Children of the C_4 World

Did a decline in carbon dioxide concentrations spur our evolution?

By RICHARD MONASTERSKY

Thure E. Cerling, a geochemist, learned how to read his whiskers as a menu of past meals. The chemistry of his hair furnished a concrete example of the dictum: "You are what you eat."

Each day for 2 months, Cerling trimmed his beard and carefully deposited the samples into individual vials. He saved the clippings while conducting fieldwork in Mongolia, where he ate little besides mutton raised on grass. He continued on the long plane ride home, where a bag of corn chips signaled a return to Western food. He kept up the routine even after resuming work at the University of Utah in Salt Lake City.

Back in his laboratory, Cerling analyzed the ratio of two carbon isotopes—the lighter carbon-12 and the heavier carbon-13—in each sample. The daily hair follicles, he found, recorded a dramatic shift in the type of carbon that he had consumed during this period. While in Mongolia, his whiskers showed a pronounced lack of the heavier carbon isotope. A few days after his return to Utah, the ratio of heavy to light isotopes shot upward.

In this short experiment, Cerling had managed to duplicate with his own body a familiar pattern in his research over the last decade. He had seen this isotopic shift time and again in fossil horses and other ancient mammals that populated the planet between 6 million and 8 million years ago. During this interval, many types of mammals started to consume plants relatively rich in carbon-13. The shift in diet appeared to be global, marking a profound change in the type of vegetation covering the planet.

Cerling and his colleagues are now chasing down the cause of this plant revolution. Their prime suspect: a drop in the atmosphere's carbon dioxide concentration. The end result, they surmise, was a massive turnover in the type of mammals populating the continents—an upheaval that set the stage for the evolution of our ancestors.

The principal figures in Cerling's research are the two major divisions of plants seen on Earth today. The older of the pair is so-called C_3 vegetation, which uses a type of photosynthesis that developed 3.5 billion years ago. C_3 plants include trees, shrubs, some grasses, and most crops, such as soybeans, rice, wheat, and barley. During the initial stages of photosynthesis, they absorb carbon dioxide from the atmosphere and combine it with a sugar to make a molecule containing three carbon atoms.

C_4 plants, in contrast, produce a four-carbon molecule as an intermediary. This type of photosynthesis evolved much more recently, sometime before 12 million years ago. It occurs in many modern grasses as well as in certain crops, including corn and sugarcane.

The two types of plants have different survival adaptations, and their battle for control plays out each year in U.S. backyards, says Cerling. The C_3 plants do better in cooler, moister climates. "So Kentucky bluegrass, which is a favorite lawn grass in the United States, does very well in April and May. It does not do well, certainly in my yard, in June and July. Crabgrass, which is a C_4 grass, does very well in the hot summer."

The same division appears on a global scale. C_4 crops and grasses dominate in the tropics, whereas C_3 crops and grasses thrive in cooler climes. In Mongolia, for example, C_3 plants have control. They provided the fodder for the sheep that Cerling ate on his trip. In the United States, livestock and chickens are often fed corn, a C_4 plant.

Cerling was able to use isotopes to track his diet because the two types of vegetation incorporate different blends of carbon isotopes during photosynthesis. The biochemical reactions in C_3 plants favor the lighter, carbon-12 isotope over carbon-13. C_4 plants are less discriminating, so they incorporate more heavy carbon into their cells. When Cerling returned from Mongolia to the United States, his diet shifted from a C_3- to a C_4-dominated diet and thereby went from a relatively light blend of carbon isotopes to a heavier blend. The change showed up in his beard clippings about 6 days later.

During their initial studies, more than a decade ago, Cerling and his coworkers did not realize that they had detected a global vegetation shift. Working in Pakistan, they were studying carbon deposits in ancient soils and fossil teeth of horses and ancient relatives of the elephants. Both the carbon deposits and the teeth indicated that C_3 plants had given way to C_4 grasses during the late Miocene epoch, starting about 8 million years ago.

Looking for a local explanation, the scientists focused on the Tibetan Plateau, which was rising during the Miocene. Climate theory suggests that the uplift of the plateau is responsible for the region's monsoonal climate, with its alternating patterns of rainy and dry seasons. This local change could have favored the loss of forests in southern Asia and the spread of C_4 grasses, which do well in the monsoonal climate, when rain falls during the hottest season.

When they discovered the same isotopic shift in North America in the early 1990s, the local explanation no longer seemed reasonable. Cerling's group suggested that there might have been a global expansion of C_4 grasses during the late Miocene.

Since then, additional data from South America and East Africa have supported that hypothesis, Cerling and his coworkers reported in the Sept. 11, 1997 NATURE. What's more, the change seems to have occurred earliest in the tropics and then spread north and south. In Kenya, for example, grazing horses switched from a predominantly C_3 diet to a C_4 one by 7.5 million years ago. In the southern United States, the change took place between 6.8 million and 5.5 million years ago.

With the evidence pointing toward a global C_4 expansion, the rise of Tibet would no longer serve as an explanation. Cerling started searching for a more pervasive change. He didn't have to look far. A few buildings away, in the University of Utah's biology department, James R. Ehleringer was experimenting with how C_3 and C_4 plants respond to carbon dioxide in the air. His data suggested that C_3 plants function better in elevated concentrations of carbon dioxide than C_4 plants do.

In the recent NATURE article, Ehleringer and Cerling propose that carbon dioxide is the key to the Miocene vegetation changes. Geochemists know, in general, that the atmosphere was once much richer in this gas. During the days of the dinosaurs, 100 million years ago, carbon dioxide had a concentration of more than 1,000 parts per million, whereas the value before the Industrial Revolution hovered near 280 ppm.

Ehleringer and Cerling speculate that as carbon dioxide values dropped slowly over time, they eventually reached a level—around 500 ppm—that inhibited the efficiency of C_3 plants. This permitted the spread of C_4 grasses, which use carbon dioxide more effectively, the scientists hypothesize.

"The reason we've linked it to carbon dioxide is that we were at a loss to explain what mechanisms other than a change in the atmosphere could have caused this to happen in North America, South America, Asia, and Africa," says Cerling.

The vegetation changes had a profound effect on the mammals of the time, contend the scientists. In Pakistan, woodland animals such as the Pakistani ape, *Sivapithecus,* disappeared, while animals that are adapted to open habitat emerged. In Africa, a similar transition took place, the scientists say. Grassland-adapted antelopes took over from relatives better suited for woodlands and shrub lands. Elephant relatives with high-crowned grass-munching teeth replaced species with low-crowned teeth.

"On most of the continents, this was an important time of change in the mammalian faunas," says Cerling. "If you read explanations for the faunal changes, most of the time they're attributed to increasing global aridity. We're suggesting that perhaps it's not a water starvation of the planet, but a carbon dioxide starvation of the planet that caused the vegetation changes."

Among the creatures affected by these shifts were the primate ancestors of humans. One theory of human origins, the savanna hypothesis, posits that the spread of African grasslands at this time favored the evolution of bipedal apes, which are adapted to walking across the open habitat. The work by Cerling and his colleagues now offers an explanation for what triggered the rise of savannas, says Nikolaas J. van der Merwe, an archaeologist at Harvard University who uses isotopic ratios to study ancient diets.

"The planet is now a different planet," says Cerling. "It's a C_4 planet, and before 8 million years ago it was a C_3 planet. So the evolution of mammals, including humans, took place in this ultralow carbon dioxide atmosphere."

Critics view Cerling's carbon dioxide theory as too simplistic. While most acknowledge that C_4 plants became more numerous during the late Miocene, they do not agree on what caused this shift or what effect it had.

Michèle E. Morgan, an anthropologist at Harvard, questions whether carbon dioxide concentrations were the sole instigator. "You can't hang it up with just one nail. There are other issues that come into play," she says.

Mural by Jay Matternes, photograph by Chip Clark/Smithsonian Institution

A collection of North American mammals inhabiting the high plains at different times during the middle and late Miocene epoch, from about 16 million to 5 million years ago. The late Miocene marked a major extinction of many forms, including the shovel-tusked, elephantlike Amebelodon *(rear left); the striped horse* Pliohippus*; the gray llamalike* Procamelus *(far right); and* Synthetoceras *(foreground), with its oddly shaped nose horn.*

One issue is climate. Morgan wonders not only whether the world was getting drier—the standard explanation—but also whether there were changes in the seasonal timing of precipitation, which would have affected vegetation. She next asks about animal fauna. Cerling's hypothesis assumes that plant changes triggered faunal turnover, but Morgan contends that shifts in animal species could alter the types of plants in an ecosystem.

John D. Kingston, an anthropologist at Yale University, also debates elements in the carbon dioxide theory. While he agrees that C_4 grasses replaced C_3 plants in the tropics, the available data do not tell exactly how the habitat changed. Evidence from horses and other animals with high-crowned teeth indicate that C_3 grasses were part of the environment long before the C_4 grasses arrived. "Maybe what we're seeing is just a replacement of C_3 grasses with C_4 grasses. That might mean that there was not a tremendous change in the landscape," says Kingston.

Rejecting the simple idea of woodlands giving way to savannas, Kingston argues that a range of habitats was available both before and after the C_4 transition. In 6.3-million-year-old rocks from Kenya, for example, he has found the fossil remnants of a rain forest only a few kilometers away from the fossils of horses, which lived on a strict diet of C_4 grasses.

"What we'd like to have is corroborating information," says Kingston. It may be difficult to come by, though. Paleobotanists would love to examine plant remains to assess precisely how habitats changed through time, but plant fossils at many key sites are rare.

The carbon dioxide hypothesis "may be true," says Kingston, "but the resolution of the data is not good enough to say 'Yes, there was a change in the habitat and yes, the animals responded to it.'"

Cerling agrees that the tropics had some grasses prior to the spread of C_4 vegetation, but the shifts in animal species suggest that grasslands expanded markedly in the late Miocene. "Afterward, I suspect there were far more grasslands and perhaps very, very little of the shrub lands present."

Scientists are only now starting to untangle the details of the C_4 revolution and to assess how it altered the course of mammalian evolution. While the facts of this transition remain fuzzy, the ancient event is becoming increasingly relevant to modern life, as people pour billions of tons of carbon dioxide into the atmosphere each year.

Without massive cuts in greenhouse gas pollution—ones that far exceed the limits adapted in Kyoto, Japan, last month—the concentration of carbon dioxide is expected to climb above 500 ppm sometime in the latter half of the next century, possibly earlier. This is the threshold value that Cerling and his colleagues identified for vegetation. Above this amount, C_3 photosynthesis has the edge over C_4 except at extremely high temperatures, suggest the researchers.

The extra carbon dioxide is pushing Earth back into a regime it has not seen in the last 8 million years. "By increasing atmospheric carbon dioxide concentrations," says Cerling, "humans may be changing the Earth's atmosphere to conditions not favorable to a 'C_4 world,' the world in which we originally evolved." □