The Mechanics of Natural Success

By INGRID WICKELGREN

Bioengineers view physics as a lever on evolution

When you have eliminated the impossible, whatever remains, however improbable, *must be the truth.*
— Sherlock Holmes, from Sir Arthur Conan Doyle's *The Sign of Four,* 1890

Eliminating the impossible may seem like a long way to the truth, but in the search for truth in nature, it could provide a shortcut. Looking at the natural world in the form of individual molecules, especially genes, makes biological variation seem boundless. But watch diverse forms of foliage fold or wildlife walk, wiggle or hang from trees, sharing the same techniques to tackle the physical world. And notice: While round and cylindrical organisms abound, there are almost no square ones, no organism's skeleton is made of metal and very few use any kind of wheel for transport. Why not? It's elementary, my dear Watson: physics.

Evolution does not seem to favor right angles, metallic skeletons or wheels because these features are not good mechanical solutions to the problems most organisms face. Flat surfaces that join at right angles function poorly, compared with curves, when they must resist internal or external pressures. Metals make good permanent structures, but not ones that must grow and adapt to environmental changes. And the planet's relative scarcity of metals makes it energetically impractical for an organism to assemble large quantities of them. Wheels are difficult to maneuver around obstacles or to keep stable over bumps, and they are nearly useless underground or in the air.

"Every organism has mechanical things to worry about, however good its reproductive capabilities might be," says biologist Steven Vogel at Duke University in Durham, N.C. Trees must withstand high winds; mammalian skeletons must remain stable but flexible; filter-feeding marine organisms must capture food from a dilute ocean; pinecones must trap pollen from the air; prairie dogs must construct burrows with plenty of ventilation. Evolution cannot tamper with gravity; nor can it alter the Earth's mineral distribution, the way the wind blows or the surface-to-volume ratio of a given size and shape. Natural selection must work with or around certain mechanical and geometric givens.

With such factors in mind, an increasing number of biologists have been mixing mechanics into recipes that explain the natural world. Their approach, called comparative biomechanics, contrasts with most of contemporary biology, which tends to focus on molecules and cells. Mechanically oriented biologists study how an organism's form and function evolved in the context of its physical environment. And their investigations reveal that many reasons for the evolved traits of living creatures lie not in genetics, cellular interactions or ecological relationships, but rather in immediate-world physical principles.

Nature's physical forces affect all organisms — animal and plant, living and extinct. They can work on an organism's insides or its outside, through fluids or directly on solids. Scientists in the field of comparative biomechanics have studied nearly every phylum on the planet and the ways in which mechanical forces have shaped their evolutionary histories. "With the aid of a little engineering, we can start recognizing the general principles underlying the mechanics of being a successful organism," Vogel says.

Comparative biomechanics dates back to the days "when biology and physics weren't really separate," Vogel says. For example, "Galileo and da Vinci worried equally about the living and the nonliving." But over the next few hundred years, biology and physics grew apart, and did not reunite until the 1930s, when Sir James Gray at England's Cambridge University began his work on mechanical principles of animal locomotion. The most recent resurgence of interest in comparative biomechanics began in the mid-1970s at Duke and Cambridge, and now about two dozen teams worldwide work in the field, Vogel says.

Applying physics to the study of biology can explain similarities among seemingly diverse creatures. By comparing the structural geometries and skeletal stresses of mammals ranging in size from squirrels to horses, one bioengineer has come up with what he proposes as the main design principle for the mammalian locomotor skeleton.

Andrew A. Biewener of the University of Chicago started with the accepted fact that all mammals, regardless of size, use the same materials in similar proportions to build their bones. The similarity exists, he suggests, because this particular ratio of these structural materials — 30 percent collagen for shock absorption and almost 70 percent calcium phosphate for strength — provides the optimal balance that enables the skeleton to hold up under its weight load during locomotion.

From this, Biewener hypothesized that all mammalian skeletons share an upper limit for the amount of stress, or deformation pressure, they can bear without breaking. "We're arguing that if animals are built of similar material elements, [natural] selection will favor a size and form of elements so that stress levels are similar [for each animal]," he says. Biewener found support for this theory when he discovered from years of research that during normal activity, many mammals of varying sizes perform at only 30 to 50 percent of the breaking strain for their skeletons, thereby maintaining a safety factor of 50 to 70 percent. "So [one] can predict that any future [evolutionary]


Biewener

Researcher guides a horse to clear a hurdle and land on a force-sensing plate. Combined with postural information, the plate's measurements help reveal mechanical principles important in the evolution of mammalian skeletons.

design would be constrained to maintain this given fraction of safety," he says.

But Biewener began to wonder how large animals maintain this margin of safety using the same materials as the smaller creatures but supporting much more weight in comparison with the cross-sectional area of their bones. For years, biologists accepted the idea that when animals evolved to larger sizes, their bones became disproportionately wider in relation to the animals' overall size increase. But when Biewener measured the length-to-diameter ratio of bones in different-sized mammals, he didn't find much variation. "There don't appear to be the kinds of shape changes that one would expect [for animals] to maintain a constant stress level," he says.

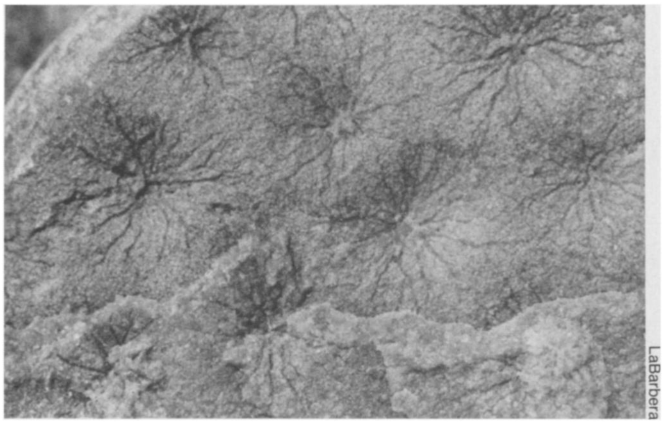
Biewener then measured the amounts and directions of forces on the skeletons of running mammals. He accomplished this by making the animals run over a rectangular force-sensing plate or by surgically placing a gauge on the surface of the animal's bone. Using a computer, he combined these measurements with postural information gleaned from movies of the animals in motion.

Biewener observed that the main difference between large and small animals in motion is posture – the way each bone is positioned in relation to the others. Larger mammals compensate for their size by running in a more upright stance, which reduces the amount of joint-twisting force, or torque, their muscles must counteract to maintain stability at speed. "So, if you're going to be large, you need to run in upright positions with weight underneath you," he explains.

An upright stance, however, means more restricted movement. That's why small animals such as rats, which run in a more crouched position, maintain much more joint flexibility than larger animals such as horses, says Biewener, whose findings are scheduled to appear in a forthcoming SCIENCE.

Comparative biomechanics can also shed light on how structure related to function in extinct organisms. Fossils, by definition, reveal hard structures – the fodder of Biewener's research. "[Biewener's work] implies that you could go back and look at a fossil and say what [that animal's] style of behavior was simply by looking at the bone proportions and what we know about the properties of bone," says Michael LaBarbera, who studies invertebrate zoology and comparative biomechanics at the University of Chicago. Some biomechanical work has focused specifically on extinct animals, including primitive fishes, dinosaurs and the flying reptiles known as pterosaurs.

This calcium carbonate fossil was once covered with living sponge tissue. The radiating lines in each centimeter-wide, asterisk-like feature represent the sponge's internal pipes, all of which were measured and found to follow Murray's law.


LaBarbera

British zoologist R. McNeill Alexander at the University of Leeds tries to figure out how fast and agile the dinosaurs were by examining their fossil remnants. From fossilized dinosaur footprints, he can determine the animals' stride lengths, which allow him to calculate their speed. Alexander finds that the herbivorous *Apatosaurus*, commonly known as brontosaurus, walked about as fast as a typical modern village-dwelling human – about 2 mph – and that carnivorous dinosaurs such as *Tyrannosaurus* walked about twice that fast, at the pace of an average city dweller.

"When we got these results, I was tempted to think that dinosaurs really were the slow, lethargic things we had imagined them to be," he recalls.

But Alexander realized that running was only an occasional activity, so fossilized footprints would be much more likely to reflect walking – rather than running – dinosaurs. At this point he started looking at dinosaur skeletons for clues to their physical capacities.

The strength of an animal's skeleton can tell scientists a lot about its athletic ability, because the faster an animal moves, the more force its bones must bear. "If one looks at it that way, it looks as though brontosaurs were about as athletic as elephants," Alexander says. Elephants can run, but they can't sprint or jump. The horned triceratops "looks as though he's about like a rhino, just about capable of galloping but that's all."

Alexander likens his approach to that of an engineer taking measurements of a bridge to determine the load it was designed to carry. "Show me an animal's skeleton," he says, "and I'll tell you what forces its evolution has designed it to carry." He described his skeletal work on dinosaurs in 1985 in the ZOOLOGICAL JOURNAL OF THE LINNEAN SOCIETY (Vol. 83, p. 1).

Organisms also must contend with fluid forces, primarily from air, water and their own blood. LaBarbera "plays with" fluid transport systems inside organisms, applying a rule known as Murray's law to fluid flow within the internal vessels of a number of creatures. For optimal fluid flow, according to the rule, a pipe's radius cubed must equal the sum of the cubed radii of each of its branches.

In combing the scientific literature, LaBarbera noticed that this mathematical relationship holds true in living organisms as varied as humans, dogs and sponges. He found the same relationship after measuring diameters of the internal cavities within an extinct fossil sponge. "If you can say there is a rule that applies to organisms as far [apart] as sponges and humans and probably everything in between, that says something interesting about natural selection," LaBarbera asserts. It not only reveals a constraint on natural selection but also suggests that the solution – independently discovered in different animals by different scientists – for the optimal circulatory configuration is a straightforward one, he says.

How does natural selection act to preserve this universal tubular architecture? In a pipe system following Murray's law, the "shear" force from fluids running parallel to the pipe walls remains the same throughout the system, regardless of the diameter or number of branches. Other researchers' experiments with mammals have demonstrated that individual cells lining vessel walls can sense the shear stress exerted by a fluid at a particular place. If that force is too great, the cells divide and the vessel grows larger in diameter, LaBarbera says.

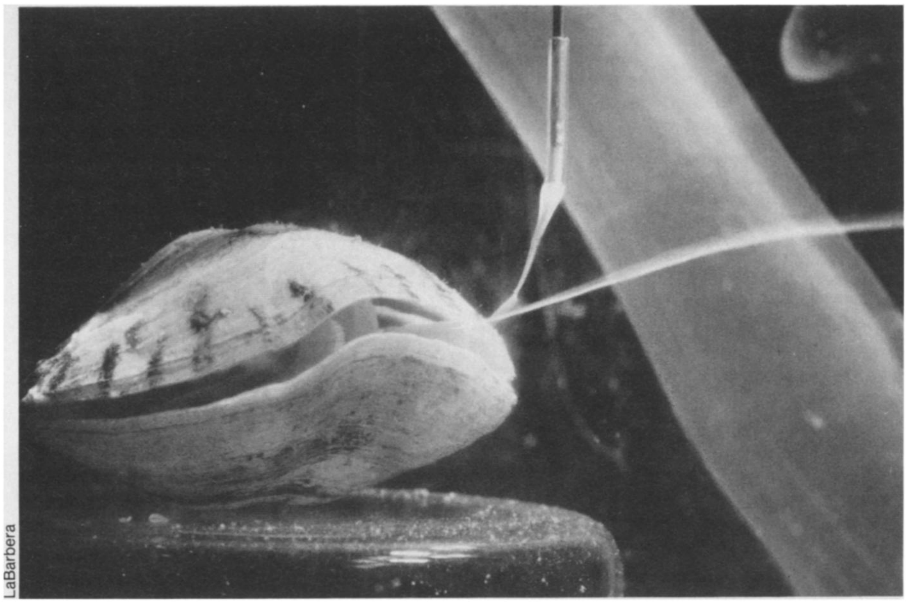
Fluid forces can also act externally. LaBarbera is now studying how fluid forces in the ocean affect feeding in marine animals such as brachiopods – invertebrate filter-feeders whose bivalve shells house a filament-bearing structure on which cilia beat to create a current that brings in microscopic food. The phylum Brachiopoda includes more than 200 living species as well as many that have gone extinct. LaBarbera's most recent work focuses on the ability of different-sized brachiopods to obtain food.

Scientists have presumed that the larger brachiopods have a food-intake handicap, reasoning that the bigger the brachiopod, the smaller the surface area of its filter-feeding organ, or lophophore, in relation to the animal's overall volume. They posited that large brachiopods solved this problem by evolving extra coils in their lophophores, thereby increasing that organ's surface area. However, LaBarbera's measurements indicate that the extra folding seen in the larger brachiopods' lophophores does not give the organs more surface area than they would have without the change in shape. This leads him to conclude that factors other than lophophore surface area must influence a brachiopod's ability to get enough food.

These factors have to do with the fluid environment in which the animals live. LaBarbera found that the viscous forces in the water play an important role in the behavior of smaller brachiopods. To minimize the energy cost of pumping water through their lophophores, he discovered, small brachiopods open their shells to a wide gape. The size of the viscous force is determined in part by the distance between the two shells.

But in larger brachiopods, viscous forces play a less important role and the "gaping" strategy becomes irrelevant, LaBarbera says. Thus, a large brachiopod can keep its shells more nearly closed. A narrower opening allows it to make a forceful jet that squirts the filtered water away from the body. This reduces the chance that the same water will be refiltered – a wasted effort in a dilute ocean.

So "the standard hypothesis is exactly backward," LaBarbera says. Instead of large brachiopods being constrained by size, "I think the actual constraint is on the small animals that need to deal with fluid dynamics."


LaBarbera

Large, 3-cm-wide brachiopod shoots a jet of dyed water (horizontal streak) through the small opening between its shells. The animal uses this technique to avoid refiltering the same seawater. Dye comes from plastic tubing in upper portion of photo.

Plants, too, must contend with fluid forces. Vogel recalls learning as a child to distinguish one type of leaf from another by its shape. But "a leaf doesn't have [its] shape for biologists to tell leaves apart," he says. "Never mind telling them apart; why are they shaped that way?"

He found part of the answer blowing in the wind. Vogel was the first to show how certain leaf shapes help trees stand up to winds that might otherwise topple them. By studying leaves and other flexible objects in laboratory wind tunnels, he found that leaves with certain shapes have 60 to 80 percent less drag than do flags of the same size constructed from a variety of different materials. While the flags flapped madly, the leaves held steady because their shapes enabled them to reconfigure into streamlined cones and cylinders that resist buffeting. Thus, says Vogel, the wind must influence the evolution of leaf shape, although other factors – such as light-capturing ability and cooling – also play a part. His findings will appear later this year in the Journal of Experimental Botany.

Comparative biomechanics highlights the contrasts between natural and human-made structures, which tend to be stiff, dry, brittle and riddled with right angles. In many ways, bioengineering is more complex than mechanical engineering, asserts Cornell University plant scientist Karl J. Niklas. He points out that an organism's environment – unlike the relatively insulated environment of machines – can change dramatically. And organisms themselves change: They grow.

"If an engineer were designing a machine, he or she would know beforehand the environment in which that machine would operate and the functions that machine would have to perform," Niklas says. "A biologist doesn't have those luxuries. A biologist has to infer what [the organism's] biological functions are."

Comparative biomechanics is unlikely to shed much light on evolutionary strategy, which involves more theoretical questions about the pace of evolutionary change and how species diverge or become extinct. Biomechanics addresses tactics – the attributes that allow organisms to function well in terms of physics. For this reason, it is an aid to explaining the natural world, not a substitute for traditional biological research encompassing chemical, thermal, cellular, behavioral and ecological variables.

In viewing the world through the lens of physics, bioengineers not only provide mechanical answers but also reveal the limits of purely biological answers. Whereas a traditional biologist might explain the evolution of an animal's posture as a mating display or as a way to promote desirable chemical reactions within bone tissue, a biomechanic might simply show that the posture works to support the animal.

Since physical laws are so well defined in comparison with most biological ones, physics can provide satisfying explanations for many biological phenomena. Niklas adapts the words of Sir Arthur Conan Doyle to his field: "Once you've stripped away all the things about an organism that can be explained by mechanics, you're left with things [that are] strictly biological." ☐