Catholic University of Louvain in Belgium, "we must find a physical process that will convince me that the inclination is the key factor in creating the 100,000-year cycle. The only answer for me is the physical mechanism."

The only possible agent of climatic change Muller can cite is the dust that asteroids and comets spew across the solar system. Asteroid dust remains largely in a disk across the solar system, and Earth periodically dips in and out of that disk as inclination varies. This interplanetary dust filters into Earth's upper atmosphere, but it has no known influence on climate. "I have to confess, I don't have a physical mechanism that works," Muller admits. "But part of the problem is our ignorance of the atmosphere and [the dust in] the nearby solar system."

Muller also points out that the physical mechanism behind the Milankovitch cycles—the amount of sunshine reaching high northern latitudes—is far from perfect. "The only real defense I have," he says, "is that if you look carefully at the Milankovitch model, the physical mechanism there was always hand waving, too." Indeed, paleoclimatologists have long recognized that the amount of Milankovitch-induced change in solar heating is too small to melt glaciers or to send Earth into a deep freeze, unless some as yet unidentified part of the climate system amplifies it.

Still, even a partial physical mechanism is better than none, researchers say. "Even though you can't pin down exactly why Earth's climate responds to Milankovitch [orbital] cycles, at least there is some physical connection, whereas Rich Muller has none," responds oceanographer Wallace Broecker of Columbia University's Lamont-Doherty Earth Observatory, who in 1970 first found a 100,000-year isotopic cycle and noted that it was roughly in step with eccentricity. "It would be hard to believe this tiny influx of dust could be having such a profound effect on climate."

"I think the chances that the 100,000-year cycles are due to inclination are exceedingly small," says Broecker, but the challenge to Milankovitch "has been healthy, because [Muller] made everybody stand up and defend what they thought. It's a fascinating problem—but unresolved."

–Richard A. Kerr

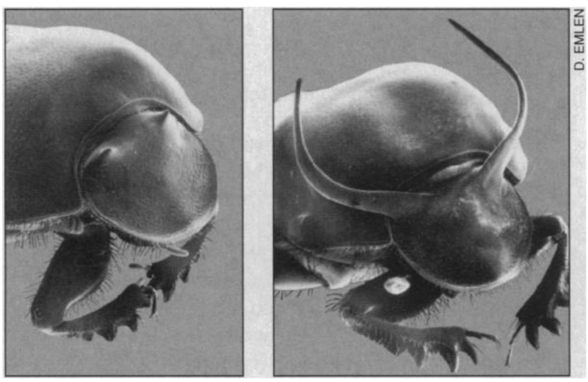
EVOLUTIONARY BIOLOGY

Sizing Up Dung Beetle Evolution

BOULDER, COLORADO—Imagine 120-kilogram antlers on an 800-kilogram moose, and you will have an idea of the outlandish proportions of the horns on some male dung beetles. The horns, which males of the genus *Onthophagus* use to repel competing suitors, have awed evolutionary biologists since Charles Darwin. Among other things, biologists have wondered what keeps the horns from getting even bigger. New experiments on these beetles now confirm a long-standing suspicion about such exaggerated traits. Horn size is limited, the studies show, because horns exact a high cost during the beetles' development: the bigger the horns, the smaller other nearby body parts.

Biologists from Darwin on have speculated about these kinds of trade-offs between body parts, but researchers had found few concrete examples. At the annual evolution meetings here,* however, evolutionary biologist Douglas Emlen of the University of Montana, Missoula, reported selective breeding and hormone experiments showing that boosting the development of *Onthophagus* males' horns causes the beetles to form smaller eyes; artificially restricting horn size leads to bigger eyes. This link, Emlen said in his talk, suggests that horns are indeed costly—and that beetles who squander too much on them are likely to be blind sided by natural selection.

The work also supports the notion that some changes in development may be a "zero-sum game," with every enhancement in one trait compensated by a reduction somewhere else, says Hugh Dingle, an evolutionary biologist at the University of California, Davis. "What Doug's work shows so nicely is that these [constraints on evolution] involve—as people have been predicting for a long time but haven't been able to show—clear trade-offs between structures."



Horns aplenty. Male dung beetles with short horns *(left)* have relatively big eyes, but big-horned beetles have tiny eyes.

Emlen, who won the American Society of Naturalists' Young Investigator Prize for his study, began his beetle work as a graduate student at Princeton University. He found that *Onthophagus* beetles have a developmental switch that turns on horn growth only if the larva has acquired enough reserves, such as body fat, before it metamorphoses into an adult beetle. Without enough fat, the larva has to save its resources to produce other adult structures and can't afford to make horns at all.

To test Darwin's suspicion that neighboring structures compete for finite resources during development, Emlen restudied the beetle specimens of his graduate work while doing a postdoctoral stint in the lab of Duke University entomologist Frederik Nijhout. He found that in *Onthophagus*, which has horns that develop just above the eyes, males with big horns did tend to have proportionally smaller eyes. "But this was just a correlation," as Emlen says; demonstrating an actual developmental trade-off would require manipulating the system.

So he and Nijhout applied juvenile hormone, which delays metamorphosis in beetles, to the beetle larvae. This postponed the onset of horn growth, producing adult males with shorter horns than untreated males. The only other trait that differed systematically between treated and control beetles was eye size: Short-horned beetles had bigger eyes.

Emlen had no comparable method to artificially make horns bigger, but he bred the beetles for seven generations and selected for large horns. The big-horned products of such selections had tiny eyes, he found, with fewer units in their compound eyes and, thus, a restricted field of vision. Carried to an extreme, Emlen says, big horns could even lead to blindness. That demonstration, says University of Maryland, College Park, evolutionary biologist Gerald Wilkinson, is "a neat trick. ... People have been writing papers about these organisms for 100 or more years, but they have all been comparative" rather than experimental.

Of course, this is just one case, and researchers exploring the links between evolution and development want more examples (*Science*, 4 July, p. 34–39). But Emlen and Nijhout say that dung beetles can likely help out. For almost every body part, there's a horn sprouting close by in one dung beetle species or another, says Emlen: "The huge variation in the morphology and location of horns should give us a big opportunity to predict how development constrains evolution."

–Wade Roush

* Joint meetings of the Society for the Study of Evolution, the American Society of Naturalists, and the Society of Systematic Biologists, Boulder, Colorado, 14–18 June.