgeously designed photosynthetic plankter could not survive a great darkness, while some marginal competitor might squeak through and become the progenitor of the next dominant group)." In the next paragraph, he shows his ability to see implications early and clearly: "Who knows? Without the great Cretaceous extinction, dinosaurs might have rallied and still dominate the earth. Mammals might still be a small group of ratlike creatures . . . ." He also notes that only one primate, *Purgatorius*, was known to exist just prior to the event. Had this one creature not found a way to make it through, probably due to "luck," we would not be here either.

HTHT 26. Chance Riches

The role of randomness, or chance, in evolution has been a source of both confusion and discomfort to many since the publication of *Origin of Species* in 1859. Darwin's two-part mechanism applies natural selection to inherent, "random" variability within a species. As both Darwin and Gould have pointed out, Darwin's use of this term differs from the common, everyday usage in some important ways. First, "random variation" within a species does not mean that the organisms can vary in any old way; each organism is constrained by its history. An animal may grow more hair or less hair than its parents, but it cannot "randomly" produce wings. Further, the second stage of Darwin's mechanism – natural selection – is not random at all, but is a directional force that will guide a linage toward more hair as the climate grows colder. Second, at a more general level, many people believe that Darwin's theory states that complex structures such as eyes, hands, and wings arise "randomly." Since common sense tells us that this is virtually impossible, they conclude that Darwin cannot be right. Gould reiterates that this is not what Darwin said, nor meant. Rather, he argued that there is a random *component* in natural selection as discussed above, again constrained by what variations the genetic code and external environment will actually allow. Finally, there is a group that equates the use of the word random with chaos or total disorder; these people believe that Darwin's theory, even if true, offers nothing but a worldview of despair and meaninglessness. Again, Gould states, the problem is a semantic one; Darwin used the term in a much more restricted way. Specifically, scientists have long known that while "random" processes do not allow one to predict very much about a single event, they do allow a great deal to be known about averages, and about how systems behave in the long run. More generally, he adds, Darwin's randomness does not offer despair; if anything, it offers freedom from universal determinism; a bit of "free will," or the opportunity for some good luck as well as bad.

Having begun this essay with the implication that it will defend the limited role of random processes in standard evolutionary theory, Gould changes course and proceeds to do something quite different. He will, he states, discuss three parts of evolutionary theory that, in the previous fifteen years or so (from the mid-sixties through about 1980), are considering a greater role for random mechanisms than before. The first of these involves *the genetic structure of populations*. Population genetics, which appeared in the first decades of the 20^{th} century as genes came to be properly understood, re-defined evolution in terms of the distribution of certain genes, or versions of genes (called alleles), within a population. In the view of the modern synthesis, natural selection decreases genetic variation within a population by eliminating the hosts of less-than-optimal genes [see ELP 28], while mutation increases it. The result is a balance, and models were developed to estimate that balance. When became possible to begin to directly measure the actual genetic variation within natural populations in the mid-1960's, the results were surprising to many; there was far more variation than expected. One new (as of about 1980) and controversial explanation is that natural selection is not eliminating many of these genetic variations because they are effectively *neutral*; they offer neither a selective advantage nor disadvantage to the resulting organism. If true, this would suggest that much of the actual genetic variation that is present inside a genome is more "random" than previously believed. This has some important evolutionary implications. If evolution is defined in terms of genetic variation, and if genes can vary and spread in ways that are invisible to the process of natural selection, then the "non-adaptive" mechanism of *genetic drift* may play a significant role in evolution rather than a minor one. Further, partially-random modifications of a genome over many generations could possibly produce something that leads to an advantage or disadvantage in the distant future; this is distinctly non-adaptive in the present.

The second component of evolutionary theory that Gould discusses involves *origin of species* (his use of the phrase). Since the founding of population genetics, it has been recognized that it is much easier to distribute a new gene widely through a small population than a large one. Thus, new species are traditionally envisioned as originating in small groups, specifically those that have become geographically isolated from the main population. Since these isolated environments are often at the margin of the species habitable range, selective (that is, adaptive, non-random) pressures can produce evolutionary change. Eventually the new group will become so genetically distinct from the parental stock that, even should the two groups re-merge, the ability to interbreed – the definition of a species – will be lost. In the 1970's, however, some other models of speciation were proposed. One of these, called *chromosomal speciation*, argues that new species may arise within the geographic range of the parent via an accidental (that is, "chance") change in the genome that precludes interbreeding. The example that the proponents offer is a change in the number of the chromosomes. [It is pointed out in HTHT 28 that one species of zebra has 32 pairs of chromosomes, while another has 46 pairs.] With whom would the first such mutant breed with? Such mutations would simply fail to reproduce in *panmictic* species (those in which a female has an equal chance of breeding with any male). However, in species that exhibit a large degree of sibling-mating and/or "harem" strategies in which several females breed exclusively with a single male, it might be possible for the mutation to take root.

Over time, the two genetically-unique species might diverge in form and behavior, even though their ranges continue to overlap.

Gould's third example involves *major patterns of rise and fall in the history of life*. In the past, the phylum of brachiopods – marine organisms with two shells hinged together – were incredibly widespread and diverse; today, "instead," clams fill most of these niches. In the traditional, adaptationist view of large-scale evolution, we would presume that clams were in some way favored by natural selection over brachiopods, and that they replaced them gradually but continuously over time. But examination of the fossil record, especially in light of the reality and importance of catastrophic events [see the previous essay], now suggests that it was the event itself that produced the large-scale change in the dominant group. Brachiopods were apparently doing fine until they were decimated in the Permian extinction event; only with this "opening" did clams begin to diversify. Gould references the work of Raup, et al. to show that 52% of all living families (the taxonomic level above genus) were lost in that extinction event; Raup calculates that this corresponds to 96% of all species. In such an event, Gould argues, it is hard to believe that the survivors were those who were better equipped over thousands of generations by natural selection. More likely, he says, they were simply "lucky"; they were winners of a game in which chance played a dominant role. [He explores this theme further in the next essay, and in TFS 15 and ELP 21 & 22.]

HTHT 27. O Grave, Where Is Thy Victory?

Gould has long lamented the fact that the term "extinction" is virtually synonymous with failure. Dinosaurs, one of his favorite groups of animals, dominated many of earth's ecosystems for 100 million years; yet the common perception is that humans, with their existence measured in hundreds of thousands of years, are superior – because we are here and they are not. One can make the general argument that extinction is the natural fate of all species, or that evolution is not about "progress," but simply short-term adaptation to local environments. However, these are less convincing to most people than the "survival of the fittest" arguments. If evolution is driven by natural selection, and if some organisms survive when others do not, does this not mean that the survivors were better adapted? If, as Darwin implied, a new species can only occupy a niche by displacing another (the metaphor of the wedge), can we not view evolution as progressive after all, and ourselves as among the reigning champs? [Richard Owen used a version of this argument in the 19th century to argue that evolution did not occur; see LSM 9.]

In fact, the fossil record does not generally support this view. First, there is little evidence of "progress" in the fossil record, only changes. Nonetheless, if competition between individuals or groups was the only mechanism leading to extinction, then we would expect the fossil record to show extinctions occurring at a relatively constant rate. However, it has long been known that there are certain geologically brief periods of time in which "mass extinctions" occur; these are followed by periods in which new groups arise almost as suddenly. Traditionally, these events have been interpreted as only minor increases in the normal rates of these processes. If mass extinctions were "real" events, it would imply that, at least in some cases, species died out not because they were out-competed, but because a natural disaster of some sort occurred. One might reasonably argue that a fish "failed" if it became extinct after another, better-adapted fish displaced it. However, if the lake simply dried up, it would not be reasonable to "blame"

(Gould's term) the species for becoming extinct. It did not fail some test it could have passed, or lose some battle it could have won; it was simply in the wrong place at the wrong time. Gould's argument in this essay is that mass extinctions, with their large degree of chance and limited role (during the event) for "survival of the fittest," plays a far greater role in life's history than was previously appreciated.

In support of this claim, he references the work of a team from the University of Chicago, led by D. M. Raup and J. J. Sepkoski. This group studied extinction rates quantitatively, and presented their results in two papers in the same issue of the journal *Science* (March 1982). The data set for the first paper measured the rates of extinctions in families of virtually all marine organisms over the last 500 million years. (Families, the taxonomic category above genera, offer two advantages over measuring the rate of extinctions of species directly. First, they are far easier to measure in the often-fragmentary fossil record. And second, families are the highest groups that continue to readily "form" in evolution; orders, classes, and phyla may go extinct, but have only rarely come into existence since the Cambrian period.) Most of the time, they found, the rate of extinction varied between 2.0 and 4.6 families per million years. However, during the five major mass extinctions (Ordovician, Devonian, Permian, Triassic, and Cretaceous, in chronological order), the average rate was 19.3 families per million years. This is about five times higher than the "background" rate, and represents a much higher ratio than was assumed by the community at that time. Gould writes: "Since these mass extinctions are even more massive than previously recognized, the scope of 'blameless' extinctions has been greatly widened." In this view, the dinosaurs were not "out-competed" by mammals; the latter simply managed to squeak through a natural disaster that the former did not. [Gould elaborates on this argument in TFS 30 and ELP 21 & 22.]

The second referenced *Science* paper deals with a smaller but more recent mass extinction event, one that does not owe its occurrence to an external catastrophe. The Isthmus of Panama arose via plate tectonics about five million years ago, connecting North America to what had previously been the island continent of South America. The latter, Gould tells us [here and earlier, in TPT 28], was like a "super-Australia," with many odd creatures and even some orders of mammals found nowhere else. All of the top predators, for example, were marsupials. The standard view of the result is that the mammals of North America – hardened by harsher climates and tempered by repeated "survival of the fittest" struggles with invaders from Asia and Europe, and thus "more evolved" – crossed the isthmus and easily decimated the isolated, stagnant South American competitors. It is certainly true that jaguars, llamas, tapirs, and peccaries all originated in North America, while in the United States the only evidence of the merger is the occasional opossum, armadillo, and porcupine. Many fascinating South American creatures became extinct, including giant sloths and those marsupial predators.

The full story, according to the researchers, is more nuanced. Their quantitative analysis shows that 14 North American families now reside in South America, accounting for 40% of the total. But surprisingly, 12 South American families moved north, accounting for 36% of the total. This is remarkably symmetric, and strongly challenges the notion that the North American mammals were inherently more advanced. Extinction rates, using data from genera instead of families, were similar as well: a 13% decrease for the South, compared to an 11% decrease for the North. [This data says nothing, of course, about why any individual family or genus survived when another did not; only that the northern mammals were not, on average, more advanced after all.] Much of the reason that these results came as a surprise is that most of the "new" North American mammals reside in the tropical regions of Mexico and Central America, and not in the more temperate regions of the United States, while those moving south seem to have occupied the entire continent fairly uniformly. (Gould notes that the North American mammals that went south have diversified more than the South American natives that migrated north.)

He closes the essay with the interesting observation that familial extinction rates have decreased from the Cambrian period (500+ million years ago) to today, from 4.6 families per million years then to 2.0 million families per year now. He offers a few speculations on why this might be the case, but no conclusions.

HTHT 28. What, If Anything, Is a Zebra?

This is an essay about cladistics. Cladistics is a way of organizing species and higher taxonomic groups that focuses exclusively on genealogical relationships, like a family tree. A "clade" is a branching diagram that attempts to show the path by which each species, living or extinct, "broke off" from its ancestral species, and reflects the goal of modeling the "tree of life" in part or in total. This differs in some important ways from the traditional Linnaean classification system that organizes life using the formal, hierarchical species-genus-family-order-class-phylum-kingdom-domain descriptors. In the Linnaean system, many species can be grouped into a genus based on certain defined characteristics; genera are then similarly grouped into families, and so on. This approach *implies* common descent – the Linnaean classes of mammals and reptiles both have backbones, placing them both in the phylum of vertebrates, which in turn suggests that both groups share a common (vertebrate) ancestor. [Interestingly, Linnaeus developed this system a century before Darwin published *Origin of Species*. Linnaeus was a creationist; the fact that his taxonomic structure was adaptable to the Darwinian revolution is a story that is told in IHL 21.] However, this system says nothing about the order in which mammals and various groups of reptiles appeared, nor what the actual lines of descent were. Cladistics is not interested in whether a genealogical group is, say, a family or an order (or a superfamily, a suborder, or something even further in between); this has advantages and disadvantages, which Gould will discuss.

Gould presents an explanation of the cladistics terminology and methodology. He begins with the definition of the term *sister group*. The term refers to two lineages – at any level from species to phylum – that share a unique common ancestor. All splittings (speciation) are of two branches only; cladistics assumes that if three lineages share a common ancestor, then two separate splittings occurred. He illustrates this with an example close to home: humans and the great apes. Cladistics, he states, considers chimpanzees and gorillas to be a sister group, on the grounds that they share a common ancestor with no one but each other. Humans, then, form a sister group with the gorilla-chimpanzee *unit* (another fundamental term in cladistics). [Later evidence – see DIH 30 – suggests that chimpanzees are actually more closely related to humans than to gorillas; that is, chimps and humans are a sister group, sharing a common ancestor more recently either did with the gorillas. This alteration of the clade does not change any of the points made in this essay; cladograms are readily and regularly modified.] Next, the chimp-gorilla-human unit forms a sister group with orangutans. This process can be applied any number of times. It can also be used to subdivide existing lineages, as would be required if extinct hominids were to be introduced into the mix.

The difficult part, Gould notes, is the proper identification sister groups. In principle, the approach is straightforward, and is the same as the process described in TPT 24; identify homologous and analogous structures, discard the analogies, and try to connect the pieces in the proper order. This is challenging enough in the Linnaean system, since it can be very difficult to tell homologies from analogies. It is even more challenging in cladistics, since the resolution – due to the requirement to determine the exact branching relationship – is so much higher. Cladists must look for a unique characteristic that is shared by each member of the sister group, but no other. (It may of course be shared by units incorporated in the sister group.) Such a characteristic is called a *shared derived character*. These are difficult to correctly identify, and one of the traps is to accidentally identify "primitive characters" (yet another cladistic term), which appear sporadically across a larger lineage, as a shared derived character. It thus becomes an operational requirement that effective shared derived characters be recently evolved.

In addition to being challenging to implement in practice [circa 1982], cladistics raises another vexing problem for taxonomists. In the earlier example, humans, chimpanzees, and gorillas are grouped (without significant controversy) into a unit, while orangutans are a sister unit. However, chimps, gorillas, and orangs – but not humans – have been collectively grouped as apes for centuries. The clade perspective thus argues that the term "ape" is not a valid category (unless it is modified to include humans). Since anything in evolutionary theory involving humans tends to be skewed, Gould offers another example: zebras.

There are seven living species in the genus *Equus*, which includes horses, asses, and donkeys; three of these seven species are zebras. One of the defining characteristics of zebras are, of course, their stripes. What originally motivated Gould to write this essay was research regarding the question: Are zebras in the same clade? Or, are stripes an analogous feature, arising independently in different lineages? Even if they are homologous, are zebra's stripes a shared derived character, or a primitive character? (That is, are stripes a new evolutionary feature shared by zebras and zebras alone, or do all members of the horse genus have the latent ability to produce stripes, while only these three not-so-closely-related species do so?) The answer, according to the work of Debra Bennett, is that two of the zebra species do form a sister group, but the third forms a sister group with a species of true horse. In Gould's professional opinion, the evidence, which is mostly morphological rather than genetic, is not airtight. (Genetics were difficult to use in this case, as no two species of *Equus* even has the same number of chromosomes.) If the argument holds up, however, it will mean that – in the cladist's taxonomy, at least – there is no such thing as a zebra.

To professionals, this is more than just a semantic argument; it is about how life is organized. [See HTHT 5, DIH 32, and IHL 21 for Gould's view on the underappreciated importance of taxonomy.] As a final example of what adopting the cladistic perspective would mean, he offers the lobe-finned fish, which includes the lungfish and coelacanth. These organisms are closely related to the direct ancestors of amphibians, reptiles, and mammals; they are more distantly related to the ray-finned fish (herring, tuna, and so on) that dominate the oceans today. The traditional Linnaean model groups dolphins with mammals and not with fish; but it also groups lobe-finned fish with ray-finned fish. The cladists, on the other hand, group the lobefins more closely with, among other things, cows. That is, technically, cladists do not consider the category "fish" to be a legitimate taxonomic term. Gould does not deny that the genealogical argument offered by the cladists is true. However, in this essay at least, he is not entirely ready to let go of categories such as "fish" because of it. Coelacanths eat, swim, reproduce, and presumably taste like "fish"; is there no place (he asks, rhetorically) for formal recognition of these facts?

[The concepts that would become cladistics first appeared in the 1960's. When Gould wrote this essay in the early 1980's, supporters of cladistics were in the minority. As genetic sequencing and computer power improved, however, their techniques became more practical and more powerful. By the early 1990's, cladistics had become the dominant method of classification. Interestingly, the concept of cladistics is highly consistent with punctuated equilibrium (TPT 17), so Gould's hesitancy in accepting it is interesting. However, he does come to fully accept it; see DIH 30.]

HTHT 29. How the Zebra Gets Its Stripes

Gould begins and ends this essay by asking a simple question: are zebras white animals with black stripes, or black animals with white stripes? The answer – and there actually seems to be one – is the latter; some abnormal zebras exhibit white splotches instead of stripes on a black animal, but the reverse is never seen. The fact that the white part formed "imperfectly" suggests that it is an overlay on the black. The researcher that discovered this curious fact was an embryologist named J. B. L. Bard. Bard also offers some speculative analysis on zebra striping patterns in the different species, and this work is the actual subject of the essay.

Biologists, Gould tells us, are loosely divisible into two personality types: those to focus on the uniqueness of each species, and those who focus on the underlying similarities. One of the legends of the latter group was D'Arcy Thompson (1860 – 1948). Thompson wrote the classic work *On Growth and Form*, which noted the mathematical structure in many organisms [logarithmic spiraling of snail shells, for example – see TPT 3] were optimal solutions to common problems. While out of the mainstream in his view of the mechanisms generating these structures, his arguments were well-made and insightful. Bard used a Thompson-like approach in his attempt to analyze the striping pattern of the three species of zebra. He proposed modeling a white-and-black-striped sheet that could be, essentially, draped over the developing zebra embryo at some stage of its development. He was referring literally to a highly regular, genetically-produced color pattern. (He did not physically observe such a structure, even though he was an embryologist; he was arguing from a theoretical position.) If such a pattern could be attached to the embryo before, say, the hind quarters underwent a specifically-observed growth spurt, then the adult zebra would have a few, wide stripes on his haunches. If the fusion came after this growth spurt, there would be a large number of narrow stripes. By assuming that the hypothetical striped sheet fused with the embryo in the third, fourth, or fifth week of development, Bard was able to argue that the result would be the striping pattern found in the three species of zebra. This is the kind of thing Thompson would have appreciated; change the timing of one factor, and the resulting form is mapped into a different but related pattern. Gould acknowledges that this is speculative, but appreciates both the approach and the execution.

Throughout the essay, he also refers to the Bard-Thompson-"unification" view as consistent with the formalist (as opposed to adaptationist) perspective that biological form is constrained by internal pathways, with the observation that small changes in the timing along these pathways can lead to significant changes in the final organism in certain directions.

HTHT 30. Quaggas, Coiled Oysters, and Flimsy Facts

The history of science is full of cases in which new facts lead to the overthrow of a reigning theory. Gould presents the opposite theme in this essay; he offers two examples in which a new theory overthrew an established fact. This touches on the scientific, as opposed to vernacular, definition of the term "fact." Rather than implying "known certainty," facts to a scientist are really only pieces of evidence that are accepted as true. Sometimes – hopefully, not often – a fact may later be found to be incorrect, and its acceptance an error. In these two examples, science was (eventually) self-correcting. Gould generalizes that no scientific theory can rest on a single fact, in large part for this very reason. [He elaborates on this in ELP 31.] He closes with a discussion of how creationists take advantage of the perceived worth of isolated "facts" to advance their distinctly non-scientific cause. He also presents a description of Darwin's own pre-Mendelian speculation about how inheritance works.

In the first example, the accepted "fact" is a now-discredited inheritance mechanism called *telegony* ("offspring at a distance"). Gould tells the story, following an article by Richard W. Burkhardt, starting with the Earl of Morton's mare. In the early 19th century, Lord Morton tried (unsuccessfully) to preserve a species of zebra called a quagga. He obtained a male, but could not find a female; so he bred the quagga with a female Arabian horse (a mare). The result was a hybrid, and it exhibited some faint zebra-like striping. He kept the quagga and the offspring, but later sold the horse mare to a friend. The mare was then bred again, this time conventionally with another horse. Surprisingly, the resulting foal was also striped. Lord Morton sent a note to the Royal Society in 1820 describing these events. It was suggested that the influence of the quagga had "remained" in the mare, affecting her later offspring. This model was later referred to as telegony; for a variety of reasons, some of which involved social politics, telegony became accepted in many circles as a fact.

Charles Darwin came to learn about Lord Morton's mare and her offspring. At first, he did not accept the telegonical explanation. Instead, he suspected that the presence of stripes on her second foal indicated that all members of the equine genus had a predilection for striping; this would indicate common descent, and therefore provide an important example in support of evolution. (This would later prove to be the correct explanation.) But he changed his mind after developing his own views on inheritance. Darwin's model, produced without knowledge of Mendel's genetics, was called pangenesis; it was consistent with telegony. Darwin postulated that each part of the body contained tiny "gemmules," which migrate to the sex cells. The male sex cells would enter the female's body, and (he argued) the gemmules would remain there, potentially ready to influence other offspring. (Darwin believed that changes to the body parts could result in changes to the gemmules that were produced. Ironically, if this were so, it would represent a form of Lamarckism.) Telegony became an important area of research in Britain at the end of the 19th century.

Finally, with the rediscovery of Mendel's work, August Weismann – a dedicated "natural selectionist" – presented his "continuity of germ plasm" argument. In this view, the genetic material inside the egg cannot be influenced by external factors; it does not behave in a Lamarckian fashion. Further, the male and female genetic materials merge during fertilization, rather than the male altering the female in some way. This new and successful Mendel-based theory stood in direct contrast to the "fact" of telegony, and led to investigation. Several high-profile breeding programs were undertaken involving horses mating first with zebras and then again with other horses; stripes appeared in many of the foals. What ended the issue was that stripes also sometimes appeared in the so-called control group: offspring of horses with other horses, none of which had ever even been exposed to a zebra. Darwin was right the first time; stripes are, apparently, a feature – latent or expressed – in all members of the horse genus. The "fact" of telegony was dethroned, due to the rise of a new theory of heredity – albeit 70 years after it was first accepted.

The second case Gould discusses involves the "fact" of over-coiling oysters. In 1922, A. E. Trueman, a British paleontologist, published a paper arguing that the extinct coiled oyster fossils found in the area were descended from earlier flat ones. At this time, natural selection was not the dominant model of how evolution proceeded. Trueman believed evolution was the result of orthogenesis [ESD 9, ELP 25], a model that argued that evolutionary trends developed a kind of momentum. Originally, he argued, the coiling was advantageous, but eventually it became so extreme that the overhanging coil prevented the other valve of the shell from moving. This trapped the organism inside, unable to feed, resulting in extinction. The proof of over-coiling was beautifully demonstrated in the "type," or name-bearing specimen of the species. This oyster and the enormous canines of the saber-tooth tiger were often used as "textbook" examples in support of orthogenesis. The over-coiling of the oyster, resulting in its own extinction, was a major problem for the supporters of natural selection; their model could not explain such a phenomenon.

Finally, in 1959, a young scientist named Anthony Hallam wrote a paper with two provocative claims. First, he argued that the coiled had not "evolved" from a flat oyster after all; the coiled oyster was a different species, and had migrated from another location. The second claim was that there was no increase in coiling in either species over time; in Gould's "punctuated equilibrium" terminology, both were in stasis. This caused a major flap, but Hallam was eventually proven correct. But where did that leave the name-bearing specimen, with one valve coiled over to pin the other shut? It turns out that this was the only specimen found in that condition. A careful reexamination, including x-rays, showed that sediment of the same color existed between the two valves; it had been deposited there post-mortem, after the oyster had led a full life. Gould reiterates the importance of not basing a theory on a single fact, no matter how "true" it appears to be.