By the same Author

Ontogeny and Phylogeny
Ever Since Darwin
The Panda's Thumb
The Mismeasure of Man

Hen's Teeth and Horse's Toes

Stephen Jay Gould

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12 | Kingdoms without Wheels

SISERA'S MOTHER thought fondly of the booty that her son might bring back—"a prey of divers colors of needlework"—after meeting the armies of Israel led by Deborah and Barak (Judges, chapters 4–5). Yet he was overdue, and she began to worry: "Why tarry the wheels of his chariots?" she inquired anxiously. And rightly did she fear, for Sisera would never return. The Canaanite armies had been routed, while Jael had just transfixed Sisera through the head with a nail (a tent post in modern translations)—ranking her second to Judith among Jewish heroines for the gory dispatch of enemies.

Generals of the biblical armies rode on chariots; their apparatus traveled on carts. But two thousand years later, by the sixth century A.D., the question posed by Sisera's mother could no longer be asked, for wheels virtually disappeared as a means of transportation from Morocco to Afghanistan. They were replaced by camels (Richard W. Bulliet, *The Camel and the Wheel,* 1975).

Bulliet cites several reasons for this counterintuitive switch. The Roman roads had begun to deteriorate and camels were not bound to them. Craftsmanship in harnesses and wagons had suffered a sharp decline. But, most important, camels (as pack animals) were more efficient than carts pulled by draft animals (even by camels). In a long list of reasons for favoring camels to nonmechanized transport by wheels, Bulliet includes their longevity, endur-

ance, ability to ford rivers and traverse rough ground, and savings in manpower (a wagon requires a man for every two animals, but three to six pack camels can be tended by a single person).

We are initially surprised by Bulliet's tale because wheels have come to symbolize in our culture the sine qua non of intelligent exploitation and technological progress. Once invented, their superiority cannot be gainsaid or superseded. Indeed, "reinventing the wheel" has become our standard metaphor for deriding the repetition of such obvious truths. In an earlier era of triumphant social Darwinism, wheels stood as an ineluctable stage of human progress. The "inferior" cultures of Africa slid to defeat; their conquerors rolled to victory. The "advanced" cultures of Mexico and Peru might have repulsed Cortés and Pizarro if only a clever artisan had thought of turning a calendar stone into a cartwheel. The notion that carts could ever be replaced by pack animals strikes us not only as backward but almost sacrilegious.

The success of camels reemphasizes a fundamental theme of these essays. Adaptation, be it biological or cultural, represents a better fit to specific, local environments, not an inevitable stage in a ladder of progress. Wheels were a formidable invention, and their uses are manifold (potters and millers did not abandon them, even when cartwrights were eclipsed). But camels may work better in some circumstances. Wheels, like wings, fins, and brains, are exquisite devices for certain purposes, not signs of intrinsic superiority.

The haughty camel may provide enough embarrassment for any modern Ezekiel, yet this column might seem to represent still another blot on the wheel's reputation (though it does not). For I wish to pose another question that seems to limit the wheel. So much of human technology arose by recreating the good designs of organisms. If art mirrors nature and if wheels are so successful an invention, why do animals walk, fly, swim, leap, slither, and creep, but never roll (at least not on wheels)? It is bad enough that wheels, as human artifacts, are not always superior to nature's handiwork. Why has nature, so multifarious in her ways, shunned the wheel as well? Are wheels a poor or rarely efficient way to make progress after all?

In this case, however, the limit lies with animals, not with the efficiency of wheels. A vulgarization of evolution, presented in many popular accounts, casts natural selection as a perfecting principle, so accurate in its operation, so unconstrained in its action, that animals come to embody a set of engineering blueprints for optimal form (see essay 11). Instead of replacing the older "argument from design"—the notion that God's existence can be proved by the harmonies of nature and the clever construction of organisms—natural selection slips into God's old role as perfecting principle.

But the proof that evolution, and not the fiat of a rational agent, has built organisms lies in the imperfections that record a *history* of descent and refute creation from nothing. Animals cannot evolve many advantageous forms because inherited architectural patterns preclude them. Wheels are not flawed as modes of transport; I am sure that many animals would do far better with them. (The one creature clever enough to build them, after all, has gotten some mileage from the invention, the superiority of camels in certain circumstances notwithstanding.) But animals cannot construct wheels from the parts that nature provides.

As its basic structural principle, a true wheel must spin freely without physical fusion to the solid object it drives. If wheel and object are physically linked, then the wheel cannot turn freely for very long and must rotate back, lest connecting elements be ruptured by the accumulated stress. But animals must maintain physical connections between their parts. If the ends of our legs were axles and our feet were wheels, how could blood, nutrients, and nerve impulses cross the gap to nurture and direct the moving parts of our natural roller skates? The bones of our arms may be unconnected, but we need the surrounding envelopes of muscle, blood vessels, and skin—and therefore cannot rotate our arms even once around our shoulders.

We study animals to illuminate or exemplify nature's laws. The highest principle of all may be nature's equivalent

of the axiom that for every hard-won and comforting regularity, we can find an exception. Sure enough—somebody out there has a wheel. In fact, at this very moment, wheels are rotating by the millions in your own gut.

Escherichia coli, the common bacillus of the human gut, is about two micrometers long (a micrometer is one-thousandth of a millimeter). Propelled by long whiplike threads called flagella (singular, flagellum), an *E. coli* can swim about ten times its own length in a second. Lest swimming seem easy for a creature virtually unaffected by gravitational forces and moving through a supporting and easily yielding fluid, I caution against extrapolating our view to a bacterium's world. The perceived viscosity of a fluid depends upon an organism's dimensions. Decrease a creature's size and water quickly turns to molasses. Howard C. Berg, the Colorado biologist who demonstrated how flagella operate, compares a bacterium moving in water to a man trying to swim through asphalt. A bacterium cannot coast. If its flagella stop moving, a bacterium comes to an abrupt halt within about a millionth of its body length. The flagella work wonderfully well in trying circumstances.

After Berg had modified his microscope to track individual bacteria, he noted that an *E. coli* moves in two ways. It may "run," swimming steadily for a time in a straight or slightly curved path. Then it stops abruptly and jiggles about—a "twiddle" in Berg's terminology. After twiddling, it runs off again in another direction. Twiddles last a tenth of a second and occur on an average of once a second. The timing of twiddles and the directions of new runs seem to be random unless a chemical attractant exists at high concentration in one part of the medium. A bacterium will then move up-gradient toward the attractant by decreasing the probability of twiddling when a random run carries it in the right direction. When a random run moves in the wrong direction, twiddling frequency remains at its normal, higher level. The bacteria therefore drift toward an attractant by increasing the lengths of runs in favored directions.

The bacterial flagellum is built in three parts: a long helical filament, a short segment (called a hook) connecting the filament to the flagellar base, and a basal structure embedded in the cell wall. Biologists have argued about how bacteria move since Leeuwenhoek first saw them in 1676. Most models assumed that flagella are fixed rigidly to the cell wall and that they propel bacteria by waving to and fro. When such models had little success in explaining the rapid transition between runs and twiddles, some biologists suggested that flagella might tag passively along and that some other (and unknown) mechanism might move bacteria.

Berg's observations revealed something surprising, hinted at and proposed in theory before, but never adequately demonstrated: the bacterial flagellum operates as a wheel. It rotates rigidly like a propeller, driven by a rotatory "motor" in the basal portion embedded in the cell wall. Moreover, the motor is reversible. *E. coli* runs by rotating the flagella in one direction; it twiddles by abruptly stopping and rotating the flagella the other way!

Berg could observe the rotation and correlate its direction with runs and twiddles by following free-swimming bacteria in his machine, but S. H. Larsen and others, working in Julius Adler's laboratory at the University of Wisconsin, provided an even more striking demonstration. They isolated two mutant strains of *E. coli*—one that runs and never twiddles and another that twiddles incessantly. They "tethered" these mutant bacteria to glass slides, using antibodies that attach either to the hook or filament of the flagella and also, fortunately, to glass. Thus, the bacteria are affixed to the slide by their flagella. Larsen noted that the tethered bacteria rotate continually about their immobilized flagella. The running mutants turn counterclockwise (as viewed from outside the cell), while the twiddling mutants turn clockwise. The flagellar wheel has a reversible motor.

The biochemical basis of rotation has not yet been elucidated, but the morphology can be resolved. Berg proposes that the bottom end of the flagellum expands out to form a thin ring rotating freely in the cytoplasmic membrane of the cell wall. Just above, another ring surrounds the flagellar base, without attaching to it. This second ring is

mounted rigidly on the cell wall. The lower ring (and entire flagellum) rotates freely, held in position by the surrounding upper ring and the cell wall itself.

Some exceptions in nature are dispiriting—the nasty, ugly, little facts that spoil great theories, in Huxley's aphorism. Others are enlightening and serve only to reinforce a regularity by identifying both its scope and its reasons. These are the exceptions that prove (or probe) rules—and the flagellar wheel falls into this happy class.

Is it accidental that wheels only occur in nature's smallest creatures? Organic wheels require that two parts be juxtaposed without physical connection. I argued previously that this cannot be accomplished in creatures familiar to us because connection between parts is an integral property of living systems. Substances and impulses must be able to move from one segment to another. Yet, in the smallest organisms—and in them alone—substances can move between two unconnected parts by diffusing through membranes. Thus, single cells, including all of ours of course, contain organelles lying within the cytoplasm and communicating with other parts of the cell, not by physical connection, but by passage of molecules through bounding membranes. Such structures could, in principle, be designed to rotate like wheels.

The principle that restricts such communication without physical connection to the smallest organisms (or to similarly sized parts of larger organisms) embodies a theme that has circulated extensively throughout these essays (see sections in *Ever Since Darwin* and *The Panda's Thumb*): the correlation of size and shape through the changing relationship of surfaces and volumes. With surfaces (length^2) increasing so much more slowly than volumes (length^3) as an object grows, any process regulated by surfaces but essential to volumes must become less efficient unless the enlarging object changes its shape to produce more surface. The external boundary is surface enough for communication between the organelles of a single cell with their minuscule volumes. But the surface of a wheel as large as a human foot could not provision the wheelful of organic matter within.

Large organisms must evolve channels—physical connections—to convey the nutrients and oxygen that can no longer diffuse through external surfaces.

Wheels work well, but animals are debarred from building them by structural constraints inherited as an evolutionary legacy. Adaptation does not follow the blueprints of a perfect engineer. It must work with parts available. Yet when I survey animals in all their stunning, if wheel-less, variety, I can only marvel at the diversity and good design that a few basic and highly constrained organic patterns have produced. Forced to make do, we do rather well.

Postscript

I did not know how many artists and writers of fiction had made up for nature's limitations until readers began to submit their favorite stories. To choose just one example in each category, G. W. Chandler told me that one of the *Oz* novels featured some four-legged rollers known as wheelers. They were, in fact, built in just the way I argued an animal could not work—with wheels for feet and the ends of legs for axles. D. Roper sent me a print of M. C. Escher's "curl-up," a lithograph showing hundreds of curious creatures wandering through a typical Escher landscape of impossible staircases. They climb by dragging a segmented body along on three pairs of humanoid legs. When they hit a flat surface, they roll up and roll along. These, of course, are permissible "one part" wheels, (like tumbling tumbleweeds), not the impossible wheel and axle combination. Still, Escher specifically created them to make up for nature's limitation since he writes that the lithograph was inspired by his "dissatisfaction concerning nature's lack of any wheelshaped living creatures. . . . So the little animal shown here . . . is an attempt to fill a long-felt want."

Still, as usual, nature wins again. Robert LaPorta and Joseph Frankel both wrote to tell me that I had missed another of nature's real wheels. They directed me to the

work of Sidney Tamm, which, I am ashamed to say, I did not know when I wrote the original article. Dr. Tamm has found wheels in single-celled creatures that live in the guts of termites. They therefore (whew!) fall into the category of permissible exceptions at small dimensions.

The body of this protist contains an axostyle (a kind of axis running the length of its body) that rotates continuously in one direction. The organelles of the anterior end (including the nucleus) are attached to the axostyle and rotate with it—"much like turning a lollipop by the stick," as Tamm notes. But, and we now encounter the more curious and wheel-like point, the entire anterior end, including the cell surface, rotates along with the axostyle relative to the rest of the body.

Tamm demonstrated this peculiar motion with an ingenious experiment in which he attached small bacteria all over the cell's outer surface. Those attached to the front end rotated continuously with respect to those adhering to the back end. But bacteria did not attach to a narrow band between front and back, and this band must therefore represent a zone of shear. Tamm then studied the structure of the cell-membrane by freeze-fracture electron microscopy and found it to be continuous across the shear zone. Tamm concludes that the entire surface must be fluid and that shear zones could, in theory, form anywhere upon it. A very strange creature! "Prais'd be the fathomless universe," Whitman wrote, "for life and joy, and for objects and knowledge curious."

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