The Panda's Thumb

TPT 1. The Panda's Thumb

This is one of Stephen Jay Gould's most famous essays. It makes the case that biological "contrivances," jury-rigged structures made from available parts, provide better evidence that evolution has occurred in natural history than structures that appear optimized for their function, such as wings or eyes. This is not an original argument, Gould notes; it was put forth by Darwin himself. Darwin also coined this use of the term "contrivance." In later essays, Gould will refer to this as "the principle of imperfection."

Gould visited the National Zoo in Washington, D.C., shortly after the famous pandas had been presented as a gift from China after President Nixon's visit. He observed that they appeared to be peeling their bamboo (to get at the shoots, the only part they eat) with the help of an opposable thumb. Being unaware that any members of the carnivore family had opposable thumbs, he looked closer, and counted the digits; including the "thumb," there were six. This was another puzzle, since while some vertebrates were known to have fewer than six digits per limb, none had more [but see ELP 4]. He went to the library and found the classic monograph on pandas: *The Giant Panda: a morphological study of evolutionary mechanism* by D. D. Davis, 1964. Davis, we are told, wrote all about this: the "thumb" is in fact an enlarged sesamoid (one of the wrist bones), manipulated by muscles and tendons that serve a different function in other types of bears.

If individual organisms were "created" from scratch (either naturally or divinely), then this unwieldy contrivance would be a very odd way of designing an opposable digit. If, on the other hand, the panda arose via decent with modification (Darwin's phrase) from a bear with more conventional paws, then a structure like the Panda's thumb makes more sense. It would have to have been formed out of parts that were available. The ancestral bear's first digit – the "real" thumb – was not available due to its earlier specialization for walking. Whether by natural selection, or a Lamarckian "need" that expresses itself as an inheritable change, or by a God who likes to tinker with established organisms rather than make new ones from scratch, the conclusion is the same: the Panda's thumb is a contrivance, and therefore evidence that evolution – modification of an earlier species to form a new one – occurred. These awkward contrivances retain evidence of natural history and provide essential evidence against creation. [An important subtlety of this view is that, if the panda were the only bear or the only carnivore in existence, this clue would not be available. Much of the evidence for evolution comes from examining a species in the context of others, both living and extinct, rather than in isolation.]

Both at the beginning and the end of the essay, Gould shows that Darwin understood this point quite clearly. His follow-up to the highly successful *Origin of Species* (1859) was not *The Decent of Man* (1871) or another book on a big-picture topic. Instead, it was *On the Various Contrivances by which British and Foreign Orchids are Fertilized by Insects* (1862). For many years, those in the profession considered this and most of his other books to be evidence that Darwin was a putterer, a not-too-bright "dilettante" who got lucky once. It took the coming 100th anniversary of the publication of *Origin* for historians of science to go back and read this apparently tedious book. What they found that it was only nominally about orchids; its true purpose was to provide detailed evidence for evolution, via the argument of contrivances. Individual species of orchids have developed structures that attract individual species of insects; these insects then pollinate only those orchids to which they are "matched." The key point, Darwin makes clear, is that all of the unique structures that all of these orchids have developed are all derived from common plant parts – leaves, flower pedals, stamens, and so on. They are all contrivances, and thus evidence that each example of this plant family evolved.

TPT 2. Senseless Signs of History

The previous essay introduced the concept of contrivances. Darwin (and Gould) define contrivances as biological structures formed out of preexisting parts that have been pressed into service, sometimes not very efficiently, to perform a new function. Contrivances are evidence of evolution, albeit not necessarily natural selection. In this essay, we are introduced to the concept of *remnants* (also Darwin's term), which can also be construed as evidence for evolution. Remnants are structures that served a function in an ancestor, but no function in the modern, descended organism. One of the classic examples is the hipbones of whales: small fragments of bone that are degenerated from the pelvis of a terrestrial ancestor. Gould refers to the teeth of baleen whales that develop in the embryonic stage, and then are re-absorbed. Remnants are evidence that the ancestors of modern organisms did not have the same form as those living today.

Gould does not present very many examples of organic remnants in this essay. He chooses instead to clarify the concept by presenting analogies from other areas. He begins with etymology, the study of word origins. "Veteran" and "veterinarian," for example, share the same root; this subtle indication of common origin, even though the words today appear to be completely unrelated, is evidence that evolution occurs in linguistics.

He spends the last half of the essay discussing the work of Archie Carr, an expert in sea turtle migration. One such species migrates every year from South America to Ascension Island in the middle of the Atlantic Ocean, to lay its eggs. Carr speculated that this difficult journey might be a remnant of an easier one, some 80 million years ago, when the Atlantic was just forming and thus the distances smaller. While the point is illustrative, Gould presents several reasons why this particular example is highly unlikely to be correct. In particular, Ascension Island is only about 7 million years old (although it sits on the volcanic mid-Atlantic ridge, and thus could be periodically re-formed), and the species of turtle in question is only about 15 million years old.

TPT 3. Double Trouble

In an earlier essay [ESD 12], Gould discusses a species of clam with a modified mantle (the fleshy part) that looks very much like a real fish, including eyespots and fins. This lure attracts real fish; when sufficiently close, the clam sprays the fish with its larvae. Some of which attach to the gills; the clam's larvae must live in this state for some time in order to mature. As Gould discussed in that essay, the lure is a great adaptation. However, it presents a challenge to Darwin's theory, which views evolution as a shortsighted process working only on individuals and not across generations. This view is consistent with the contrivance of the Panda's thumb, but "perfection" requires some additional explanation. Half a wing, half an eye, and (by analogy) half a fish lure would not seem to offer any selective advantage for natural selection to work on. In that essay, Gould argues that intermediate structures may have served other purposes.

This essay begins with the discovery of an anglerfish with a "lure" made from a modified dorsal spine that also closely resembles a small fish. The lure is another contrivance, like the Panda's thumb, albeit a very good one. The existence of a very similar adaptation twice, in two very different lineages (a mollusk and a vertebrate), could be interpreted as a reflection of the power of natural selection. Others, however, have viewed this similarity as a problem for Darwinism. Natural selection, Darwin said, acts on random variations. The probability, so the argument goes, that natural selection would lead to something approaching a fish lure once is unlikely but possible; but the probability of it occurring twice, independently, would seem to be "unlikely squared," or virtually impossible. Therefore, the argument continues, some force other than natural selection must be acting to guide the evolutionary process towards this goal. One of the more famous proponents of this view was Arthur Koestler, who had recently published a book that included this argument. Koestler's primary example was the skull of the so-called "Tasmanian wolf" (a marsupial), which closely resembles the corresponding skull of the more common placental wolves.

[Koestler was more widely known for his novels, in particular the 1940 classic *Darkness at Noon*. Gould does not discuss Koestler's career in literature or how it may have influenced his scientific views, or vice versa, but he does something similar with Vladimir Nabokov in IHL 2.]

Gould attempts to counter Koestler's argument with three lines of reasoning. The first is to note that the similarities of the two skulls (and the two lures) are really only superficial; an expert can easily tell them apart. This attacks the "squared" part of the argument, on the grounds that the structures are not "the same," merely similar in outward appearance. Each lineage retains the evidence of its natural history. Gould introduces one of the most famous examples of convergence: the physical shape of fish, dolphins, and ichthyosaurs (extinct marine reptiles). All have arrived at a similar shape and function in similar ways, but all retain clear evidence of their ancestral past. Louis Dollo, he continues, studied the problem of convergence in the late 19th century. In 1890, he is credited with introducing Dollo's law: "Evolution is not reversible." This is really a statistical generalization, not an actual law, but its point is that natural history is apparent in all biological structures. A fish was ancestral to a terrestrial reptile, which in turn was ancestral to the marine ichthyosaur. However, the ichthyosaur's fins do not revert to the structure of the ancestral fish. Instead, they retain clear evidence of the terrestrial phase of its heritage. The *differences* in the resulting convergent structures are therefore also evidence of evolution, which is in part why Gould grouped this essay with the previous two. [He returns to Dollo's law in general and ichthyosaurs in particular in ELP 5.]

Gould's second counter is to argue that Koestler and similar thinkers misunderstand Darwin's view of "random variations." Darwin saw these as small changes, heavily constrained by current structure; Koestler appears to believe that Darwin thought them to be much more powerful and unconstrained. In Darwin's view, the vast majority of significant modifications were "filtered out" by natural selection. If an organism really could evolve in any direction without constraints, then the probability of a truly identical development occurring twice is truly highly improbable. However, this is not the case.

The third line of attack against the argument that convergence implies additional guiding forces is to point out that sometimes, certain solutions really are optimal. Any large aquatic vertebrate must propel itself by undulating its tail, and stabilize itself with projections such as fins, and streamlining the body reduces the energy required to move through the water. Similarly, carnivore skulls almost require binocular vision and a combination of stabbing and tearing teeth. Natural selection can, he argues, produce similar shapes from different lineages simply because (in some cases, at least) certain shapes are more-or-less uniquely adaptive. Gould briefly mentions the work of D'Arcy Wentworth Thompson, author of a famous 1942 treatise *On Growth and Form*. Thompson identified the selective advantages of many fundamental shapes for biological systems, including the logarithmic spiral and the hexagon. (Gould notes that Thompson's vision was highly unorthodox and, in many ways, certainly wrong: he believed that the fundamental shapes physically "impressed" themselves in some way on the living structures. Despite his odd worldview, many of his observations on nature and mathematics were very insightful.)

Gould acknowledges that his arguments are circumstantial. His point is that there are ways to interpret convergence in nature that are consistent with Darwin's view: that evolution is a long series of gradual changes, each one of which offers a slight advantage to the individual, with no externally-defined direction or goal. Nonetheless, another problem remains: how does an organism evolve a fish lure from a dorsal spine, or a paddle from a leg, when probably hundreds of changes are required to act in an apparently coordinated fashion? This is one of the major puzzles of evolution, and Gould closes with an interesting line of speculation. A colleague used a computer model (circa late 1970's) that drew shapes based on an algorithm and exactly three user input parameters. By changing these three parameters, the resulting shape could be changed from something that closely resembled a snail to a clam, and then a nautilus. It might be the case, Gould speculates, that certain genes control rates of activity, or groups of other genes; change just a few of these, and the resulting organism could change its structure significantly and coherently. He references a recent paper that claims to identify a small number of structural changes that could turn a more common bear into something like a panda. Perhaps, he offers, this could even offer a mechanism by which gradual changes on certain genes led to "episodic alteration" of the final shape – a reference to his own model of punctuated equilibrium [TPT 17 -- also see ESD 7 & 8, and HTHT 14 & 15].

TPT 4. Natural Selection and the Human Brain: Darwin vs. Wallace

Charles Darwin, Gould reminds us, first developed his theory of evolution via of natural selection in 1838. Alfred Russell Wallace developed it independently some twenty years later, also after being inspired by Malthus' *Essay on Population*. Interestingly, Darwin's vision and Wallace's vision were not exactly the same. Wallace would look at an organism, and see each and every facet of it – both structural and behavioral – as being optimally honed by natural selection. Wallace, partly to honor Darwin and probably also in part to capitalize on his fame, referred to this "functionalist" or "adaptationist" view of natural selection as "Darwinism." Gould presents the following 1867 quote from Wallace in support of this position.

> None of the definite facts of organic selection, no special organ, no characteristic form or marking, no peculiarities of instinct or of habit, no relations between species or between groups of species, can exist but which must now be, or once have been, useful to the individuals or races which possess them.

Proponents of this view were referred to either as Darwinists or "pure" or "strict" Darwinists. Importantly, Darwin himself was not in this camp, and spent a great deal of effort arguing against it. In other words, Darwin was not a Darwinist – and neither was Gould, who sides with Darwin over the "ism." [See HTHT 10 for a discussion of Gould's personal conversion on this issue, with further discussion in ELP 1.] Darwin believed in a messier reality with multiple evolutionary mechanisms, and his frustration with strict Darwinism led to the following uncharacteristically bitter statement in the last edition of *Origin of Species* (quoted by Gould).

> As my conclusions have lately been much misrepresented, and it has been stated that I attribute the modification of species exclusively to natural selection, I may be permitted to remark that in the first edition of this work, and subsequently, I placed in a most conspicuous position – namely, at the close of the Introduction – the following words: 'I am convinced that natural selection has been the main but not the exclusive means of modification.' This has been of no avail. Great is the power of steady misrepresentation.

The other "means of modification" that Darwin considered fell into two categories. The first included adaptive mechanisms other than natural selection, the dominant example being sexual selection. This category was itself divided into two subcategories: those adaptations in which the males competed with each other for the females (e.g., antlers), and those in which the female chose directly based on perceived attractiveness (e.g., the male peacock's tail plumage). Wallace acknowledged the possibility of the first, but not the second [see BFB 14 for a related example]. In the other major category were the non-adaptive mechanisms. One such mechanism, which Darwin referred to as "correlations of growth," capitalized on his view that adaptive changes in one structure within an organism could also lead to non-adaptive changes in others. Another was his belief that an organ shaped by natural selection for one function could, under some circumstances, be available for others. Wallace never seriously accepted the validity of any non-adaptive mechanisms.

While Darwin and Wallace politely skirmished over the relative degree of dominance that natural selection played in the formation of new species, they struggled far more intensely over its role on the human brain and, more to the point, human consciousness. On one side, Darwin believed that the theory of evolution must apply to "the citadel itself" (Darwin's phrase). On the other side, after stating that natural selection completely controlled almost everything else, Wallace concluded that it could not have produced the human mind. This structure had to be the result of some higher, nonevolutionary power. Wallace, being a religious man, readily concluded that this higher power was God.

Most scholars today conclude that Wallace "lost his nerve," while Darwin had the integrity to followed his argument to its logical conclusion. Gould now introduces the crux of the essay by stating that this conclusion is fair to Darwin, but not to Wallace. Wallace was in the minority of British subjects in his position on race, Gould explains; specifically, he did not believe that other races were inherently inferior. He certainly believed that Western culture (and especially British culture) was superior to all others, but unlike most of his contemporaries, he believed that the "savages" that were rapidly becoming subjects of the Empire had the same inherent mental capabilities that he did. He based his view on two lines of reasoning. The first was anatomical; there seemed to be no difference in brain size or structure between Brits and any other group. The second was cultural. He was familiar with cases where members of other cultures had been brought to England, and saw that they could learn to speak and write English, play musical instruments, and generally function in their new land. This posed a great problem for Wallace's view of evolution, for the following reason. Both he and Darwin agreed that natural selection could not "select" for features that would serve a future purpose, but not a current one. Natural selection, they agreed, worked only on individuals competing to adapt to their local environment. However, if this is the case, then how does one explain a brain that is capable of learning to play the piano when such a function would never be considered a selective advantage in its "natural state?" How could the latent ability to write be adaptive in a culture with no written language? Wallace was not, Gould argues, an intellectual coward; he took his "strict Darwinist" perspective to its logical conclusion, which was that it could not explain the human brain. Darwin, with his more flexible position, had no difficulty with the concept that the brain evolved for certain purposes, but once in existence could be pressed into service for other purposes – including writing and playing the piano. This was one of the non-adaptive mechanisms that Wallace believed could not play a significant role in evolution; thus, he was consistent. [Gould discusses Wallace again at some length in LSM 10.]

This debate did not receive very much attention at the time. *Origin of Species* had convinced people that evolution occurred, but few were convinced that natural selection was a mechanism capable of creating new species. This changed with the acceptance of the "modern evolutionary synthesis" [TPT 18], which was developed in the 1930's and 40's. The modern synthesis, among other things, identifies natural selection as the primary mechanism behind evolutionary change. However, the version of natural selection that was adopted was essentially Wallace's. Gould makes clear his objections to "neo-Darwinism," which he argues is very similar to Wallace's "strict Darwinism," and (in his view) suffers from the same problems and limitations.

[Gould presented a famous and controversial talk to the professional community on this topic in 1977. The presentation was entitled "The Spandrels of St. Marco and the Panglossian Paradigm," and argued pointedly that the community was, at most, paying lip service to non-adaptive evolutionary mechanisms. Doctor Pangloss is a character in Voltaire's 1759 political satire *Candide*. Pangloss consistently argues that everything that exists or happens serves a purpose, and the result was always an optimal world (or, by analogy, an optimal organism). It was lost on no one that Voltaire was mocking the absurdity of this viewpoint in his play. Spandrels are components of cathedral architecture that are highly decorated, and thus often perceived to be of fundamental importance, but have no structural role. Gould uses spandrels as a metaphor for biological structures that originally evolved for non-adaptive reasons, and only after their formation were they pressed into service for their current function. While Gould does not address it in this essay, in this presentation he states his preference for an alternative view to adaptationism, which is referred to in Europe as formalism.]

TPT 5. Darwin's Middle Road

Gould, a historian of science as well as a scientist, describes two conflicting paradigms of how scientists achieve fundamentally new understandings of nature. The first one, inductivism, had held sway for many decades. It states that good scientists collect objective facts over a period of time, without presupposing any underlying theoretical viewpoint. When all of the important facts are in place, the open mind should then be able to see the new theory. [Gould discusses his view that humans must interpret all facts in light of some theory in several other essays.] The second paradigm, which Gould refers to as "eureka-ism," says that the great scientists almost always develop their new understanding in a brilliant flash of insight, and only afterwards collect the necessary facts to substantiate it. Neither of these is true, Gould argues. In addition to being incorrect, he states that he finds both of the paradigms to be distasteful. He dislikes the inductivist model at an emotional level, because it paints science as soulless and scientists as drones. He dislikes the eureka argument in part, he tells us, because supporters invariably imply that these flashes can only come to a chosen few, which strikes Gould as elitist. He does, however, acknowledge the importance of understanding how the creative process actually does occur within science.

Both inductivists and eurekaists have used Darwin's development of the theory of evolution by natural selection to support their positions. Gould describes two contemporary historical analyses of Darwin's meticulous notebooks shed new light on the actual process. Gould references these studies, along with his own reading of Darwin's notebooks, to refute both views.

The inductivists argue that Darwin slowly accumulated his unbiased facts in South America, the Galapagos, and then Australia. When he had the pieces in place, he formed his theory. Darwin's own autobiography (intended, Gould claims, as a source of inspiration for his children rather than for publication) supports this position, but the actual writings in his journals at the time do not. The record clearly shows two things: first, that the evolutionary significance of many of the "facts" as he gathered them, including the famous Galapagos finches, were not obvious to him at the time. Second, and perhaps more importantly, his journals clearly show him postulating theory after theory during the critical period, and rejecting them one by one while gathering additional information. Darwin did not develop his theory in a straight line.

The eurekaists, on the other hand, quote other passages from Darwin that suggest his theory was developed in a flash of insight after reading Mathus' *Essay on Population*. Again, Darwin's actual journals contradict this. By the time he read Malthus, according to Gould's references, he already knew what it would say from other sources. Even so, there is no sudden burst of creative writing immediately following his notes on Malthus. In fact, he turned to other topics.

So, how did Darwin develop his theory? His journals indicate an iterative process between fact gathering and brainstorming – that is, the middle road of the essay's title. To this, however, Gould adds an additional technique. This technique is *analogy*, the power of gleaning insight into one field by noticing something analogous in another. During the critical period where Darwin's concept gels, the most influential source seems to come not from biology, but from economics: Adam Smith's 1776 *Wealth of Nations*, and other later authors who wrote about this work. Darwin's last step (or leap, depending on one's perspective) appears as an analogy to the "unseen hand" of Smith's market economy – that order can appear if individuals are left to act only in their own interest. (Karl Marx, an admirer of Darwin, is quoted here as appreciating the irony that *Laissez Faire* works better in nature than it does in economics.) Only after this step did Darwin seek to develop quantitative support via statistical studies, which led him to Malthus. In support of his argument for this third component, Gould writes, "If genius has any common denominator, I would propose breadth of interest and the ability to construct fruitful analogies between fields." [Gould returns to the details of the role the Galapagos fauna played in Darwin's development of natural selection in TFS 23.]

TPT 6. Death Before Birth, or a Mite's *Nunc Dimittis*

This essay begins with a seemingly simple question: Why, in most species, are the numbers of male and female individuals approximately equal? It is not, as one might think, a simple random "coin flip"; in humans, for example, slightly more males are born than females, but more girls survive so there is a small variation in favor of women. Darwin's theory implies that survival favors those species that can produce the most offspring. Therefore, if the ratio of male to female in offspring is variable, it would appear to make sense for a ratio of, say, ten females to every male, since one male can fertilize more than one female. Yet the ratio for most animals, including humans, is close to one-to-one. Is this fact, then, in conflict with Darwin's view of natural selection?

The now-standard answer to this evolutionary puzzle was first proposed by the mathematical geneticist R. A. Fisher, one of the founders of population genetics in the 1920's. His argument is that we should expect to see such an asymmetry *if* natural selection worked on populations or on species. If, however, natural selection works on individuals, as Darwin proposed, then a 50-50 ratio makes perfect sense. Fisher proposed the following hypothetical scenario: natural selection works on individuals, but at the beginning of a virtual experiment, the ratio of female offspring to male offspring is ten to one. In such a world, any male that produced two male offspring in ten would have an advantage over the other males within that population, for his offspring would go on to produce twice as many grandchildren as his fellows. This, in turn, would increase his percentage of the population's total gene pool. This trend would continue until males that only produced one male offspring in ten were removed from the population. The same argument holds true if females outnumbered males; equilibrium is achieved at a one-to-one ratio. Thus, based on this simple mathematical argument and basic observations, Fisher concludes that Darwin was correct in his claim that natural selection works on individuals, and not on groups.

This is a fully plausible explanation, supported by some limited quantitative analysis, but how can we know if it is true? There are undoubtedly many possible explanations for a one-to-one sex ratio. The best way to test a model such as Fisher's, Gould states, is to look for exceptions to the rule – in this case, species with markedly asymmetric male-to-female ratios – and see if they can be reconciled with the theory. Nature's oddities, Gould notes, are an essential tool with which to probe the limits of biological "laws."

One creature with just such an asymmetry is a species of mite in the genus *Adactylidium*. A mature female attaches itself to the egg of a thrips (a type of insect). Using this egg as a food source, it produces five to eight offspring – exactly one of which is a male. (The total number of offspring that can mature – male or female – is limited by the amount of food available in the thrips egg.) Careful examination shows that this species performs "sibling mating"; in this case, the one male fertilizes all of his sisters. In non-incestuous reproduction, each of these eight or so offspring would have half of their mother's genes, and the grandchildren would have one quarter. By Fisher's reasoning, this would result in equal numbers of male and female offspring – say four males and four females. Each of these would have to find a mate; then the females and the mates of the males would have to find a thrips egg. The odds are poor that all eight would mate; only those that do would be able to capitalize on a thrips egg if they came across one.

However, with sibling mating, seven of the eight offspring would be fertilized females. Each daughter that finds a thrips egg will produce grandchildren. Most importantly, each of these grandchildren will have half of the original mother mite's genes (a quarter from the son, and another quarter from each daughter). If the goal of the individual is to increase one's genome within the population, then this can be a successful strategy. Of course, there are genetic drawbacks as well as advantages, and this highly simplified mathematical argument does not prove the validity of Fisher's argument that natural selection is responsible for the popular one-to-one sex ratio. However, "the exception that proves the rule" does show consistency with Darwin's view of evolution.

This approach would backfire if the lone male dies before he can fertilize the females. Perhaps, then, it is another adaptation that this species of mite protects her offspring by hatching them inside her body. As in ESD 10, the offspring then proceed to eat their mother from the inside out; while still inside her carcass, the offspring mate. The fertilized females then break through the empty shell of their late parent, and go off to seek their own thrips eggs. The male also emerges, and then promptly dies. If a casual observer did not know the full life cycle of this species, it would appear that the male served no function at all. He is born; then, without eating, mating, or even walking around much, expires. (It was this behavior that first attracted more detailed scrutiny.) In a closely related species, the male does not emerge at all; it dies inside his mother's body, having never been "born," thus giving the essay its title. [Gould identifies a similar question – why are males comparable in size to females – in HTHT 1.]

TPT 7. Shades of Lamarck

Gould wrote this essay on the 150th anniversary of the death the great French biologist Jean Baptiste Lamarck (1744-1829). He begins by stating that Lamarck was a fine scientist who made several substantial contributions. Nonetheless, the essay's primary purpose is to compare the mechanisms of Lamarckism to Darwinism, and then to show how shades of Lamarckism are still popping up today (and are still wrong). All that most people today know of Lamarck's evolutionary theory is the concept "inheritance of acquired characteristics," which was not original with him. This was only a piece of his evolutionary theory, Gould tells us. Lamarck saw life as moving actively and "progressively" up an evolutionary ladder, driven by an internal mechanism of some sort, and often blocked by environmental constraints that led to numerous and suboptimal designs. This mechanism, Lamarck speculated, involved the organism's need to respond anatomically to the new environment, and – importantly – the ability to pass these acquired changes on to offspring. It was only the last part of Lamarck's model that was resurrected after publication of *Origin of Species* in 1859, Gould states. [For a more detailed discussion of Lamarck's evolutionary theory, see LSM 6.]

Both Lamarck's and Darwin's evolutionary mechanisms are based on organisms adapting to their environments over multiple generations. The essential difference is that Lamarck's is a one-stage process, while Darwin's requires two separate stages. In the Lamarckian view, an animal would recognize that the climate is getting colder, and would actively respond – not consciously, but nonetheless in direct response to it – by becoming hairier. Few if any such animals would become less hairy in this model. This is referred to as "directed variation." (The modifications are then inherited by offspring, which continue the trend.) In Darwin's view, when the climate gets colder, individual animals will be born that are hairier, but others will be born with less hair; the same thing happens when the climate is heating up, and also when it is stable. There is no preferred direction at the individual level. Then the second Darwinian stage comes into play; those born without more hair die, while those born lucky get to live and reproduce. In Darwin's model, the variation is not directed; it is natural selection – in the form of innumerable individual deaths without issue – that leads to a shaggier population. Gould claims that it is unfortunate that the Darwin model refers to these undirected variations as "random," since the more common use of this term implies that the variation can go in any direction. Evolutionary variations are constrained by the available structures; that is, by the natural history of the organism. Mammoths will not develop feathers when it gets cold, even if they work better than fur.

Gould then proceeds to give some examples of how professional biologists confuse the two mechanisms, even today. First, he refers to an article in the prestigious journal *Lancet*, in which the author notes that there are situations in which viruses can induce genetic changes into a bacterium by introducing a fragment of DNA. While true and fascinating (much progress has been made on this since 1979), the author claims that this is a case in which the Lamarckian model is more appropriate than the Darwinian model, since the genetic change was "acquired." Not so, says Gould, because there is no *preferred* direction of variation associated with this process. Yes, this is a modification of the genome, but it fits perfectly well under what we refer to, not entirely appropriately, as Darwin's first stage of "random" variation. Mutagens, both radiological and chemical, also fall into this category; they generate variations, but not in any preferred direction, and therefore they are not Lamarckian.

After discussing some other examples, he comes to a book entitled *The Case of the Midwife Toad* by Arthur Koestler. The subject of this book is the work of a 20th century Australian Lamarckian named Paul Kammerer. Midwife Toads are a species of purely terrestrial toad that is descended from aquatic ancestors. The ancestral species (or another aquatic descendent) has a certain characteristic that the terrestrial toads have lost: roughened ridges called nuptial pads on their forefeet that support mating in water. Kammerer's experiment was to force midwife toads to mate (and lay eggs) in the water, most of which did not hatch. He repeated this process for several generations with those that did hatch, and found that these toads did have rudimentary nuptial pads. He argued that he had demonstrated a Lamarckian effect; the toads needed to develop these pads, and over several generations they did, and were able to pass the changes on to their offspring. Not at all, says Gould. By using only the eggs that survived and hatched in the water, Kemmerer was "selecting" those that varied in the ways that were best adapted to aquatic living. But why the pads again; why not some new approach? Gould addresses this by referring to combinations of genes, where whatever changes that allow midwife toad eggs to hatch in water also support the growth of other latent but associated characteristics. [He elaborates on this point in HTHT 14.] It is also consistent with Darwin's views on correlated variation, as discussed in *Origin of Species*.

Gould closes this essay with a discussion of why Lamarckian views remain so popular. First, he argues, from a distance, evolution does appear to be Lamarckian – if one only considers the survivors, and does not examine the individual offspring too closely. But much of it, he argues, is social; people work hard, make progress, learn things, and pass them on to the next generation. There is no doubt that human culture progresses via a Lamarckian process. It would be reassuring if the natural world did as well. Most people are uncomfortable with the thought of randomness guiding (or not guiding) their lives, and would like nature to have a preferred direction, toward a goal, involving some purpose. Darwin's view eliminates this for biological evolution and natural history; both he and Gould encourage us to seek comfort elsewhere.

TPT 8. Caring Groups and Selfish Genes

The theory of natural selection postulates that variations among individuals, coupled with harsh environmental constraints, leads to the formation of new species via the preferential survival and reproduction of those born with certain advantages. In this view, any stability one finds in the living world is not the product of a design or plan, but simply an unintended side effect of the selective process. Those individuals who are "selected" by nature or chance to reproduce pass on some of their characteristics; the rest do not. But how, then, does one explain sterile workers in social insects, or bees that die after stinging an animal that is attacking the hive? (Darwin himself struggled with this problem, and discussed these examples in *Origin of Species*.) Altruism and cooperative behavior in general are difficult to explain in terms of individuals being the sole unit upon which natural selection acts; what is the selective advantage in helping a competitor get access to finite resources? One proposed alternative is that natural selection may, under some circumstances, work at levels other than the individual, such as the group or the species. Groups of (say) bees that have members willing to die stinging an attacker may fare better in the long run than other groups that do not. If this behavior can be passed on biologically to the next generation, then descendents of this group might eventually displace the others. In this hypothetical example, natural selection operates on the group in addition to the individual.

The rise of the modern evolutionary synthesis in the 1940's reemphasized the importance of selection at the level of the individual. The modern synthesis is an extension of population genetics; this field incorporated Mendel's concept of the gene, a "particle" of inheritance that retained its characteristics from generation to generation. Different versions of a gene are called alleles; one allele might correspond to a white flower, another for a purple flower. Difference in species, in this paradigm, reflected differences in genes; evolution is viewed as changes in allele frequency within a population. Inside an organism, genes make copies of themselves, but – with the exception of the rare mutation – can only produce exact copies. Neither the external environment nor the individual itself can modify these genes [thus demolishing the evolutionary theory of Lamarck – see previous essay]. Since individuals die, the gene patterns that continue are those that are copied into offspring. This, in turn, requires the gene host to successfully reproduce – which is to say, "Be selected." Only those genes that produce successful individuals get the chance to try again; it was this argument that led the supporters of the modern synthesis to adopt Darwin's natural selection as the mechanism behind evolution. (Darwin, of course, worked before Mendelian genetics was widely known and understood.) Followers of the modern synthesis came to refer to themselves as Darwinists, strict Darwinists, neo-Darwinists, and by other names, in part for this reason. Since it is individuals that either succeed or fail to pass on their genes, they settled on the individual as the sole unit on which natural selection acts. Genes, via mutation, become the source of variation of individuals within a species. As the neo-Darwinist expression went, "Genes vary, individuals are selected, and species evolve." After this introductory discussion, Gould proceeds to discuss two challenges to the view that individuals are the key target of selective forces: one from above, and one from below. He begins with a discussion of the Scottish biologist V. C. Wynne-Edwards (1906-1997).

Wynne-Edwards precipitated a heated battle with the Darwinists with the publication of his 1962 book *Animal Dispersion in Relation to Social Behavior*, by presenting an argument that evolution could and did, under some circumstances, select for groups. His starting point was the observation that, in many species, the population remained relatively stable, as opposed to the boom-and-bust levels that one might nominally expect of a group of self-interested automatons. (This type of behavior is observed widely by many species, and is fully consistent with the "economic" argument of Malthus that was so inspirational to Darwin. However, Wynne-Edwards noted, there are species that do appear to maintain relatively stable populations in the presence of surpluses and shortages, and these must be explained too.) His argument is that, if a biologically-based behavior arose in one group of individuals (by chance) to deliberately moderate reproductive activity during good times, such a group would have a better chance of not being completely eliminated in bad times. He argued that male lions who lost a struggle for dominance "accepted their fate" of not mating (not consciously, but presumably hormonally). More importantly, he also argued that the "swarming" behavior of some animals and the "chorusing" of others is actually a census-taking procedure that, when compared to the available resources, allows the population as a whole to "calculate" the optimal number of offspring. Reproductive decisions are made, in this perspective, in the best interests of the group as a whole, to the detriment of at least some individuals.

Key members of the still-new modern synthesis school rejected Wynne-Edwards' argument for group selection. They acknowledged the validity of his observations, but reinterpreted them in ways that were consistent with the Darwinist view that individuals were, in fact, acting in their self-interest in all of these cases. One of the specific arguments that was brought to bear was kin selection [ESD 33], a mathematical argument that helping multiple siblings survive and reproduce (apparently altruistic) produced the same genetic result in the next generation as reproducing oneself, and thus could be interpreted as a self-serving act after all. Assistance to strangers was explained in terms of "reciprocal kin selection" (perhaps a stranger might help your offspring someday), and therefore, again, consistent with selection exclusively at the level of the individual. Gould does not take sides in this debate (in this essay). He simply notes that at the time of publication, the Darwinists held the dominant position within the community, although a few pockets of resistance remain. [Group selection would see its fortunes brighten in the 1990's. Gould himself comes around to the perspective that selection does act at multiple levels, including the group. It is one of the tenants of Gould's posthumous 2002 tomb, *The Structure of Evolutionary Theory*.]

The second challenge to the standard model that Gould refers to is "the selfish gene" concept of Richard Dawkins, who had recently published a book of the same name on this topic. [Dawkin's 1976 book was very influential in both the scientific community and in the popular press. Gould and Dawkins debated this and other fundamental issues in evolutionary theory until Gould's death.] The selfish gene concept is an expanded, more rigorous version of the old joke that a hen is an egg's way of getting to another egg. Dawkins' position is that the fundamental level at which natural selection acts is the gene, and not on individual; in this way he differs from Wynne-Edwards, who argued for multiple levels of selection. Dawkins writes that "we are robots, programmed by these genes for their own benefit," which is the creation of more copies of themselves. Gould explicitly acknowledges that Dawkins is speaking metaphorically about genes "wanting" anything; this is simply shorthand, he tells us, for stating that those genes that happen to operate in such a fashion multiply at the expense of those that do not. Such behavior could easily replace the kin selection arguments associated with altruistic behavior, which were proposed to support selection at the level of the individual.

Gould remained neutral in the earlier argument, but here he openly sides against Dawkins' paradigm. His primary line of attack is that individual genes cannot be selected for; the entire genome, inside the organism, lives or dies as a group. Such an approach might work, Gould states, if individual genes mapped linearly to structures and behaviors. In this view, a cheetah is fast because it has genes for "fast." But as many people before Gould (notably Ernst Mayr) have noted, genes do not generally work this way. [It may actually be considered a fluke that Mendel was able to identify as many one-to-one gene alleles – tall or short pea plant, wrinkly or smooth pea, and so on – as this is not the general case.] Many genes are involved in the production of a given structure, and a single gene may influences several different structures. Further, most genes do not code for anything at all [see HTHT 13 and ELP 28]. The overall result is, Gould claims, that natural selection cannot "see" individual genes, and thus cannot act on them individually. Dawkins' argument is fundamentally based on the reductionist or atomist view of life that Mendel's original work implies but Gould rejects: that an organism can be understood purely in terms of its components, with little concern for interactions between these components [ESD 32 and 33].

[One might also argue that Dawkins is extending the neo-Darwinist paradigm, which emphasizes the role of gene distributions in evolution. It is worth noting that Dawkins was one of the early critics of Wynne-Edwards' group selection argument. Gould never accepts the "selfish gene" concept, but he will later be at least intrigued to a partially-related idea by Francis Crick called "selfish DNA" – see HTHT 13. It is worth noting that Gould does express strong support for a more limited form of "modularity" of both structures and behaviors in the presence of natural selection; these views are discussed in ELP 17.]

TPT 9. A Biological Homage to Mickey Mouse

Gould wrote this essay on the 50^{th} "birthday" of Mickey Mouse, who first appeared in the cartoon *Steamboat Willie* in 1928. His emphasis is on the way in which Mickey has metaphorically "evolved," especially over his first few decades. In the early days, his personality was "mischievous, to say the least," and he was drawn to appear much more adult-like than in later years. Later, as he became nicer, his features changed: his head grew in size relative to the rest of his body, his eyes got bigger, and his ears moved back, suggesting more forehead. All these are changes that we associate with youth, both in human babies and in those of other mammals such as kittens and puppies. He uses this to illustrate his first point: that, as Konrad Lorenz noted in several important papers, these sorts of juvenile features evoke strong feelings of affection and nurturing. (Lorenz was referring to human adult reaction to animals, not cartoons, but the point remains.) As a second point, Gould notes that humans are neotonic; we retain many embryonic features into childhood, and many childlike features into adulthood. This point is discussed in ESD 7.

TPT 10. Piltdown Revisited

Stephen Jay Gould was fascinated with the famous Piltdown hoax. He wrote three essays about it: this one, and two more in his next collection [HTHT 16 and 17]. There are two parts to his fascination, the first of which is the question of who perpetrated the fraud. The man who "discovered" the evidence is believed to have done it, although Gould states that no definitive proof exists. It remains more uncertain, however, whether or not he acted alone, and if not, who his co-conspirators might have been. This topic is still debated, and Gould wholeheartedly joins in the fray in the postscript to this essay, and then in even more detail in the next two. Thus, "whodunit" is one question; the second, perhaps more important one is, why did it take so long to unmask the hoax? And for that matter, why were these rather crude fakes able to fool the world's experts at all? This second line of query is the primary subject of this essay.

Gould begins with an overview of the historical events, and introduces us to the main characters. In 1908, a lawyer and amateur archeologist named Charles Dawson claimed to have obtained some skull fragments from a gravel pit in Piltdown, which is located in southeastern England. The skull fragments were unusually thick, but otherwise completely modern in form. Since the geologic age of the Piltdown site was older than those of the Neanderthal and Cro-Magnon remains that had been found in Germany and France, the anthropological implications were vast. Dawson, along with another man named Pierre Teilhard de Chardin (who would later become moderately famous as a scientist, theologian, and author; see HTHT 18), continued to periodically work the site. A few years later, in 1912, Dawkins brought the material to Arthur Smith Woodward of the London Museum. Smith Woodward was impressed, and convinced of both the authenticity and the relative ancientness of the skull fragments. The three men together went out to the site later that year. This time, Dawson found a jaw fragment with two molars still embedded. The jaw was much more ape-like than the skull fragments. While the incompleteness of the fragments made it impossible to determine if the skull and jaw fragments were from the same creature, it would be fascinating if they were – a human-like brain case with an ape-like jaw could easily have been considered "the missing link" between apes and humans that scientists had been searching for. There was further supporting evidence for all of this. First, both the skull fragments and the jaw were deeply stained by minerals that were present in the groundwater at Piltdown, suggesting that they were in fact ancient and not recently deposited there. Second, the teeth, while ape-like in form, were worn in a way that is consistent with human, but not ape, usage [Gould does not provide details on this]. Third, other material was found as well – some stone tools, and fossil fragments of mammals that did not currently live in England such as elephants.

Smith Woodward, a renowned professional, was convinced that skull and jaw came from a single creature; he presented a report stating as much to his colleagues at the end of 1912. Even at the time, several professionals concluded that the skull belonged to a modern human and the jaw to an ape; a few even speculated that fraud might be involved. Then, a few years later, Dawson made another "discovery." At a nearby site, he found another ape-like molar tooth (worn in the human fashion), and another human-like skull fragment. If the two pieces were from different species, finding them in the same general location once might be a coincidence; but finding this association twice seemed virtually impossible, Smith Woodward believed. He and a handful of other senior members of the British scientific community declared Piltdown man to be real, and gave it the formal name *Eoanthropus*. Meanwhile, in 1914, Teilhard joined the French army as a stretcher-bearer in the Great War. Dawson died unexpectedly in early 1916. While doubt remained in many circles, Smith Woodward's consensus held for forty years.

In 1949, Kenneth P. Oakley applied a new dating technique based on fluorine. (Oakley apparently believed, like most, that the fossils were legitimate, and was seeking to refine their age.) Bones acquire fluorine at a rate that is proportional to how long they have been buried and in contact with groundwater, which carries the dissolved mineral. Oakley found that there was virtually no fluorine in the Piltdown fossils, proving that they were modern. Still, natural explanations were sought for several more years. Finally, Oakley considered fraud. Once he did, he quickly found that the bones had been artificially stained, and the teeth had been "worn" with a file. The skull was from an anatomically modern human; the jaw was from an orangutan. The stone tools also turned out to be modern recreations, and the mammal fossils, while real, were identified as being imported from elsewhere. [After writing this essay, Gould ends up meeting Oakley and discusses the Piltdown case with him; see HTHT 16.] Piltdown was formally announced as a hoax in 1953. Smith Woodward had died a few years earlier, before the bubble burst but after he had dictated his last book, about Piltdown Man, entitled *The First Englishman* (1948). One of Oakley's colleagues, J. S. Weiner, published *The Piltdown Fraud* in 1955. In it he presents (we are told) a sufficient amount of circumstantial evidence to preclude Dawkins' innocence, although he is unable to come up with either a "smoking gun" or a motivation. He also concludes that Smith Woodward was innocent of any wrongdoing; he was merely duped. Teilhard was interviewed by Oakley about the subject, but not suspected at the time. He died in 1955.

Gould tells us that he has seen the fossils, and to him it seems obvious that they are fakes. Why, he asks, did it take so long for the obvious to become apparent, at least to the most influential players? He offers four lines of reasoning. The first is "the imposition of strong hope upon dubious evidence." The French were bragging about their ancient hominid fossils; England seemed to have none, until Piltdown. Next, he offers "reduction of anomaly by fit with cultural biases." It was the conventional wisdom of the period that our simian ancestors evolved large brains first, and bipedal posture later, or at least they evolved together [see ESD 26]. Piltdown Man, with a large brain case but an ape-like jaw beautifully supported this perspective. It must be true! Gould also notes that the brain size was bigger than those of the hominids found in China, Indonesia, Europe, and Africa; this also played into the cultural prejudices of the English establishment. Third, Gould proposes "reduction of anomaly by matching fact to expectation." Many of the writings of the period note all sorts of simian characteristics to what we now know is a modern human skull; meanwhile, the orangutan jaw is also "found" to have several uniquely human features. Even scientists can see things that are not there, if they want to! The fourth and final line of reasoning is "prevention of discovery by practice." The fossils were considered so valuable that they were locked up in a safe. None other than Louis Leakey asked to examine them in support of a book he was writing on early man in 1933; he was allowed to examine plaster replicas of the fossils, but not the pieces themselves. Since the replicas did not reproduce the fraudulent information, the problem of detecting fraud – even by a skeptic, which Leakey was – was greatly inhibited. (Oakley had access to the real material.) This, of course, does not explain why a man of Smith Woodward's skills and reputation would be taken in; for this, we must draw on the first three lines of reasoning.

TPT 11. Our Greatest Evolutionary Step

This essay was prompted by the 1979 announcement of the discovery of a new and ancient species of hominid, *Australopithecus afarensis*. The find, announced by discoverers Donald Johanson and Tim White, includes the famous "Lucy" skeleton. Lucy, they declare, is ancestral to both the later australopithecines (*A. africanus*, *A. robustus*, and others), and to our own line of *Homo* (including *H. habilis*, *H. erectus*, and ourselves, *H. sapiens*).

Gould begins with an update and correction to an earlier essay on human evolution, ESD 6. The material in question are whether the discovery of some important fossils announced by Mary Leakey in 1975 were really *H. habilis*, as she claimed, or *A. afarensis*, which Johanson and White argue for. Gould sides with Johanson and White, while noting that this does not alter his conclusion of that earlier essay regarding the bush versus ladder paradigms in evolutionary theory. The importance of these facts for this essay is that the material found by Johanson and White range from 2.9 to 3.3 million years, while Leakey's material is between 3.35 and 3.75 million years old. Reclassifying Leakey's finds as *A. afarensis* would extend the existence of Lucy's kind from 400 thousand years to upwards of a million years – with virtually no change, Gould notes.

A critical aspect of this discovery is that, while *A. afarensis* had an ape-sized brain (400-550 cubic centimeters), it was fully bipedal – like modern humans, but unlike any ape. Gould focuses on a false understanding of the significance of this find, as reported in the popular press. He quotes from the January 1979 New York Times: "The evolution of bipedalism was thought to have been a gradual process involving intermediate forerunners of modern human beings that were stooped, shuffle-gated 'ape-men,' creatures more intelligent than apes but not as intelligent as modern human beings." Not quite, says Gould; the scientific community has known that early hominids had small brains but walked upright since the 1920's. The significance of *A. afarensis* is just how close to the chimpanzee-human split that the origin of bipedalism appears to be.

With *A. afarensis*, the origin of bipedal posture in our ancestors is moved from 2.5 million years to almost 4 million years. To illustrate the significance of this extra 1.5 million years, Gould turns to progress that had been made in the previous fifteen years regarding the genetic "molecular clock." To the surprise of some, it turns out that the rate of change of many amino acids within a chromosome proceeds at a relatively steady rate. Once this rate has been determined, the amount of time since two species shared a common ancestor can be estimated by comparing their DNA, at least in theory. He tells us that human DNA has been found to differ from chimpanzee DNA by about 0.8 per cent. This corresponds to a time span of about 5 million years (plus or minus about 1 million years, as of the time this essay was written). Thus, moving the origin of bipedalism from 2.5 to 3.8 million years places it much closer to the chimpanzee-human split. Our lineage, as distinct from the other great apes, was apparently bipedal almost from the beginning.

Further, if we assume that this common ancestor was not bipedal, it implies that the change to upright posture happened within a relatively short period – on the order of a million years or less. The tripling of brain size came much later, over a period from 2 to 1 million years ago. The increase in brain size was probably simpler to accomplish genetically, he argues; larger brains can be brought about via neoteny with just a few changes to some regulatory genes [see ESD 7]. Upright posture, on the other hand, involved a complex series of changes to both the pelvis and the foot. Bipedalism, he concludes, is thus the major event in human evolutionary history, and the apparent abruptness with which it arose is the true significance of the Lucy find.

[In 2009, Tim White published a description of an even older member of the hominid family, *Ardipithecus ramidus*, whose remains were actually found in the early 1990's. "Ardi," as one relatively complete skeleton is known, is 4.4 million years old. Its brain is even smaller than Lucy's; it is estimated at 300 – 350 cubic centimeters, about the same size as a chimpanzee. Despite having an opposable toe (like apes), other details from the toe and hip suggest that Ardi was fully bipedal.]

TPT 12. In the Midst of Life . . .

This is an essay about Man's place in nature. It begins with a discussion of the views of Charles Lyell, one of the founders of modern geology as well as friend and mentor to Charles Darwin. Lyell's uniformitarian view was that, after formation, the Earth settled down to a stable and steady existence, with no direction and no "progress." When forced to explain the disappearance of dinosaurs and other large reptiles, followed by the appearance of large mammals, he did not reconsider his uniformitarian paradigm. Instead, he postulated the existence of a very slow cycle of warmer and cooler periods in Earth's history. The dinosaurs had lived in a warmer time; now it was cooler, he argued, and so now there were mammals. Millions of years from now, when the climate warms up again, we might again see ichthyosaurs (or something very much like them) swimming in the seas, and dinosaur-like reptiles walking on land.

However, Lyell writes, there is one exception to this cyclical process: Man. Man's "moral attributes" must have been imbedded in him by forces greater than those normally at work. Gould refers to such special treatment for our species as a "picket fence," separating us from the rest of nature. He discusses two kinds of picket fences that proponents have historically advocated. The first, which he calls *transcendence*, argues that the history of man has been driven by processes that have not occurred on the earth before. In a restricted sense, Gould agrees with this – our culture, as we define it, does appear to be unprecedented. But in the strict sense (he tells us), human culture does not transcend evolution, it acts as a layer on top of it. Only when advocates claim that the rules of evolution no longer apply – when they have been transcended in the more literal sense – does he object. There is very little of this in the professional community currently, Gould writes. The other general approach, which he finds more reprehensible, is *preparation*. This view postulates that Earth's natural history has been a prelude to our inevitable arrival. Lyell argued that the steady-state earth "yearned" for conscious beings to appreciate it. Wallace, in a more spiritual view, argued for the existence of a universal consciousness awaiting the arrival of a species that it could take form in [see TFS 26 for more on Wallace's views]. Again, this "classic" version of preparation has virtually no professional support today. However, there is a modern version of it that is quite widespread – and, he argues, quite wrong.

The modern picket fence does not involve a divine or spiritual force guiding evolution toward Man; instead, it draws on the concepts of predictability and inevitability. He writes: "[This version] holds that the fully natural process of organic evolution follows certain paths because its primary agent, natural selection, constructs ever more successful designs . . . . If we could go back to that primordial bacterium and start the process again, evolution would follow roughly the same path." That path, proponents argue, inevitably ends with a self-aware organism capable of language and thought. Rather than challenge the presumption that intelligence is the epitome of evolution, or even argue (as he does elsewhere) that there is no epitome, only survivors whose day too shall pass, he takes a different tack. First, he argues that if there is a gradual, more-or-less continuous progression in the history of life on Earth, it ought to be apparent in the fossil record; there is no such evidence. Second, he draws on certain specific events in natural history that, had they occurred differently or not at all, would have precluded not only humans but vertebrates and even multicellular life. Specifically, he draws on the Cambrian explosion, the relatively sudden event in which all modern animal phyla first appeared. This event occurred some 540 million years ago, which is more than 3 billion years after life first appeared on earth. No one knows why it occurred as late (or as early?) as it did, he states, but notes that if it happened a few billion years later, our sun might be about to enter its red giant phase – which would eliminate all life on earth. That is, he concludes, it is almost certainly wrong to see human intelligence – or something very similar – as inevitable. [Gould elaborates on the Cambrian explosion and his "contingency of history" or "tape of life" argument in his 1989 book, *Wonderful Life*. He critiques other views of man's place in nature in HTHT 18. His most detailed essays on his views of the absence of progress in natural history are ELP 21 & 22.]

TPT 13. Wide Hats and Narrow Minds

Is there a correlation between the weight of an individual's brain and the intelligence of that individual? One might think so – humans have larger brains than, say, chimpanzees, and are also more "intelligent" (however that might be defined). This essay describes a famous battle that played out in the professional proceedings of the Anthropological Society in Paris for several months in 1861. On one side was Paul Broca, founder of the society and the world's leading craniometrician (one who studies head sizes and shapes). He argued that head size and brain weight were most definitely correlated with intelligence, and with moral character. (Like most European males of that era, he was convinced that European males were the highest grade of human in the world. He also believed that male European heads and brains were the largest in the world.) On the other side was Louis Pierre Gratiolet. He also believed that European males were superior to other races and sexes (see the next essay), but did not believe that head size or brain weight were correlated with this supposed fact. The debate was inevitably extended to the issue of whether men of genius within the European male demographic could be identified via their skull size.

The question as to whether a correlation between human brain size and intelligence exists is, Gould argues, scientifically legitimate. (The answer turns out to be "no.") The battle in question, however, devolved into a specific debate over the size of one particular brain – that of Georges Cuvier [HTHT 7]. Cuvier (1769 – 1832) was unquestionably a genius, by any definition of the term. He was the greatest anatomist of his time, founded the science of paleontology, and convinced the world that extinctions had occurred in natural history. He survived the French Revolution unscathed, dying in bed many years later. He also had an enormous head. At the time of his death, his brain was reported to weigh 1830 grams, far more than the average brain weight of about 1400 grams. The debate, which sounds ludicrous today, involves whether the reported weight could be substantiated (this was almost 30 years later), versus his available but less impressive hat size – the hat itself was offered into evidence. While Cuvier's brain represented only a single data point, it was an important one for illustrative and debating purposes.

Broca, Gould tells us, won the debate, albeit only temporarily. It became apparent with time that many other men of letters did not have exceptionally large brains. Further, it also became clear that there were diseases that could enlarge both the skull and brain, if they affected the individual in childhood. Nonetheless, there were proponents who often used slanted evidence to reinforce the biases of the social establishment for decades (see Gould's 1981 book *The Mismeasure of Man*). The fascination with brain size continued well into the 20^{th} century; Gould was motivated to write this essay after news reports that part of Albert Einstein's brain had been found in a mason jar in Kansas. Einstein's brain had been removed when he died in 1953 for purposes of measurement; it was found to be of average size.

TPT 14. Women's Brains

Paul Broca (1824 – 1880; see previous essay) was the leading craniologist of his day, and the leader of an important academic group in Paris. At a time when there was a strong consensus that brain size (weight or volume) was correlated with intelligence, Broca presented himself as a purely objective researcher. One of his most important findings was that the brains of men were larger than the brains of women, with inevitable consequences for social order. Gould quotes some of these, which usually (and condescendingly) condemn attempts to educate women or to allow them access to the professions. By extension and careful selection of data, these same arguments were used to justify domination over other races.

Following along with Broca's approach, Gould examines the original data and analysis [as research for *The Mismeasure of Man*, 1981], and this essay discusses his findings. He credits Broca and his team with meticulous and accurate measurements, but challenges some of their assumptions. As expected, Broca finds that women's brains are, on average, smaller than men's brains, by 181 grams, or about 14%. However, Gould notes, Broca did not correct for height. (Body weight is an ineffective measurement, since a person's brain weight does not vary with degree of obesity.) Further, his measurements were made via autopsy of bodies from the equivalent of nursing homes, and the women there were, on average, much older than the men; brain weight decreases with age. When Gould corrects for these factors, he is able to reduce the difference but not eliminate it. He then presents an additional tactic: brain size is also correlated to height (in both men and women), and no one suggests that taller people are inherently smarter than shorter people.

Craniology has, of course, fallen out of favor. Modern intelligence testing shows no significant difference between men and women – or, for that matter, between any groups of people based on brain size. But as Gould notes in these and many other essays, the results of intelligence testing of groups is often used to the same ends, which he strongly dislikes. He closes with a lament for all of the women who never had the chance to make a contribution to society due to prejudices that were rationalized by scientists.

TPT 15. Dr. Down's Syndrome

This essay presents an insight into 19th-century Victorian thinking. It mixes the Victorian's growing but still limited understanding of biology and natural history with both the awakened imagination and the arrogance of the power that science had brought them. It is only tangentially about Down's syndrome, which results in a number of debilitating physical and mental attributes, and which we know today is correlated with an extra copy of chromosome 21. Rather, it is about the thought process behind how Down's Syndrome came to be known as Mongolian idiocy, or mongolism. The connection was only in small part due to the fact that many people with Down's syndrome have slightly yellowish skin and a small epicanthic fold, a characteristic of the oriental eye.

Dr. J. L. H. Down was the medical superintendent of the Earlswood Asylum for Idiots ("idiot" then being a formal medical term) in Surrey, England, in the mid-1800's. The scientifically-oriented members of the British upper classes were searching for a set of criteria by which to classify mental defects. Dr. Down published a paper in 1866 in *London Hospital Reports*, entitled "Observations on the Ethnic Classification of Idiots." The paper attempts to organize the hospital's afflicted according to some of the quasi-scientific beliefs of the day. The essential factors are the recapitulation theory of Ernst Haeckel, and the so-called "threefold parallelism," often associated with Louis Agassiz.

Haeckel's theory of recapitulation [ESD 7, TPT 24], summarized by the phrase "ontogeny recapitulates phylogeny," argues for a linear relationship between the development of an embryo and the complete evolutionary history of that organism's ancestors. Mammals, in this model, pass through a fish stage (explaining the gill slits that appear and are later reabsorbed), an amphibian stage (a tail that appears and then disappears), and a reptile stage (recognized by the early presence of a three-chambered heart, which later develops into the mammal's four-chambered heart). Throughout the 19th and well into the 20th centuries, recapitulationists worked to extend this model, not just to humans, but to races and other groups within humanity. Europeans "ranked" races, with themselves at the top (naturally), traditionally followed by Orientals, American Indians, Malay, and finally, Africans. In their view, Europeans were more advanced than Orientals because they were more developed, embryologically and evolutionarily [ESD 27]. "Born criminals" were argued to be atavisms, or throwbacks, to these earlier evolutionary stages [ESD 28].

In what became known as the threefold parallelism, some scientists argued that there was a correlation between embryology, paleontology, and comparative anatomy. The connection between the first two implies that modern humans are "more evolved" than our ancestors. An important additional implication was that our adult ancestors were mentally equivalent to modern children; this followed from the argument that the orthogenetic process did not stop at birth, but continued through growth to adulthood. The third parallel offers that modern members of non-White races are analogous to our ancestors. Continuing this logic, adult Africans are the developmental equivalent of European children, at least mentally. This argument was often used to justify the imperialist and colonialist policies of the age. Down was part of an informal movement that wanted to extend the threefold parallelism to a fourth area: mental health. [See IHL 8 for how this view influenced Sigmund Freud.] Down, in short, attempted to classify mental deficiencies by correlating them with the five or so racial "stages" of the threefold parallelism. Correlations to the other groups were quickly forgotten, but references to the Oriental group – which Down referred to as "the great Mongolian family" – made their way into the medical mainstream.

Gould includes a discussion of the social and racist positions of the time. He notes that Down himself was a liberal of his day, in that he believed in a common ancestor for all races, rather than "lower" races representing separate acts of creation [see the following essay]. Down's theory attracted some interest, but never swept the field. Discovery of Down's syndrome in oriental and all other racial groups was only one problem that led to the collapse of his mental defect model, although the recognition of this coherent set of symptoms remained. Recapitulationism itself suffered greatly with the rediscovery of Mendelian genetics in 1900, but did not fall away completely until the modern synthesis took hold in the 1930's and 40's. Nonetheless, the term "mongolism" was still a recognized medical term when Gould wrote this essay in the 1970's. He argues that it should be formally retired, not simply because it is derisive, but because it is wrong. [Not long after he wrote this, it was; the condition today is simply known as Down's syndrome.]

TPT 16. Flaws in the Victorian Veil

Louis Agassiz was the first great American natural historian, although like so many great Americans, he was born elsewhere – in this case, Switzerland. In Europe, he was a student of the legendary Georges Cuvier; he became the world's leading expert on fossil fishes, and discovered the existence of ice ages. After coming to America in the 1840's, he built the original wing Harvard's Museum of Comparative Zoology in 1859. He believed in the ancientness of Earth (that is, more than 6000 years), but died in 1873 as one of the last holdouts against evolution. What inspired Gould to write this essay, however, was not his contributions to science, but rather how this great Victorian gentleman viewed race in both America and the world. Differences between the glowing pseudo-biography written by his widow Elizabeth – herself the founder and first president of Radcliff college – led Gould to track down his original letters, which happened to be kept in the very building in which he worked. These letters make it clear that Agassiz had a viscerally negative and fearful reaction to the black servants at the Boston clubs he attended (he had met no blacks in Europe). While a loyal ally of his adopted Union and an opponent of slavery, he was no egalitarian; these blacks might be human, but they were in no way equal to whites. His later writings argued for continued separation of the races, so as to maintain the white's "ethnic purity." As to the large number of clearly mixed-race people in the South, he blamed the seductive powers of the black women with subverting the otherwise-virtuous southern gentlemen.

In the middle of this essay, Gould presents some additional background on the racial views held by the educated upper classes America at this time. One of the debates in the decade before the Civil War, we are told, was this: was Adam the ancestor of all people, or only white people? That is, are blacks (and Indians) the brothers of Americans, or separately-created species with many resemblances? On one side of this debate were the *polygenists*, who held that each major race had been created as a separate species. On the other side were the *monogenists*, who advocated a single origin (with Adam), and that the different races were created in different regions, and represented different levels of degeneration since then. As Gould notes, there were no egalitarians in the debate, nor any evolutionists. Agassiz had been in the monogenist camp when he first came to America, but converted to polygenesis after his exposure to black servants. Gould presents some quotes from Agassiz's letters that are shocking today. Gould reiterates his view that it is important to study and understand the views of earlier generations on such matters, rather than to forget them.

TPT 17. The Episodic Nature of Evolutionary Change

This is Gould's first explicit discussion of punctuated equilibrium [sometimes written in the plural, punctuated equilibria] in his monthly essays, although he has alluded to parts of it previously (see ESD 6, for example). [Gould and his colleague, Niles Eldredge, first published their seminal and controversial paper on this topic in 1972. It was based in part on earlier work by Ernst Mayr and others. This essay was written some five years later, in 1977.] Punctuated equilibrium, also referred to as "punk eek" and PE, made Gould and Eldredge famous (and to many, infamous) within their professional community. The phrase was borrowed from the old soldier's saying that war is "long periods of boredom punctuated by short periods of terror." In this essay, Gould discusses the history of thought on how new species arise, beginning with Darwin, and then discusses the key points of PE within this historical context.

Gould begins by quoting parts of a letter from Huxley to Darwin on the eve of the publication of *Origin of Species* in 1859. Huxley promises to fight tooth and nail for the concepts of evolution and of natural selection, but questions Darwin's commitment to slow and continuous evolutionary change. His argument is that the fossil record does not clearly support it, and that his theory does not require it. Darwin, Gould claims, is following the gradualist or "uniformitarian" reasoning brought to geology by his friend and mentor, Charles Lyell [ESD 18]. Darwin (we are told) believed that species are continuously "drifting" in form as time goes by in response to the environment: sometimes faster, sometimes slower, but rarely static. In this view, a species is not a true entity in nature; it is merely a snapshot in time of a continuously evolving sequence.

[To be sure, Darwin's view of *phyletic gradualism* does allow for the creation of new species as well as the continuous modification of existing ones. A given species is continuously producing "variants," much as new breeds of pigeons are produced by breeders; with enough time, those variants that survive and continue to evolve will become new species, and even new genuses and families. The only figure in *Origin of Species* appears in the critical Chapter 4, on natural selection itself; it shows evolution as a branching bush, not a ladder. The main differences between Darwin and Eldredge/Gould are how quickly new species can actually arise, and – just as importantly – the rate at which evolution proceeds once the species is established.]

What the fossil record appeared to show in Darwin's time were geologically abrupt extinctions, followed by the similarly sudden appearance of new, "fully formed" species. Darwin attributed this to the highly fragmentary nature and low time resolution of the fossil record. He believed that, as more and better strata were found, the record would bear out the gradual nature of speciation, phyletic change, and extinction. In fact, the opposite occurred. More and better strata were discovered, but both the appearance and disappearance of the fossils in this record were found to be more abrupt than ever. Further, during the millions of years in between, each species remained virtually unchanged; this is referred to as *stasis*. [Both Eldredge and Gould started their careers looking for gradual changes over time, expecting to find them. Gould looked at land snails, Eldredge at trilobites. Eldredge once reportedly commented – in frustration – that the trilobites almost seemed to not *want* to change.]

What their 1972 paper did, in essence, was to suggest that the fossil record was not a false representation of nature (due to poor preservation), but actually an accurate one. They argue that virtually all evolutionary change occurs during the punctuations of speciation, and almost none during the periods of stasis. This is primarily an empirical argument; the key point is that this appears to be what the fossil record says. They add, however, that mutations can make their way through small populations far more easily than large ones; this would be consistent with stasis in large populations, along with the sudden appearance in the fossil record of apparently "new" species – once their numbers grow large. Much of their argument goes to the point that their model does not challenge Darwin's mechanism of natural selection; rather, they claim it only challenges Darwin's unnecessary argument for gradual but continuous change. Gould adds that PE requires no new evolutionary mechanisms. The paper and the essay also carefully point out that by “sudden” species formation, they are still referring to a geologic and sedimentary timescale. In this essay, Gould states that the time required to create a new species is on the order of hundreds to thousands of years. [Elsewhere he uses an even higher range.] This process is still far too slow to be observed by any of the organisms living through it, he argues; but it is quite short compared to the lifetime of a typical species. Gould includes an extended discussion on how the culture that scientists live in can affect their thinking toward concepts such as gradualism (“stability” and “progress”) and sudden events (“catastrophes” or “revolutions”). [He discusses punctuated equilibrium in detail next in TFS 11 and ELP 19.]

TPT 18. Return of the Hopeful Monster

In 1940, geneticist Richard Goldschmidt wrote a book arguing that evolution did not always proceed in a gradual, continuous fashion. That is, he argued, macroevolution was not in all cases – or even in most cases – simply microevolution plus great amounts of time, as Darwin believed. The timing of the book’s publication coincided with the formation of the modern evolutionary synthesis, a new consensus and soon-to-be orthodoxy (in Gould’s words) that concluded the opposite. Goldschmidt became one of the faces of the opposition for the synthesis community. In this essay, Gould argues that many of Goldschmidt’s arguments are indeed valid, and states his expectation that he will be at least partially vindicated in years to come. He adds that, despite claims by both the neo-Darwinist supporters of the modern synthesis and Goldschmidt himself, these views are not in conflict with Darwin’s theory of evolution.

The modern synthesis derives its name from its unification of knowledge from geneticists, paleontologists, field naturalists, embryologists, and members of other fields. It is an extension of population genetics, which argues that what we observe macroscopically as evolution is correlated microscopically with changes in gene frequency within a population [see TPT 8]. The modern synthesis concludes that Darwin’s two-stage statistical process (random variation, then natural selection), rather than a single-step “directional” process such as orthogenesis or Lamarckism, is the dominant mechanism behind evolutionary change. Another important tenant of the synthesis is Darwin’s view of continual gradualism in evolution. This view implies that all phyletic change is accomplished by a large number of very small steps, each of which offers a slight advantage to the host, and is thus selected for. Goldschmidt concurred with the first of these two tenants (as does Gould, in this essay), but opposed the second. While agreeing that microevolution worked as the neo-Darwinist consortium claimed, he argued that macroevolution was *not* a simple extension of this process; some of the key changes were, in fact, abrupt. He agreed that most such macromutations would be highly disadvantageous, if not immediately fatal, for the creature in question. Nonetheless, occasionally, such a change could lead to a significant advantage. He referred to such organisms as “hopeful monsters.” Goldschmidt had studied embryology, and offered evidence from this field to support his views. In this partially political struggle, the neo-Darwinists won and Goldschmidt lost.

Gould proceeds to make a series of arguments in support of Goldschmidt's views. The first is that, in his opinion, continuous change cannot explain all macroevolutionary events. He begins by reiterating a point from the previous essay: empirically, there is little evidence in the fossil record for continuous transitions at the species level. [This argument has been abused by creationists to argue against the process of evolution generally. Gould, of course, refutes this interpretation in many essays. He also notes that there are numerous cases of gradual transitions in the fossil record at higher levels; see ELP 6 and DIH 28.] He next raises the familiar challenge to Darwin's theory of how half a wing or half an eye could be adaptive, and thus selected for. The standard response, he argues, is *preadaptation* (also referred to in these essays as *exaptation* and *coaptation*); this proposes that many important structures originally supported another purpose, and only when available were pressed into service for their current function. Gould is a great supporter of this mechanism [TPT 1, BFB 9 & 20], but argues that it cannot explain everything. One of the examples he presents is that of certain snakes on the island of Mauritania that have an upper jaw split into two parts, front and back, which are connected by a hinge. This feature appears in no other vertebrate, but is a useful adaptation in that it allows the snake to eat food it would not otherwise be able to. Gould references a paper suggesting that such a modification almost had to have occurred via a discontinuous transition, rather than a gradual sequence of intermediate steps.

Another of Gould's arguments is that the sorts of transitions proposed by Goldschmidt are not in conflict with Darwin's theory. The historical context of this debate is whether natural selection, Darwin's preferred mechanism, can act as a *creative* force in evolution, or only as an executor of the unfit. The latter view dominated most evolutionary thinking until the rise of the modern synthesis; one of the most important aspects of the synthesis is the acceptance of natural selection as a mechanism by which new species can arise. The neo-Darwinists saw Goldschmidt's views as a threat to the acceptance of this mechanism, and thus the entire synthesis. Goldschmidt himself concurred that this undercut Darwin's original argument. Gould, on the other hand, argues that there is a place for both. In the case of the snake just described, a macroscopic change might first have created the split upper jaw, but it then took more conventional microevolutionary processes to create the species that exist today. Further, numerous other gradual changes to both the physical structures of the snake and its behavior to capitalize on the new design would then likely have occurred. The neo-Darwinists, Gould claims, misrepresented Goldschmidt's position by claiming that he argued that the new species would have come into existence, wholly formed, in a single step. This would be virtually impossible, on the grounds that it would require multiple simultaneous and adaptive genetic changes. [This position, a form of saltationism, was advocated after the rediscovery of Mendel's genetics in 1900; it seemed to make sense that a change or mutation in one gene would lead directly to a new species. Early experiments with fruit flies quickly showed that this was not the case. The modern synthesis notably rejects saltationism.]

Gould concludes with a discussion of the evidence that Goldschmidt offered in defense of his model, and finds most of it to be valid. Goldschmidt studied the embryological development of gypsy moths. He found that small changes in the *timing* of the development of the embryonic insect resulted in major changes in the coloration patterns of the mature caterpillars. Remarkably, he identified the genes responsible for these small changes in timing (in 1918!). His recognition that some genes did not code directly for structures, but rather controlled the timing and activity rate of other genes, is both fundamentally important, and (in Gould's view) underappreciated. Goldschmidt's 1940 book explicitly discusses how a single change in these important "rate genes" can lead to significant changes in the structure of the adult organism. [Gould argues that the difference between human and chimpanzee brain size is likely attributable to such a change in ESD 7. While Gould does not mention it here, Goldschmidt's perspective is clearly supportive of his punctuated equilibrium model. He continues the discussion of regulatory genes and in HTHT 14 & 15.]

TPT 19. The Great Scablands Debate

The first half of this essay is a case history in the debate between catastrophism and gradualism in geology in the 1920's, with the revolutionary catastrophists winning out over the dogmatic gradualists. When Charles Lyell had established the principles of gradualism in the early science of geology in the 1830's, he banished large-scale catastrophic events, virtually without exception [see ESD 18]. This perspective became the new orthodoxy of both the geological and paleontological communities, Gould states. He advocates a more pluralistic perspective. [Gould had a vested interest in this struggle, of course, as his model of punctuated equilibrium is consistent with geologically sudden events.] In the second half, however, he describes how his research into this particular case shows a more nuanced story.

The scablands are a huge area in eastern Washington, covering thousands of square miles. Part of the Columbia River plateau, the land was formed by ancient basaltic lava floods, which were then covered by a layer of loess (wind-borne, loosely-packed sediments built up during the ice age.) Today, there are dozens of interlaced channels, some miles wide, carved through the loess and deep into the basalt. By the 1920's, everyone agreed that the channels were carved by water. The pervading "gradualist" view at that time, as expressed by the US Geologic Survey, was that the channels had been carved by glacial meltwater, with flows a few times larger than the Columbia River that flows around the area today. A scientist named J Harlen Bretz (no period after the "J," we are told) started a controversy in 1923 by arguing that the entire scablands were instead carved by a single, catastrophic flood. He based his argument on the geological evidence he had gathered at the site, which included unlikely locations for huge boulders and deep gouges and scrapes in the hard basaltic bedrock. These characteristics, he said, were not consistent with a steady-state river. In 1927, Bretz presented his arguments directly at a meeting of his scientific opponents, who remained unconvinced (Gould presents a list of quotes from some of the more powerful members). The geological sticking point, as opposed to the philosophical opposition to anything catastrophic, was a source for the huge amount of water that all agreed would have been required to do the carving. Bretz offered no serious proposals; he did not know, he said, but argued that it was irrelevant to his point. Some years later, the source of the (liquid) water was discovered: it was a large lake formed from glacial meltwater over an extended period.

This fossil lake, now known as Lake Missoula, was on the other side of the Idaho panhandle in Montana. The lake was dammed by the edge of the retreating glacier, and when this dam collapsed the flooding resulted. Catastrophism wins – and the gradualist orthodoxy has to admit defeat!

Not so fast, Gould tells us. In reviewing the minutes of the 1927 meeting, Gould concludes that the establishment was not being unreasonable when they objected to Bretz's model. First of all, the amount of water required was indeed huge, and no one could figure out how to melt the glacier that fast. (Before the existence of the fossil lake was discovered, it was assumed that the glacier itself had to be the source of the water. No one could – then or now – come up with a supportable mechanism to melt the amount of ice that Bretz's argument required so quickly.) That is, no one could come up with a rational mechanism. Gould makes an analogy to the theory of continental drift; until a mechanism for how something can occur is established (in that case, plate tectonics), no amount of geologic, stratographic, or fossil evidence would turn the tide [see ESD 20]. Bretz could point to boulders and gouges forever; until a source for that much water could be determined, the community at large would not – and, arguably, should not – modify the established paradigm.

The story continues. The geological establishment had their own evidence to present as well; it was apparent even then that the scablands could not have been formed all at once. In fact, we now know that there were at least eight [and as many as 100] separate times in which the ice dam broke and then reformed, refilling the lake. When aerial photos of the scablands were finally taken, a new feature was observed: gigantic "ripples" in the streambeds, some more than 20 feet high. Bretz never noticed them because they were too large to be recognized from the ground. Scientists and engineers determined the flow rate from the size of these fossil ripples. The biggest floods were certainly catastrophic by any standards: water 250-300 meters deep, moving at 15-25 km/hr (50 mph!), with the lake taking a week to drain. However, this also confirmed that even this huge fossil lake did not contain enough water to form the entire scablands at one time. Gould admires Bretz for sticking by his observations and his guns. But he also acknowledges that Bretz was "wrong" in his argument for a single catastrophic event (he later changed his position on this). He notes in closing that Bretz lived long enough to see his (modified) position accepted. The Geological Society of America awarded him the Penrose medal, their highest honor, in 1979.

TPT 20. A Quahog is a Quahog

One of the issues raised by any theory of evolution – Darwin's, Lamarck's, or others – is simply: "Are species real?" They certainly appear to be; we have distinct Latin names for every species of bird we have discovered, for example. Plato thought of species as abstract, perfect "forms," which individual organisms could only approach [HTHT 6]. Most western pre-Darwinian biologists, including Agassiz and Linnaeus himself, thought of species as individual thoughts in the mind of God [IHL 21]. Evolutionary thought, in contrast, requires a different perspective. Instead of individual, fixed creations, each modern species arose from an earlier one via some transformational process. In such a paradigm, does the concept of species as a natural, “real” entity still exist? Both Lamarck and Darwin concluded that it did not; that what we think of as permanent species were only momentary snapshots of a continuously changing lineage. Despite this, we are told, both men formally named and described thousands of such temporary fictions. At the end of the essay, Gould discusses how the punctuated equilibrium model restores the “reality” of the species concept, albeit not during the (geologically short) period of speciation itself.

The majority of this essay focuses on a slightly different and more recent form of this debate. One of the founders of population genetics and the modern evolutionary synthesis, J.B.S. Haldane, wrote in the mid-20th century: “The concept of species is a concession to our linguistic habits and neurological mechanisms.” On the other side, another great evolutionary biologist of the 20th century, Ernst Mayr, countered: “Species are the product of evolution and not of the human mind.” Mayr argued from the perspective that members of a species not only resembled each other more than other organisms, but that they interacted via interbreeding. Whom shall we follow? Gould sides with Mayr, and credits him with the “offbeat but . . . persuasive line of evidence” that follows. (Gould mentions that Mayr encouraged him to write this essay.)

If species as we know them are simply a product of the human mind (Mayr asks), would we not expect other, non-western cultures to group individuals differently? Mayr himself, as a young man, studied birds on the island of New Guinea. During this period, he lived in the forests with the “stone age” Fore people. Mayr was impressed to discover that individuals in this community had names for virtually all of these “species” as well, and that there was an almost perfect one-to-one correspondence between the Fore names and the western, Latin names. Later, in 1966, another young scientist named Jared Diamond published a more extensive study of the Fore people, and confirmed the correlation of their “folk taxonomy” to ours. [Diamond would go on to more widespread fame later as the author of the 1997 book *Guns, Germs, and Steel*.] The essay goes on to discuss further examples from other parts of the world. Mayr concludes, and Gould concurs, that this evidence supports the perspective that “species” (as westerners understand the concept) is not a culturally-dependent invention, like music or language, but a representation of an external reality.

Gould notes a second interesting lesson from the folk taxonomy studies. Our western taxonomic structures above the species level – genus, family, order, and so on – are recognized as artificial. Non-western cultures categorize these larger groups as well, but with far less similarity to our Linnaean taxonomy. The main differences involve relative importance to humans, rather than what we now recognize as degree of common descent. We do the same things in our own lives all the time, Gould says; bugs are bugs, for the most part. He recounts a story of how he was “corrected” by a New Englander when he referred to a quahog – a type of shellfish – as a “clam,” a term which he used more generically (literally). This exchange produced the essay’s title.

TPT 21. An Early Start

In the 1950's, the prevailing paradigm regarding the origin of life on Earth was that it had taken a long, long time to develop. The age of the earth was known to be some 4.5 billion years by then, but there was no evidence of life at that time prior to about 600 million years. Since even the simplest single-celled organisms are remarkably complicated, the conclusion was that the steps required to go from amino acids to the first cell took billions of years. During the next few decades, however, evidence appeared that indicated bacteria and other prokaryotes (small, simple one-celled organisms with no nucleus or other organelles) existed at least two billion years ago. In this essay, Gould discusses two important scientific papers published in 1977 that strongly indicate that life first appeared well before this, in fact not long after earth's crust solidified and oceans formed. The significance, Gould tells us, is that life can form very quickly, once certain conditions such as liquid water are met. If so, this would suggest that the formation of life may be almost inevitable under such conditions. This has implications for the existence of single-celled life on other worlds. [A recurring theme of Gould's is that the "inevitability" of prokaryotic life in this environment should not be confused with the inevitability of intelligent life. He believes the probability of the latter is remote indeed; see LMC 18, and his books *Wonderful Life* and *Full House*.]

In the 1950's, Harvard paleobiologist Elso Barghoorn, with Stanley Tyler, discovered prokaryotic microfossils in the Gunflint Formation, which is located along the northern edge of Lake Superior. The Gunflint Formation consists of fine, alternating layers of iron-rich deposits and silica-rich chert, and has been dated at about 2 billion years. This discovery proved that prokaryotic life existed that far back, but still left billions of years for the "slow development" paradigm to work. In 1967, Barghoorn and colleagues found microfossils in the geologically similar Fig Tree Series of South Africa, dated at 3.1 billion years. However, these structures were not very well preserved, and there were serious questions about whether they were produced organically. The first paper from 1977 that Gould draws on is again from Barghoorn; this time he offers almost irrefutable evidence of bacterial and algal prokaryotic life in the Fig Tree Series. The evidence that these microscopic, sphere-like bodies were in fact remnants of bacteria is as follows. First and second, the average size and the size distribution of the structures are consistent with modern bacteria. Third, many are distorted in a way that is consistent with what bacteria do when they die. Fourth, a significant percentage appears to be dividing. And finally, the ratio of carbon-12 to carbon-13 is consistent with organic processes (bacteria preferentially choose carbon-12 out of the environment when performing photosynthesis.) Also, better dating put the age of these fossils at 3.4 billion years.

The second 1977 paper arguably pushes the origin of life back even further. Carl Woese, a scientist from the University of Illinois, used genetic sequencing – then in its infancy – to discover that certain types of methane-producing prokaryotes were not bacteria at all. In a seminal paper with G.E. Fox and others, Woese demonstrated that these methanogens are far more like each other, genetically, than they are like any of the bacteria or blue-green algae. Later studies of their biochemistry confirmed these results. Woese argued (Gould states) that these methanogens should be classified as a sixth kingdom of life. [See ESD 13 for a discussion of the other five.]

[In fact, the final result would be a more revolutionary taxonomy. A category above kingdom was created, called *domain*. The methanogens were all placed into the domain of Archaea. Bacteria, blue-green algae and other prokaryotes with "conventional" biochemistry were placed in the domain Bacteria. Finally, all organisms containing eukaryotic cells (with nuclei and other internal organelles) were collected into the domain Eucaryota. Thus, Eucaryota includes the kingdom of Eukaryotes (single-celled organisms with nuclei) as well as the more familiar multicellular kingdoms of plants, animals, and fungi. Interestingly, the Eucaryota, which includes ourselves, are more closely related to the Archaea than they are to the Bacteria. This has important implications regarding the origin and descent of eukaryotes and multicellular life.]

Bacteria, blue-green algae, and all eukaryotes can survive in the presence of oxygen; methanogens cannot. (They exist today in many anaerobic environments, from swamps to the digestive tracts of many animals, including us.) Since Earth's early atmosphere contained no free oxygen but lots of carbon dioxide (which methanogens can tolerate), it seems highly likely that methanogens existed before bacteria. Further, all of these organisms must have shared a common ancestor; we infer this from the fact that they all use the same genetic material and code. Since the microfossil evidence of Barghoorn demonstrates that bacteria were thriving some 3.4 billion years ago, it seems highly likely that the common ancestor of bacteria and methanogens existed even earlier. Life – at least, very simple life – appears to have arisen on Earth not long after the oceans formed.

TPT 22. Crazy Old Randolph Kirkpatrick

Randolph Kirkpatrick was a scientist and curator at the British Museum from 1886 to 1927, and continued to work until his death in 1950. One of his areas of expertise was sponges, both living and extinct, and he frequently traveled to obtain specimens. In 1912, he went to a small volcanic island in the Atlantic Ocean off the coast of Morocco. He was after a puzzling species of sponge that seemed to have both calcareous and silica components. [Marine life makes "hard parts" out of only three substances: silica, which is silicon dioxide, like quartz and glass; calcium phosphate, known mostly for vertebrate bones and teeth although also found elsewhere; and calcium carbonate, which makes up almost everything else, including shells and coral skeletons. The term "calcareous" refers to calcium carbonate.] Many sponges have no hard parts at all. Some have "spicules" (small, sharp rods or "stars") made of silica; others build more massive calcareous structures. At the time, it was believed that no sponge could include both silica and calcite structures; yet this, and a few other species from the Pacific, appeared to. (More have been found since then, Gould reports.) Others had argued that the silica spicules had contaminated the clearly calcareous sponges in some way. Kirkpatrick effectively showed that they grew within the sponge; they generated both materials.

The coral-like characteristics of the calcareous skeleton reminded Kirkpatrick of something he had seen elsewhere: the extinct, mysterious fossil *stromatoporoids* and *chaetetids*. These fossils were grouped with corals due to their structure and calcareous composition, but had many anomalous features, and were one of the major taxonomic puzzles of the day. Kirkpatrick's creative mind sparked, and he looked for something in a preserved stromatoporoid that no one else had thought to look for: silica spicules. He found them, and thus resolved the mystery; stromatoporoids were sponges. However, his work was ignored at the time, and not rediscovered until the 1960's. The reason is that, on a separate front, he began to argue for a theory that was so crazy that it discredited everything he did.

While on that volcanic island in the Atlantic in 1912, a coworker brought him a piece of volcanic rock from the island's summit. Examining it, Kirkpatrick believed he saw traces of nummulites. Nummulites are a type of calcareous fossil, associated with single-celled forams, but can grow quite large – an inch or more in diameter. They are disk-shaped, resembling coins. (They are actually tight spirals, comprised of thousands of separate, adjoining living chambers.) Finding these objects in sedimentary rocks is quite common; there are types of limestone that are entirely composed of them. But finding them in volcanic rock was certainly unexpected; the heat associated with the formation of igneous rocks is sufficient to preclude the preservation of fossils of any type. Also, volcanic rocks are made of mostly silicate materials. Somehow, Kirkpatrick concluded that the volcanic rock did not simply *contain* nummulites; he convinced himself it was entirely composed of them. Therefore, he continued, these rocks could not actually be "igneous" in origin, but must reflect a sedimentary process. He proceeded to examine volcanic rocks from all over the world, and everywhere he saw the characteristic disk-shapes of nummulites. (Apparently no one else could. He began publishing his papers himself when all of the reputable journals appropriately refused to publish his work.) On a roll now, he established a new paradigm of early life: that the seas, free of predators, had originally been packed nothing but nummulite-producing forams, which he named *Eozoon* ("dawn animal"). The seafloor was not comprised of igneous basalt, but rather of the heated, compressed, and silica-infused remnants of trillions of Eozoon skeletons. Much of this ancient sea floor was now land.

This is all just plain crazy, Gould acknowledges. But he defends Kirkpatrick the man, if not the nummulitic theory. It is the same attributes of assembling seemingly disparate facts, and sticking to his conclusions in the face of general (if not universal) resistance from his peers, that allowed him to solve the problems of coralline sponges and the puzzling fossil stromatoporoids. Gould notes that the final price that Kirkpatrick paid for his "crackpot" theory of nummulites was not to be vilified, but forgotten – even for his legitimate accomplishments.

TPT 23. Bathybius and Eozoon

Prior to the 19th century, it was widely believed that living and non-living things were composed of different kinds of matter. By Darwin's time, it was known that life was composed of common elements, albeit their chemical structures were exceedingly complex. This posed no problem for the creationists of the day (which included most scientists); God simply created each of these complex species as they now existed, along with the ability to reproduce. Evolutionists, however, faced a problem: they had to assume that, at some point in Earth's history, life evolved from non-living material. What might these intermediate states have looked and acted like? The fossil record was of little help; it showed evidence of "fully formed" organisms appearing in the Cambrian period, and nothing before then. [Simpler prokaryotic cells were later found in pre-Cambrian rocks; see TPT 21.] This left the proponents of evolution to speculate on the nature of this proto-life between inorganic and organic matter. This essay discusses the "discovery" of two such organisms, both of which turned out to be something else entirely. Gould uses these examples to reiterate his perspective that scientists do not and cannot see "facts" in a purely objective manner; all facts must be viewed in the context of some sort of model or theory.

Ernst Haeckel (1834 – 1919), a key supporter of Darwin's theory in Germany, argued that the "missing link" between these two worlds would most likely be composed of unorganized protoplasm. (He correctly recognized that even the single-celled amoeba was too complex, as it included sophisticated structures such as a nucleus.) Thomas Henry Huxley (1825 – 1895), friend and defender of Darwin, read Haeckel's hypothesis and was swayed by it. Huxley considered the deep sea floor to be a likely place to look for evidence, and in 1868 examined a sealed container of mud dredged from the bottom of the Atlantic some eleven years earlier. He found what he was looking for, or so he thought: a gelatinous substance that permeated the mud, without a well-defined structure. Under the microscope, there were no nuclei or other organelles, but embedded throughout there were small disks made of calcium carbonate, called coccoliths. Huxley identified the jelly-like substance as Haeckel's primordial organism – still, apparently, in existence – with the coccoliths as the proto-skeleton. He named the material *Bathybius haeckelii*, after Haeckel, who was pleased. Other stored samples from around the world's seafloors showed similar results.

Slightly earlier, in 1858, a Canadian geologist thought he found evidence for pre-Cambrian life in rocks from the area around Ottawa. The structures consisted of interleaved layers of silica and calcium carbonate. Some better specimens were found in 1864 and shown to J. William Dawson, Canada's leading paleontologist. Dawson (1820 – 1899) found "canals" through the carbonate material, and concluded that the rock was indeed organic in origin; he concluded that it was probably the amalgamated skeletons of a large foraminifer, a type of algae. Its age and relative simplicity again met the expectations of what the evolutionist community was looking for. Dawson named the organism *Eozoon canadense*, or "Canadian dawn animal." Darwin himself was sufficiently impressed with this find to mention it in a later edition of *Origin of Species*. Some argued that *Eozoon* represented a more developed stage of *Bathybius*.

Together, *Bathybius* and *Eozoon* were a hot topic for several years. But in the 1870's, during the famous *Challenger* voyage to explore the world's oceans, no samples of *Bathybius* were found in any of the deep-sea dredges – until alcohol was added to the samples as a preservative. It turned out that the gelatinous substance that Huxley had found was a precipitate caused by the reaction of the alcohol with the seawater and mud, and not organic at all. All of the examples that Huxley had examined had been similarly preserved. (The coccoliths turned out to be organic in origin, but are actually fragments of plankton skeletons.) When informed, Huxley behaved properly and published a letter in the journal *Nature* retracting his views. *Eozoon* lasted longer, but suffered from the fact that the rocks in which it was found were all metamorphic. Having been exposed to great heat and pressure, it was always difficult to support an organic origin; blocks of limestone ejected from Mt Vesuvius in 1894 that contained *Eozoon* ended all remaining support for an organic origin. [The *Eozoon* that Kirkpatrick claimed to identify in the 1950's – see the previous essay – was quite different.]

Gould returns to his point that scientists do (and must) view data with some sort of theory in mind, in order to make sense of what they see. With great frequency, these models are incorrect, and as a result the data is often misinterpreted. This is the nature of science; however, such errors often lead to fruitful lines of research. Science, at its best, is self-correcting – although sometimes this can take a long time [see, for example, TPT 10]. Gould expresses his admiration for Huxley for quickly recanting his views when the evidence showed them to be wrong. He goes on to state that the assumptions that early life had to be homogeneous, diffuse, and formless were both unfounded and incorrect; early life is small and without nuclei or organelles, but are certainly well-defined [TPT 21]. [Gould does not discuss the fact that the origin of these early prokaryotic cells from non-living chemicals remains a mystery.]

TPT 24. Might We Fit Inside a Sponge's Cell

With *Origin of Species*, Darwin convinced the scientific community that current life evolved from earlier life, and that all life shared a single common ancestor in the distant past. With the acceptance of this paradigm shift, one of the primary tasks became the mapping of the "tree of life" back to this origin. The most popular areas of research, naturally, involved our own ancestry: the origin of vertebrates, of land-dwelling tetrapods, of mammals, and of man. The example Gould discusses in this essay goes back even further: the origin of multicellular life. However, the focus of this essay is the development of the methodology by which we determine what the proper genealogical relationships are.

When biologists believed that species were permanent and immutable, there was little insight to be gained from the recognition that human arms, bat wings, and dolphin flippers all employed differently shaped versions of the same bones [but see IHL 21, regarding Linnaeus]. Once the reality of evolution is accepted – via natural selection or some other mechanism – these similarities took on an important new significance: they indicate a common ancestry. At some point, there was a single "tetrapod" with four limbs, each with this characteristic structure; all reptiles, mammals, and birds are its descendents. Structures such as this are called homologies, and the term indicates a common origin. Other characteristics, such as the bones of the inner ear, are shared only by mammals. Since this feature is not shared by all modern tetrapods, we can conclude that mammals formed at some later time. By studying the detailed anatomy of living and fossil organisms, we can find homologies that allow us – in principle – to determine the structure of life's history.

There are two major obstacles facing this approach. The first is the fact that the fossil record is sparse, and that only hard parts fossilize (with some rare exceptions). Thus, in most cases, we must try to construct genealogical lineages using only living organisms. Since the common ancestors we seek to identify have been extinct for ages, this greatly complicates the issue. The second problem is that there are also many cases where structures that appear to be similar are not homologies at all, but are instead examples of convergent evolution. One of the most famous examples is the wing of birds, bats, and insects: all support flight, but none of these shared a common ancestor that could fly. Each of these groups evolved flight independently. Such structures are known in the profession as "analogies." If one confuses an analogous structure between two groups for a homologous structure, one is sure to err in the construction of their genealogical relationship. Thus, the biologist confronting the task of deciphering the tree of life is to recognize the analogies, separate them from the homologies, and then construct the evolutionary sequence using only the latter. In principle, this is a straightforward if tedious and complex task, for at the detailed level analogous structures always show far more differences than homologous structures. [The branch of biology known as comparative anatomy focuses on mastering these subtle similarities and differences in both living and extinct organisms. The great scientist Louis Agassiz came to Harvard and founded its Museum of Comparative Zoology, where Gould would later become curator.] In practice, however, it can be very difficult to determine whether a similar-looking bump on the bones of two different groups is a homology or an analogy.

With the great improvements in the microscope during the 19th century came investigations of, among many other things, developing embryos. It was realized that the budding field of embryology offered another window into the history of life. [Barnacles, for example, were finally recognized as crustaceans when the microscope showed their larvae to be very similar to those of other crustaceans; the adults are so different as to be essentially unrecognizable.] It was widely observed that the embryos of all vertebrates developed gill slits; these remained for fish and sharks, but were later reabsorbed by reptiles and mammals. From this and other valid and fascinating late 19th-century observations, some scientists proposed that embryos were actually re-living their evolutionary history as they developed. Credit for the theory of "recapitulism" is usually given to Ernst Haeckel, and known by its catchphrase, *ontogeny recapitulates phylogeny*, although a great deal of earlier work had been done [see IHL 27]. (Ontogeny refers to the development of an individual from egg to adult, and phylogeny refers to the evolutionary history of that species' ancestors.) The essential assumption of recapitulationism is that evolutionary change occurs only at the end of the procession; thus, the evolutionary history of a lineage can be physically observed by watching the development of the embryo. As Gould describes it, the importance of Haeckel's "biogenetic law" was that it was intended to be a means to use embryology to separate analogies from homologies, and thus advance the effort to understand the structure of the tree of life.

Unfortunately, Haeckel's theory of recapitulation turned out to be worse than incorrect; it proved to be fruitless. It was found that, in embryological development, many steps were usually missing, while others worked in different orders. Contradictory conclusions ruled the day, and scientists were left with only speculation and frustration. The model became doomed with the rediscovery of Mendelian genetics in 1900. Once it was recognized that ontogeny was controlled by a genetic "program," and that all the components of this program were in place from fertilization, it no longer made sense that changes could only be added at the end of the embryo's development. Changes in the genetic code could produce changes at any point, although very early variations in the developmental process are usually fatal. [Nonetheless, Gould acknowledges an affinity for studies involving the intersection of embryology and evolution. Gould's first book, *Ontogeny and Phylogeny* – published in 1977 and aimed at the professional community – discusses these subjects. Near the beginning of this essay, he writes in regard to the connection: "I happen to maintain a strong fondness for it. I also believe that new methods will revive it as a major concern for the remaining decades of our century." He was largely vindicated in this 1979 prediction; the tools of genetic sequencing led to the formation of a new and dynamic field connecting embryology and evolution, known as evolutionary developmental biology or "evo-devo."]

With this discussion completed, Gould turns to one of the most fundamental evolutionary developments in the history of life on earth: the formation of multicellular life ("metazoans") from single-celled organisms that monopolized the planet for most of its history. He presents the two most popular proposed paths. The first, *amalgamation*, hypothesizes that groups of individual cells came together to live as a colony, then differentiated into different types of cells, and eventually developed a technique by which the "group" could reproduce collectively instead of individually. The second, *differentiation*, begins with a larger single-celled organism that develops internal divisions. Hoping for the discovery of fossil evidence is almost certainly futile [but see LSM 21], so we must employ the sorts of techniques described above. The first question that arises is, did multicellular life arise only once, or did it arise multiple times? That is, is the multicellular aspect of (say) plants and animals a homology or an analogy? Most scientists, Gould states, believe that each of the three multicellular kingdoms (plants, animals, and fungi) not only arose independently, but also several times within each of these kingdoms. [This is also mentioned in ESD 15 and LSM 21.]

The simplest members of the animal kingdom are sponges; many have only two types of cells. Some of the most convincing evidence that sponges arose by amalgamation is that certain species can be separated into individual cells by passing them through a fine filter; the individual cells then move independently and re-aggregate themselves into a functional sponge. If all animals arose from sponges – which would imply that multicellularity in animals is homologous – then all animals (including us) arose via amalgamation. But most scientists believe that sponges are not ancestral to any other group of animals. The next group Gould considers is the cnidarians (the "c" is silent), which include corals and related organisms. The consensus is that these also formed by amalgamation; the question that follows is whether corals are themselves the ancestors of other animal phyla or not. If the answer is "no," then one may still argue that the "higher animals" (which include vertebrates) may have formed by differentiation. Gould discusses the work of the scientist who championed this perspective: Earl Hanson of Wesleyan University. Hanson and his allies argued that a group of small and simple but multicellular flatworms (phylum Platyhelminthes) are about the same size as ciliates (a group of single-celled organisms that includes *Paramecium*.) Some species of ciliates have multiple nuclei within their single membrane. Both are about the same size, and have some other important similarities as well, along with significant differences. Within the context of this essay, the question becomes: are the similarities between these two groups homologous or analogous? Gould summarizes the arguments of both sides. He appears to lean toward Hanson's critics, but argues that new techniques involving gene sequencing should soon resolve the issue. If Hanson is correct, Gould concludes, and flatworms (and thus the rest of the animal kingdom) did achieve multicellularity via differentiation, then the bodies of all higher animals are the homologs of a single cell. On the other hand, sponges, (probably) corals, and other multicellular groups are homologs of *colonies* of single cells, via amalgamation. In such a case, the entire human body would be the homolog of a single cell of a sponge; hence the essay's title.

TPT 25. Were Dinosaurs Dumb?

Gould was always fond of dinosaurs. Growing up in the 1940's and 50's, he resented the standard presentation of dinosaurs as stupid, plodding morons who were no match for upstart mammals who presumably stole their eggs and drove them to extinction. By the time he wrote this essay, their reputation had improved significantly. For example, it was recognized that the large sauropods walked on land rather than wallowing in rivers like hippos to support their weight, and that they appeared to live in herds. It had been known for some time that mammals and dinosaurs arose about the same time, and that larger mammals arose only after dinosaurs mysteriously became extinct. Despite this, because the dinosaurs are extinct and mammals are not, most people assumed that mammals out-competed them – presumably because dinosaurs were dumber. [This essay was written shortly before the discovery that the source of this extinction was the result of an asteroid or comet impact; see HTHT 25.]

But were dinosaurs as dumb as textbooks claimed for decades? While noting that brain size and intelligence are not the same thing – he notes that human brain sizes vary from 900 to 2500 cubic centimeters, with no correlation in IQ – he does recognize that the ratio of dinosaur brain to body size is small. However, it has been well-established that brain size in modern animals scales only at about 2/3 that of body mass [see ESD 22]. Gould references the work of Harry Jerison, who found that the average brain size of ten groups of dinosaurs fell almost exactly on the line for reptiles. (Warm-blooded animals of the same body size have larger brains than cold-blooded animals, but both have slopes of about 2/3.) That is, dinosaurs are about as "brainy" as one would expect for a reptile of their size. People do not generally think of snakes or alligators as particularly stupid, and both can prey on mammals. Nonetheless, Jerison found a great deal of variation around this mean. Another investigator, James A. Hopson, examined the data further and found that carnivorous dinosaurs were brainier than herbivores, and more defenseless herbivores such as the duckbills were brainier than the large sauropods or the armored stegosaurs. This is consistent with modern animals, and supports the perspective that dinosaurs were not particularly dumb.

TPT 26. The Telltale Wishbone

This essay discusses the "dinosaur renaissance" efforts of John Ostrom and Robert T. Bakker that began in the late 1960's. These scientists played a large role in convincing both the scientific community and the public at large that dinosaurs were not the slow, primitive, dim-witted extinction-bait that so many believed [see the previous essay]. They are most famous for arguing two points about dinosaurs: first, that they may have been warm-blooded, and second, that birds are in fact living dinosaurs. They proposed a revised taxonomic structure: that dinosaurs should not be classified as an order of reptiles, but rather as a separate class (the next highest Linnaean category, which includes reptiles and mammals) and grouped with birds. All members of this new class, which would be called Dinosauria, are warm-blooded. Gould discusses all of these topics, from the perspective of the late 1970's. He states that he has not made up his mind on the subject, but finds the arguments original and appealing.

To begin with, Gould tells us that the connection of birds with dinosaurs is not new; it dates back to the discovery of *Archaeopteryx* in 1861, only two years after Darwin published *Origin of Species*. T. H. Huxley, Darwin's colleague, argued for such a connection; the structural similarities between Archaeopteryx and a group of smaller dinosaurs called coelurosaurs was striking. This view fell into disfavor in the early 20th century, for a very good reason. While many pre-dinosaurian groups possessed a clavicle, or collarbone, it appeared that no dinosaurs did. Yet birds – including Archaeopteryx – all have "wishbones," which are modified clavicles called furcula. One of the statistical "laws" of evolution is that, once a feature is lost, it cannot reappear later in anything like the same form [see TPT 3; also HTHT 14 for some interesting exceptions]. Thus, scientists argued, birds must be descended from an earlier group of reptiles that were ancestral to both birds and dinosaurs. The likely candidate was a group of Triassic thecodont reptiles called pseudosuchians. Later, however, some species of coelurosaurians were found to have clavicles after all. Later still, John Ostrom of Yale University reexamined in detail the remains of Archaeopteryx, the clavicle-bearing coelurosaurians, and the pseudosuchians. The extreme similarity of the Archaeopteryx to the coelurosaurians convinced him (and Gould) that numerous key structures were homologous [see ESD 24], indicating a direct genealogical relationship. That is, birds are descended from dinosaurs after all. However, Gould strongly cautions, this does not mean that stegosauruses evolved into hummingbirds. All it means is that the direct ancestor of all birds was a single group of small dinosaurs – the coelurosaurians – rather than the older pseudosuchians. [See IHL 23 for Gould's lament regarding this ongoing misunderstanding.]

This may seem anticlimactic to the public, Gould comments, but it is very important to scientists who consider it their task to understand the history of life. It also touches on an important taxonomic debate: the difference between cladistics, which groups organisms strictly by their chronological branching from parent groups, and "traditional" taxonomies [in particular, *phenetics*] that consider shared derived characteristics (e.g., "form") as well as ancestry. In the traditional perspective, lobe-finned fish are grouped with the far more common ray-finned fish on the grounds that they are all "fish." In cladistics, lobe-finned fish are more closely grouped with mammals than ray-finned fish, because lobe-finned fish and mammals share a more recent common ancestor than lobe-finned fish and ray-finned fish. [Cladistics had only been introduced in the 1960's; this essay was written in 1977. However, due in part to multivariate techniques and the reduced cost of computing power, which Gould used to obtain his doctorate – see DIH 27 – and also in part to advances in genetic sequencing, it became the dominant taxonomic paradigm in the 1990's. In a real sense, cladistics is a return to phylogeny; see ESD 24. At this point in his career, despite his previously-stated fondness for phylogeny, Gould states that he tends toward the traditionalist rather than the cladist perspective. In later essays it is clear that he has changed his mind; see DIH 30. The debate may seem esoteric when applied to fish or even birds and dinosaurs, but as one of the figures in this essay shows, it also applies to the relationship of man to the great apes.]

We now arrive at the essay's central question: should birds be recognized as living dinosaurs, or "merely" as their descendents? With the groundwork in place, Gould rephrases this question: should dinosaurs and birds be grouped into the same taxonomic category, i.e., the class Dinosauria? He approaches the problem from the traditional [phenetic] perspective: if birds only obtained "wishbones" from dinosaurs and little else, then the differences in body plan and lifestyle should preclude such a conclusion, and dinosaurs should continue to be grouped with reptiles. If, on the other hand, birds shared other important features with at least the coelurosaurian dinosaurs, then the case would be much stronger. Two key features, required for the fundamental avian characteristic of flight, would be feathers and endothermy (warm-bloodedness). Could birds share these features with at least some dinosaurs?

At this point Gould reintroduces Robert Bakker, John Ostrom's former student, who argues that they do. [Bakker would go on to write the best-selling 1986 book *The Dinosaur Heresies* on this subject. He would also become a technical consultant on the 1993 film *Jurassic Park*.] Gould summarizes what he considers to be Bakker's four main arguments in favor of warm-bloodedness in dinosaurs. The first is bone structure: cold-blooded animals living in areas with pronounced seasons exhibit growth rings in their bones, corresponding to the outside temperature; warm-blooded animals do not. No dinosaur bones show growth rings. Second, dinosaur remains are found in places that, at the time, were close to the poles. No cold-blooded animals today are found at these latitudes. [Critics argued that the poles were much warmer then than they are now.] Third, the ratio of individual carnivores to herbivores seems to match the ratio of warm-blooded mammals today, and not higher ratio of today's cold-blooded reptiles (who need to eat less). And fourth, newer reconstructions of dinosaur anatomy suggests that they are lighter and more agile than previously thought, consistent with a more active, and therefore warm-blooded, lifestyle. [Interestingly, Gould does not discuss the point raised in the previous essay: that brain-to-body sizes differ between warm-blooded and cold-blooded animals, and dinosaurs appear to be consistent with the latter.]

The next topic is feathers, which has traditionally been a problem for Darwinists. Until feathers (and wings) have evolved to the point where they can support flight, what evolutionary advantage would they offer that would give them a selective advantage? Gould and Bakker both support the view that feathers started out as insulation. Coelurosaurs were small dinosaurs, and archaeopteryx were even smaller; and smaller creatures lose heat much more rapidly than larger creatures do, due to their larger surface area to volume ratio. If these creatures were warm-blooded, the need for insulation of some type would be more pronounced. Gould notes that Ostrom believes that Archaeopteryx was not even capable of flight. [Some 20 years after Gould wrote this essay, fossils of dinosaurs – that is, non-avian dinosaurs – with very distinct feathers were discovered in China; see IHL 23.] If, Gould summarizes, it can be shown that birds acquired not only wishbones but also warm-bloodedness and feathers from their dinosaurian ancestors, then he would support grouping birds with dinosaurs in a separate class. It would therefore follow that birds are, by these criteria, living dinosaurs. [As of this writing, the community still appears to be divided on the issue; no such reorganization has occurred.]

TPT 27. Nature's Odd Couples

The extinction of one member of an ecosystem does not usually result, Gould begins, with the collapse of the entire ecosystem. However, there are cases in which one species is completely dependent on another, and extinction of one invariably leads to the extinction of the other. He discusses two such examples in this essay. The first example dates from his days as a graduate student, studying land snails in Bermuda. He often noticed members of a species of large hermit crab (all of which are famous for occupying the shells of deceased snails) struggling with the small size of available shells. One day, he saw a hermit crab in a larger whelk shell, which was much better suited to its needs. It turned out that the whelk shell in question was actually a fossil, washed out of a nearby cliff. There are no living whelks on the island; he discovered that they had all been eaten for food a few centuries before by newly-arrived Europeans. Without a source of new shells, the hermit crabs were forced to contend with shells from unsuitably small snails, and the occasional fossil. Gould laments that such fossils are small in number and will not last indefinitely, and thus the hermit crabs will someday perish as well.

The second example deals with the legendary dodo and a tree called *Calvaria*, which produces fleshy fruit with a robust pit at the center. Both organisms lived on the island of Mauritius in the Atlantic, until the dodos were wiped out in the late 1600's (again by Europeans, with help from the hogs that they brought with them). In 1977, Stanley A. Temple of the University of Wisconsin reported the following story. Only a few of the formerly Calvaria trees still existed, he claimed, and they all appeared to be hundreds of years old. They produced fruit with seeds each year, but none sprouted; it seemed that the pit was too thick. Temple references old reports of dodos swallowing the fruits whole; their stone-filled gut would have significantly worn down the shells of the pits. Sure enough, when the Calvaria pits were artificially abraded, they sprouted. Temple concluded that these new sprouts may have been the first produced in 300 years; Gould is delighted that we may actually have saved a species from human-induced extinction.

In an extended postscript, several of the assumptions in Temple's publication (which partially motivated Gould to write this essay) were later challenged by a local Mauritanian scientist. The challenger concluded that the Calvaria tree was not completely dependent on the dodo, and that there were other reasons for its decline, including invasive species. Gould presents the short version of this rebuttal verbatim, and then presents Temple's counter-rebuttal. Gould credits both sides with good arguments, and declares his own revised position as undecided (although rooting for Temple on emotional grounds).

TPT 28. Sticking Up for Marsupials

South America was an island continent for about 70 million years; during this period, many unique animals evolved there. Then, some two or three million years ago, continental drift brought it close enough to North America for the isthmus of Panama to form. The result was a mass movement of animals between these continents, which also led to a significant mass extinction as "invasive species" drove many natives out. Opossums and armadillos are among the animals that moved from south to north. However, on a large scale, far more animals moved from north to south [but see HTHT 27], resulting in the extinction of many South American mammals, including all of the top predators. Two entire orders of mammals were eventually lost: the notoungulates and the litopterns. (Today, Gould mentions, there are about 25 orders of mammals). Many of these animals superficially resembled camels, horses, rhinos, and rabbits, due to the phenomenon of evolutionary convergence. [The similarity of litopterns to camels led Darwin to make one of the most fruitful mistakes in natural history; see LMC 7.]

Because the South American predators faired so poorly as a group against the North American invaders (primarily the jaguar and other cats), scientists have looked for a structural explanation. The southern predators, it turns out, were all marsupials, while the northerners were all placentals. Therefore, one obvious hypothesis is that the placental form of reproduction is, in and of itself, a sufficiently better adaptation to any given environment than the marsupial form – at least for predators. Gould offers a counterargument, based on the work of his colleague John Kirsch and others, and concludes that this hypothesis is likely false (hence the essay's title).

The immune system of all animals is adept at recognizing the difference between "self" and "non-self" at a genetic level; when working correctly, it will attack the latter and ignore the former. Placental mammals have developed a mechanism by which this process is suppressed for the internally-developing fetus, which is genetically half "non-self." Marsupials, on the other hand, have not developed such a mechanism; they expel the "fetus" after a mere ten days or so of gestation, after which – if fortunate – it makes its way to the mother's pouch, where it completes its development. Kirsch offers a theoretical argument, based on energy invested by the parent, that the marsupial approach is at least as adaptive as the placental approach. Gould goes on to discuss Kirsch's additional argument that Australia and South America, where most marsupials live today, do not represent refuges for mammals that were too inferior to compete with placentals, but were themselves centers of creative evolutionary development.

Yes, Gould acknowledges, carnivorous marsupials were replaced by carnivorous placentals when Panama rose from the ocean. However, he continues, it is probably not safe to conclude that the reproductive strategies themselves were the underlying source of this event. What else could it be? He references some work by Robert Bakker [the same Bakker of warm-blooded dinosaur fame; see TPT 26]. Bakker points out that the carnivores of North America experienced two major extinction events during the Tertiary period, with new groups arising in each case; no similar events occurred in South America. Perhaps, following Bakker's observations, it was these "tests" that produced designs that proved superior to the southern carnivores. Gould adds that H. J. Jerison [TPT 25] has found that the relative brain size of both North American carnivores and herbivores increased significantly over the Tertiary period, perhaps as a result of these extinctions, while those of South America did not. The fact that the two orders of extirpated South American mammals mentioned at the beginning of this essay were both placentals further supports this perspective.

TPT 29. Our Allotted Lifetimes

Many aspects of life do not scale proportionally with size; leg bones of elephants must be relatively thicker than bones of mice, for example [see ESD 21]. In ESD 22, Gould introduced the concept of the mouse-to-elephant curve, which can be used to empirically demonstrate how different features scale with body mass. In that essay, he showed that brain mass scales at a rate of about 2/3 of body mass. However, there is a fair degree of variation around this line. Humans brains, it turns out, lie well above the line; our brains are smaller than those of large whales, but the ratio of human brain size to human body size is the largest in the animal kingdom. He suggests that the mechanism responsible for our unusually large brain is the phenomenon of neoteny [ESD 7 & 8 and TPT 9].

In this essay, he returns to the mouse-to-elephant curve approach to discuss how lifetimes scale with body mass in the animal kingdom. He reports on several studies that show, first of all, that heart rate and respiration rate do scale proportionally over a huge range of body size; in almost all cases, there are about four heartbeats per breath. (Humans follow this closely.) Next, he offers evidence that both of these metabolic functions also scale with body size, albeit not linearly; larger animals breath more slowly and have lower heart rates. However, the number of heartbeats an animal performs over its natural lifetime turns out to be about 800 million, regardless of size. Gould ponders whether a mouse, which lives only a year or two, "lives" as much as a whale, based on this premise. [He returns to explore this line of speculation in LMC 20.] Once again, there is some variation in this rule of thumb, and once again humans are well above the curve; our natural lifetimes exceed this average by about a factor of three. Gould concludes that neoteny, with its general "slowing down" of so many human developmental characteristics, is again probably responsible.

TPT 30. Natural Attraction: Bacteria, the Birds and the Bees

In 1975, a University of New Hampshire scientist named Richard Blakemore published a paper about bacteria that "grew" microscopic magnets inside their bodies. These bacteria were found in ocean sediments off the coast of Massachusetts. The "magnets" were actually strings of about twenty cubes of magnetite (Fe_3O_4), each about 500 angstroms on a side. [An angstrom is one-tenth of one-billionth of a meter, or 10^{-10} meters.]

An MIT-based colleague of Gould's and an expert in magnetism, Richard B. Frankel, collaborated on the study. Frankel showed that the size of each cube was critical; much larger or much smaller and the magnetite would not have been magnetic. He also showed that the aggregate collection of these cubes within each bacterium was sufficiently large to allow the host to determine its orientation with respect to Earth's magnetic field. In fact, he reports, the bacteria have been observed to preferentially move north and south, as opposed to east and west.

What would a bacterium do with a built-in compass, considering it is likely to move at most a few inches in its lifetime? Frankel points out that Earth's magnetic field has a vertical component as well as a horizontal component (except near the equator), and thus can orient an organism up and down as well as azimuthally. Humans usually have no need for this information, as it is invariably obvious which way "up" is via gravity. However, bacteria are so small that gravity plays virtually no role in their lives. Frankel hypothesizes that the hosts might benefit significantly from a sensor that allows them to reliably tell up from down. One way to test this hypothesis, Gould states, is to see if bacteria in the southern hemisphere move the opposite way under similar circumstances. In a postscript, Gould reports that Frankel, Blakemore, and others appear to have found such behavior in magnetic bacteria off the coasts of New Zealand and Tasmania. [Other scientists have proposed that the organisms use the navigation aid to move in and out of oxygen-poor areas, as most types are found in such regions, and the gradients can be steep.]

In closing, Gould notes that some bees have magnetite in their abdomens, and there is some evidence that the orientation of their communicative dances can be modified by external magnetic fields. Also, some pigeons have a magnetite structure between their skull and brain. The structure is also composed of grains of the correct size to be natural magnets, and the structure might therefore serve them as a navigation aid as well.

TPT 31. Time's Vastness

The Earth's rotation is currently slowing down at a rate of about two milliseconds per century, or about one second every 50,000 years. The source of this deceleration is tidal forces, which are in turn due to Earth's gravitational interaction with the Moon. Gould briefly notes the discoverers of this effect (Edmund Halley in the 18th century) and its cause (the famous philosopher Immanuel Kant). The Moon's gravitational pull creates tides, which move uniformly over the oceans of the Earth as it rotates. When these tides encroach on the shallower water near land, a great deal of energy is dissipated as friction, and the Earth slows ever so slightly. As a result, the length of a day is now longer than it used to be. In addition, these tidal forces produce a coupling between the angular momentum of Earth's rotation and that of the Moon's orbit around it. Some of Earth's rotational velocity is converted into an increased distance between the Earth and the Moon, and therefore [via Kepler's third law] an increase in the amount of time the moon takes to complete a cycle. That is, the moon is significantly farther away now than it was in the distant past, and there are more days between full moons.

Due to human's recent ability to keep time accurately to nanoseconds, we can not only directly detect the phenomenon of Earth's slowing rotation, we must correct for it. "Absolute time" is truly constant [neglecting Einstein's relativistic effects, a safe assumption for life on Earth], but the length of a "day," as we have just seen, is not. The result of the integration of this two-milliseconds-per-century deceleration is that, every few years, a "leap second" must be added to our official timing references, which are now based on atomic clocks. (Gould begins this essay by noting Guy Lombardo's admittedly minor failure to properly account for one such leap second during his musical countdown to the end of 1978.)

So, how many hours were in a "day" during, say, the Cambrian period some 500 million years ago? This turns out to be a very difficult question for physics and astronomy to answer with precision, for two reasons. First, the magnitude of Earth's tidal-induced deceleration is strongly influenced by how far away the moon is from the Earth – and, and we have seen, this distance itself has varied with time. Secondly, deceleration is also a function of the fraction of the Earth that is covered with shallow seas; more shallow sea, more frictional interactions, and more deceleration. But this is also a function of time, due to plate tectonics and the rising and falling of sea levels throughout natural history. (Gould notes that the fraction of the Earth covered by shallow seas has been far greater in the geologic past than it is now.)

Perhaps, Gould continues, paleontology can come to our aid. Since the number of "atomic clock" seconds in a year really is (almost) perfectly constant, one implication of shorter days in the distant past is that there would be more days in a year. Are there any fossils that might preserve a record of both days and years that we could use to determine the ratio? Gould discusses the work of John West Wells and others, who have studied microscopic banding in certain groups fossil corals. Some corals show two types of banding: thicker ones that clearly define seasons (and thus years), and thinner laminations within these bands. Wells carefully examined some modern corals with this behavior, and found that there were about 360 of the fine laminations to every band. It may be reasonable to propose, he continues, that the fine laminations are correlated with a day-night cycle of some sort. (The difference between "about 360" and "precisely 365" striations per band might be due to a small number of very cloudy days, Gould suggests later.) Wells then searched the fossil coral record for specimens that preserved the fine laminations. There were very few, but he found one 370-million-year-old sample that had, on average, 400 laminations per band. This would correspond to a 22-23 hour day; paleontology (perhaps) confirms a physical theory! (The essay's title is drawn from the observation that even a change of one second per 50,000 years will result in an hour or more during the several hundred million years of fossilized history.)

Can paleontology provide supporting evidence for the change in the Earth-Moon distance over the eons? Via Kepler's third law, a closer Moon would imply fewer "atomic clock" seconds in a month, and thus fewer days per month. (However, the number of "days" per "month" would suffer from the problem that *both* vary with time.) Nonetheless, some scientists have attempted the challenge; Gould reports on some work by Kahn and Pompea on the chambered nautilus. The nautilus lives in a constantly-growing spiral shell, such that the opening grows with the animal itself. The shell exhibits fine growth lines that correspond to the day-night cycle; the animal approaches the surface at night, while living more deeply in the water column during the day. Periodically, it will also grow internal partitions called sepia. These serve to strengthen the shell, and to form a "back wall" to the creature's living space within it. Kahn and Pompea counted the growth lines between sepia, and found an average of about 30. Perhaps, they hypothesized, sepia production is tied to the lunar cycle (many things in the living world are), noting that there are 29.5 days per month today. There happen to be many well-preserved nautiloid fossils, and Kahn and Pompea studied several of them. They found, Gould reports, 25 lines per sepia in 25-million-year-old fossils, and only 9 lines per sepia in those 420 million years in age. If their assumptions are valid, this would certainly correspond to a much closer Moon during these periods. (Gould goes on to conclude that the assumption that the sepia-building is tied to the lunar cycle is almost certainly false. The results of Kahn and Pompea suggest an Earth-Moon distance increase of 94.5 centimeters per year, while direct physical measurements place the modern rate of increase at about 5.8 centimeters per year. Nonetheless, he expresses excitement and hope that continued work in this field will produce interesting and important results.)