From Stephen Jay Gould, *The Panda's Thumb*

I. The Panda's Thumb

FEW HEROES LOWER their sights in the prime of their lives; triumph leads inexorably on, often to destruction. Alexander wept because he had no new worlds to conquer; Napoleon, overextended, sealed his doom in the depth of a Russian winter. But Charles Darwin did not follow the *Origin of Species* (1859) with a general defense of natural selection or with its evident extension to human evolution (he waited until 1871 to publish *The Descent of Man).* Instead, he wrote his most obscure work, a book entitled: On the Various Contrivances by Which British and Foreign Orchids Are Fertilized by Insects *(1862).*

Darwin's many excursions into the minutiae of natural history—he wrote a taxonomy of barnacles, a book on climbing plants, and a treatise on the formation of vegetable mold by earthworms—won him an undeserved reputation as an old-fashioned, somewhat doddering describer of curious plants and animals, a man who had one lucky insight at the right time. A rash of Darwinian scholarship has laid this myth firmly to rest during the past twenty years (see essay 2). Before then, one prominent scholar spoke for many ill-informed colleagues when he judged Darwin as a "poor joiner of ideas ... a man who does not belong with the great thinkers."

In fact, each of Darwin's books played its part in the grand and coherent scheme of his life's work—demonstrating the fact of evolution and defending natural selection as its primary mechanism. Darwin did not study orchids solely for their own sake. Michael Ghiselin, a California biologist who finally took the trouble to read all of Darwin's books (see his *Triumph of the Darwinian Method),* has correctly identified the treatise on orchids as an important episode in Darwin's campaign for evolution.

Darwin begins his orchid book with an important evolutionary premise: continued self-fertilization is a poor strategy for long-term survival, since offspring carry only the genes of their single parent, and populations do not maintain enough variation for evolutionary flexibility in the face of environmental change. Thus, plants bearing flowers with both male and female parts usually evolve mechanisms to ensure cross-pollination. Orchids have formed an alliance with insects. They have evolved an astonishing variety of "contrivances" to attract insects, guarantee that sticky pollen adheres to their visitor, and ensure that the attached pollen comes in contact with female parts of the next orchid visited by the insect.

Darwin's book is a compendium of these contrivances, the botanical equivalent of a bestiary. And, like the medieval bestiaries, it is designed to instruct. The message is paradoxical but profound. Orchids manufacture their intricate devices from the common components of ordinary flowers, parts usually fitted for very different functions. If God had designed a beautiful machine to reflect his wisdom and power, surely he would not have used a collection of parts generally fashioned for other purposes. Orchids were not made by an ideal engineer; they are jury-rigged from a limited set of available components. Thus, they must have evolved from ordinary flowers.

Thus, the paradox, and the common theme of this trilogy of essays: Our textbooks like to illustrate evolution with examples of optimal design—nearly perfect mimicry of a dead leaf by a butterfly or of a poisonous species by a palatable relative. But ideal design is a lousy argument for evolution, for it mimics the postulated action of an omnipotent creator. Odd arrangements and funny solutions are the proof of evolution—paths that a sensible God would never tread but that a natural process, constrained by history, follows perforce. No one understood this better than Darwin. Ernst Mayr has shown how Darwin, in defending evolution, consistently turned to organic parts and geographic distributions that make the least sense. Which brings me to the giant panda and its "thumb."

Giant pandas are peculiar bears, members of the order Carnivora. Conventional bears are the most omnivorous representatives of their order, but pandas have restricted this catholicity of taste in the other direction—they belie the name of their order by subsisting almost entirely on bamboo. They live in dense forests of bamboo at high elevations in the mountains of western China. There they sit, largely unthreatened by predators, munching bamboo ten to twelve hours each day.

As a childhood fan of Andy Panda, and former owner of a stuffed toy won by some fluke when all the milk bottles actually tumbled at the county fair, I was delighted when the first fruits of our thaw with China went beyond ping-pong to the shipment of two pandas to the Washington zoo. I went and watched in appropriate awe. They yawned, stretched, and ambled a bit, but they spent nearly all their time feeding on their beloved bamboo. They sat upright and manipulated the stalks with their forepaws, shedding the leaves and consuming only the shoots.

I was amazed by their dexterity and wondered how the scion of a stock adapted for running could use its hands so adroitly. They held the stalks of bamboo in their paws and stripped off the leaves by passing the stalks between an apparently flexible thumb and the remaining fingers. This puzzled me. I had learned that a dexterous, opposable thumb stood among the hallmarks of human success. We had maintained, even exaggerated, this important flexibility of our primate forebears, while most mammals had sacrificed it in specializing their digits. Carnivores run, stab, and scratch. My cat may manipulate me psychologically, but he'll never type or play the piano.

So I counted the panda's other digits and received an even greater surprise: there were five, not four. Was the "thumb" a separately evolved sixth finger? Fortunately, the giant panda has its bible, a monograph by D. Dwight Davis, late curator of vertebrate anatomy at Chicago's Field Museum of Natural History. It is probably the greatest work of modern evolutionary comparative anatomy, and it contains more than anyone would ever want to know about pandas. Davis had the answer, of course.

The panda's "thumb" is not, anatomically, a finger at all. . It is constructed from a bone called the radial sesamoid, normally a small component of the wrist. In pandas, the radial sesamoid is greatly enlarged and elongated until it almost equals the metapodial bones of the true digits in length. The radial sesamoid underlies a pad on the panda's forepaw; the five digits form the framework of another pad, the palmar. A shallow furrow separates the two pads and serves as a channel way for bamboo stalks.

The panda's thumb comes equipped not only with a bone to give it strength but also with muscles to sustain its agility. These muscles, like the radial sesamoid bone itself, did not arise *de novo.* Like the parts of Darwin's orchids, they are familiar bits of anatomy remodeled for a new function. The abductor of the radial sesamoid (the muscle that pulls it away from the true digits) bears the formidable name *abductorpollicis longus* ("the long abductor of the thumb"—*pollicis* is the genitive of *pollex,* Latin for "thumb"). Its name is a giveaway. In other carnivores, this muscle attaches to the first digit, or true thumb. Two shorter muscles run between the radial sesamoid and the pollex. They pull the sesamoid "thumb" towards the true digits.

Does the anatomy of other carnivores give us any clue to the origin of this odd arrangement in pandas? Davis points out that ordinary bears and raccoons, the closest relatives of giant pandas, far surpass all other carnivores in using their forelegs for manipulating objects in feeding. Pardon the backward metaphor, but pandas, thanks to their ancestry, began with a leg up for evolving greater dexterity in feeding. Moreover, ordinary bears already have a slightly enlarged radial sesamoid.

In most carnivores, the same muscles that move the radial sesamoid in pandas attach exclusively to the base of the pollex, or true thumb. But in ordinary bears, the long abductor muscle ends in two tendons: one inserts into the base of the thumb as in most carnivores, but the other attaches to the radial sesamoid. The two shorter muscles also attach, in part, to the radial sesamoid in bears. "Thus," Davis concludes, "the musculature for operating this remarkable new mechanism—functionally a new digit—required no intrinsic change from conditions already present in the panda's closest relatives, the bears. Furthermore, it appears that the whole sequence of events in the musculature follows automatically from simple hypertrophy of the sesamoid bone."

The sesamoid thumb of pandas is a complex structure formed by marked enlargement of a bone and an extensive rearrangement of musculature. Yet Davis argues that the entire apparatus arose as a mechanical response to growth of the radial sesamoid itself. Muscles shifted because the enlarged bone blocked them short of their original sites. Moreover, Davis postulates that the enlarged radial sesamoid may have been fashioned by a simple genetic change, perhaps a single mutation affecting the timing and rate of growth.

In a panda's foot, the counterpart of the radial sesamoid, called the tibial sesamoid, is also enlarged, although not so much as the radial sesamoid. Yet the tibial sesamoid supports no new digit, and its increased size confers no advantage, so far as we know. Davis argues that the coordinated increase of both bones, in response to natural selection upon one alone, probably reflects a simple kind of genetic change. Repeated parts of the body are not fashioned by the action of individual genes—there is no gene "for" your thumb, another for your big toe, or a third for your pinky. Repeated parts are coordinated in development; selection for a change in one element causes a corresponding modification in others. It may be genetically more complex to enlarge a thumb and *not* to modify a big toe, than to increase both together. (In the first case, a general coordination must be broken, the thumb favored separately, and correlated increase of related structures suppressed. In the second, a single gene may increase the rate of growth in a field regulating the development of corresponding digits.)

The panda's thumb provides an elegant zoological counterpart to Darwin's orchids. An engineer's best solution is debarred by history. The panda's true thumb is committed to another role, too specialized for a different function to become an opposable, manipulating digit. So the panda must use parts on hand and settle for an enlarged wrist bone and a somewhat clumsy, but quite workable, solution. The sesamoid thumb wins no prize in an engineer's derby. It is, to use Michael Ghiselin's phrase, a contraption, not a lovely contrivance. But it does its job and excites our imagination all the more because it builds on such improbable foundations.

Darwin's orchid book is filled with similar illustrations. The marsh Epipactus, for example, uses its labellum—an enlarged petal—as a trap. The labellum is divided into two parts. One, near the flower's base, forms a large cup filled with nectar—the object of an insect's visit. The other, near the flower's edge, forms a sort of landing stage. An insect alighting on this runway depresses it and thus gains entrance to the nectar cup beyond. It enters the cup, but the runway is so elastic that it instantly springs up, trapping the insect within the nectar cup. The insect must then back out through the only available exit—a path that forces it to brush against the pollen masses. A remarkable machine but all developed from a conventional petal, a part readily available in an orchid's ancestor.

Darwin then shows how the same labellum in other orchids evolves into a series of ingenious devices to ensure cross-fertilization. It may develop a complex fold that forces an insect to detour its proboscis around and past the pollen masses in order to reach nectar. It may contain deep channels or guiding ridges that lead insects both to nectar and pollen. The channels sometimes form a tunnel, producing a tubular flower. All these adaptations have been built from a part that began as a conventional petal in some ancestral form. Yet nature can do so much with so little that it displays, in Darwin's words, "a prodigality of resources for gaining the very same end, namely, the fertilization of one flower by pollen from another plant."

Darwin's metaphor for organic form reflects his sense of wonder that evolution can fashion such a world of diversity and adequate design with such limited raw material:

> Although an organ may not have been originally formed for some special purpose, if it now serves for this end we are justified in saying that it is specially contrived for it. On the same principle, if a man were to make a machine for some special purpose, but were to use old wheels, springs, and pulleys, only slightly altered, the whole machine, with all its parts, might be said to be specially contrived for that purpose. Thus throughout nature almost every part of each living being has probably served, in a slightly modified condition, for diverse purposes, and has acted in the living machinery of many ancient and distinct specific forms.

We may not be flattered by the metaphor of refurbished wheels and pulleys, but consider how well we work. Nature is, in biologist Francois Jacob's words, an excellent tinkerer, not a divine artificer. And who shall sit in judgment between these exemplary skills?

II. Wide Hats and Narrow Minds

IN 1861, FROM February to June, the ghost of Baron Georges Cuvier haunted the Anthropological Society of Paris. The great Cuvier, Aristotle of French biology (an immodest designation from which he did not shrink), died in 1832, but the physical vault of his spirit lived on as Paul Broca and Louis Pierre Gratiolet squared off to debate whether or not the size of a brain has anything to do with the intelligence of its bearer.

In the opening round, Gratiolet dared to argue that the best and brightest could not be recognized by their big heads. (Gratiolet, a confirmed monarchist, was no egalitarian. He merely sought other measures to affirm the superiority of white European males.) Broca, founder of the Anthropological Society and the world's greatest craniometrician, or head measurer, replied that "study of the brains of human races would lose most of its interest and utility" if variation in size counted for nothing. Why, he asked, had anthropologists spent so much time measuring heads if the results had no bearing upon what he regarded as the most important question of all—the relative worth of different peoples:

> Among the questions heretofore discussed within the Anthropological Society,

> none is equal in interest and importance to the question before us now. . . . The great importance of craniology has struck anthropologists with such force that many among us have neglected the other parts of our science in order to devote ourselves almost exclusively to the study of skulls. ... In such data, we hope to find some information relevant to the intellectual value of the various human races.

Broca and Gratiolet battled for five months and through nearly 200 pages of the published bulletin. Tempers flared. In the heat of battle, one of Broca's lieutenants struck the lowest blow of all: "I have noticed for a long time that, in general, those who deny the intellectual importance of the brain's volume have small heads." In the end, Broca won, hands down. During the debate, no item of information had been more valuable to Broca, none more widely discussed or more vigorously contended, than the brain of Georges Cuvier.

Cuvier, the greatest anatomist of his time, the man who revised our understanding of animals by classifying them according to function—how they work—rather than by rank in an anthropocentric scale of lower to higher. Cuvier, the founder of paleontology, the man who first established the fact of extinction and who stressed the importance of catastrophes in understanding the history both of life and the earth. Cuvier, the great statesman who, like Talleyrand, managed to serve all French governments, from revolution to monarchy, and die in bed. (Actually, Cuvier passed the most tumultuous years of the revolution as a private tutor in Normandy, although he feigned revolutionary sympathies in his letters. He arrived in Paris in 1795 and never left.) F. Bourdier, a recent biographer, describes Cuvier's corporeal ontogeny, but his words also serve as a good metaphor for Cuvier's power and influence: "Cuvier was short and during the Revolution he was very thin; he became stouter during the Empire; and he grew enormously fat after the Restoration."

Cuvier's contemporaries marveled at his "massive head." One admirer affirmed that it "gave to his entire person an undeniable cachet of majesty and to his face an expression of profound meditation." Thus, when Cuvier died, his colleagues, in the interests of science and curiosity, decided to open the great skull. On Tuesday, May 15, 1832, at seven o'clock in the morning, a group of the greatest doctors and biologists of France gathered to dissect the body of Georges Cuvier. They began with the internal organs and, finding "nothing very remarkable," switched their attention to Cuvier's skull. "Thus," wrote the physician, in charge, "we were about to contemplate the instrument of this powerful intelligence." And their expectations were rewarded. The brain of Georges Cuvier weighed 1,830 grams, more than 400 grams above average and 200 grams larger than any non-diseased brain previously weighed. Unconfirmed reports and uncertain inference placed the brains of Oliver Cromwell, Jonathan Swift, and Lord Byron in the same range, but Cuvier had provided the first direct evidence that brilliance and brain size go together.

Broca pushed his advantage and rested a good part of his case on Cuvier's brain. But Gratiolet probed and found a weak spot. In their awe and enthusiasm, Cuvier's doctors had neglected to save either his brain or his skull. Moreover, they reported no measures on the skull at all. The figure of 1,830 g for the brain could not be checked; perhaps it was simply wrong. Gratiolet sought an existing surrogate and had a flash of inspiration: "All brains are not weighed by doctors," he stated, "but all heads are measured by hatters and I have managed to acquire, from this new source, information which, I dare to hope, will not appear to you as devoid of interest." In short, Gratiolet presented something almost bathetic in comparison with the great man's brain: he had found Cuvier's hat! And thus, for two meetings, some of France's greatest minds pondered seriously the meaning of a worn bit of felt.

Cuvier's hat, Gratiolet reported, measured 21.8 cm in length and 18.0 cm in width. He then consulted a certain M. Puriau, "one of the most intelligent and widely known hatters of Paris." Puriau told him that the largest standard size for hats measured 21.5 by 18.5 cm. Although very few men wore a hat so big, Cuvier was not off scale. Moreover, Gratiolet reported with evident pleasure, the hat was extremely flexible and "softened by very long usage." It had probably not been so large when Cuvier bought it. Moreover, Cuvier had an exceptionally thick head of hair, and he wore it bushy. "This seems to prove quite clearly," Gratiolet proclaimed, "that if Cuvier's head was very large, its size was not absolutely exceptional or unique."

Gratiolet's opponents preferred to believe the doctors and refused to grant much weight to a bit of cloth. More than twenty years later, in 1883, G. Herve again took up the subject of Cuvier's brain and discovered a missing item: Cuvier's head had been measured after all, but the figures had been omitted from the autopsy report. The skull was big indeed. Shaved of that famous mat of hair, as it was for the autopsy, its greatest circumference could be equaled by only 6 percent of "scientists and men of letters" (measured in life with their hair at that) and zero percent of domestic servants. As for the infamous hat, Herve pleaded ignorance, but he did cite the following anecdote: "Cuvier had a habit of leaving his hat on a table in his waiting room. It often happened that a professor or a statesman tried it on. The hat descended below their eyes."

Yet, just as the doctrine of more-is-better stood on the verge of triumph, Herve snatched potential defeat from the jaws of Broca's victory. Too much of a good thing can be as troubling as a deficiency, and Herve began to worry. Why did Cuvier's brain exceed those of other "men of genius" by so much? He reviewed both details of the autopsy and records of Cuvier's frail early health and constructed a circumstantial case for "transient juvenile hydrocephaly," or water on the brain. If Cuvier's skull had been artificially enlarged by the pressure of fluids early during its growth, then a brain of normal size might simply have expanded— by decreasing in density, not by growing larger—into the space available. Or did an enlarged space permit the brain to grow to an unusual size after all? Herve could not resolve this cardinal question because Cuvier's brain had been measured and then tossed out. All that remained was the magisterial number, 1,830 grams. "With the brain of Cuvier," wrote Herve, "science has lost one of the most precious documents it ever possessed."

On the surface, this tale seems ludicrous. The thought of France's finest anthropologists arguing passionately about the meaning of a dead colleague's hat could easily provoke the most misleading and dangerous inference of all about history—a view of the past as a domain of naive half-wits, the path of history as a tale of progress, and the present as sophisticated and enlightened.

But if we laugh with derision, we will never understand. Human intellectual capacity has not altered for thousands of years so far as we can tell. If intelligent people invested intense energy in issues that now seem foolish to us, then the failure lies in our understanding of their world, not in their distorted perceptions. Even the standard example of ancient nonsense—the debate about angels on pinheads— makes sense once you realize that theologians were not discussing whether five or eighteen would fit, but whether a pin could house a finite or an infinite number. In certain theological systems, the corporeality or non-corporeality of angels is an important matter indeed.

In this case, a clue to the vital importance of Cuvier's brain for nineteenth-century anthropology lies in the last line of Broca's statement, quoted above: "In such data, we hope to find some information relevant to the intellectual value of the various human races." Broca and his school wanted to show that brain size, through its link with intelligence, could resolve what they regarded as the primary question for a "science of man"—explaining why some individuals and groups are more successful than others. To do this, they separated people according to a priori convictions about their worth—men versus women, whites versus blacks, "men of genius" versus ordinary folks—and tried to demonstrate differences in brain size. The brains of eminent men (literally males) formed an essential link in their argument—and Cuvier was the *creme de la creme.* Broca concluded:

> In general, the brain is larger in men than in women, in eminent men than in men of mediocre talent, in superior races than in inferior races. Other things equal, there is a remarkable relationship between the development of intelligence and the volume of the brain.

Broca died in 1880, but disciples continued his catalog of eminent brains (indeed, they added Broca's own to the list —although it weighed in at an undistinguished 1,484 grams). The dissection of famous colleagues became something of a cottage industry among anatomists and anthropologists. E.A. Spitzka, the most prominent American practitioner of the trade, cajoled his eminent friends: "To me the thought of an autopsy is certainly less repugnant than I imagine the process of cadaveric decomposition in the grave to be." The two premier American ethnologists, John Wesley Powell and WJ McGee made a wager over who had the larger brain—and Spitzka contracted to resolve the issue for them posthumously. (It was a toss-up. The brains of Powell and McGee differed very little, no more than varying body size might require.)

By 1907, Spitzka could present a tabulation of 115 eminent men. As the list grew in length, ambiguity of results increased apace. At the upper end, Cuvier was finally overtaken when Turgenev broke the 2,000-gram barrier in 1883. But embarrassment and insult stalked the other end. Walt Whitman managed to hear the varied carols of America singing with only 1,282 g. Franz Josef Gall, a founder of phrenology—the original "science" of judging mental worth by the size of localized brain areas—could muster only 1,198 g. Later, in 1924, Anatole France almost halved Turgenev's 2,012 and weighed in at a mere 1,017 g.

Spitzka, nonetheless, was undaunted. In an outrageous example of data selected to conform with a priori prejudice, he arranged, in order, a large brain from an eminent white male, a bushwoman from Africa, and a gorilla. (He could easily have reversed the first two by choosing a larger black and a smaller white.) Spitzka concluded, again invoking the shade of Georges Cuvier: "The jump from a Cuvier or a Thackeray to a Zulu or a Bushman is no greater than from the latter to the gorilla or the orang."

Such overt racism is no longer common among scientists, and I trust that no one would now try to rank races or sexes by the average size of their brains. Yet our fascination with the physical basis of intelligence persists (as it should), and the naive hope remains in some quarters that size or some other unambiguous external feature might capture the subtlety within. Indeed, the crassest form of more-is-better— using an easily measured quantity to assess improperly a far more subtle and elusive quality—is still with us. And the method that some men use to judge the worth of their penises or their automobiles is still being applied to brains. This essay was inspired by recent reports on the whereabouts of Einstein's brain. Yes, Einstein's brain was removed for study, but a quarter century after his death, the results have not been published. The remaining pieces— others were farmed out to various specialists—now rest in a Mason jar packed in a cardboard box marked "Costa Cider" and housed in an office in Wichita, Kansas. Nothing has been published because nothing unusual has been found. "So far it's fallen within normal limits for a man his age," remarked the owner of the Mason jar.

Did I just hear Cuvier and Anatole France laughing in concert from on high? Are they repeating a famous motto of their native land: *plus (a change, plus c 'est la meme chose* ("the more things change, the more they remain the same"). The physical structure of the brain must record intelligence in some way, but gross size and external shape are not likely to capture anything of value. I am, somehow, less interested in the weight and convolutions of Einstein's brain than in the near certainty that people of equal talent have lived and died in cotton fields and sweatshops.