EDITOR'S INTRODUCTION *Conservationists by nature look out upon a world of wounds, but perhaps only the most astute among us—those who have suffered the deepest penalty of an ecological education—see the ghosts that inhabit the land. Like the protagonist in the recent film* The Sixth Sense, *Connie Barlow can see the dead; not the ghosts of people, however, but giant ground sloths, mastodons, gomphotheres, and other now extinct megafauna. In this article, and the wonderful new book from which it is excerpted,* The Ghosts of Evolution, *she considers the fascinating relationship between large tropical fruits and the megaherbivores with which they coevolved, and mourns the loss of an ancient pact between certain plants and the animals who helped disperse their seeds.* —TB

Haunting the Wild Avocado

by Connie Barlow

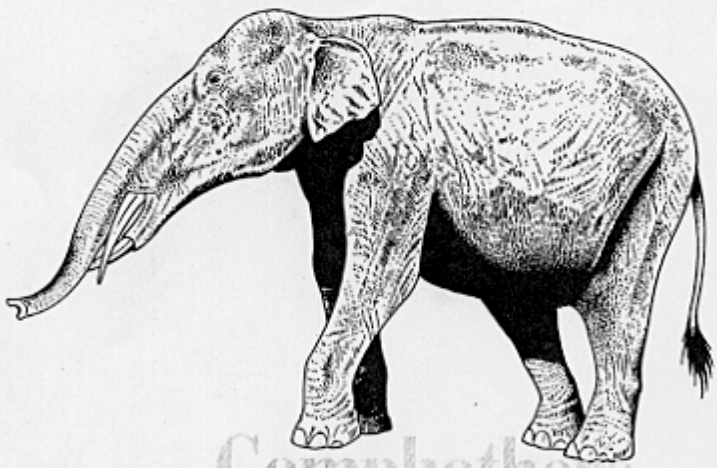
We live on a continent of ghosts, their prehistoric presence hinted at by sweet-tasting pods of mesquite, honey locust, and monkey ear.

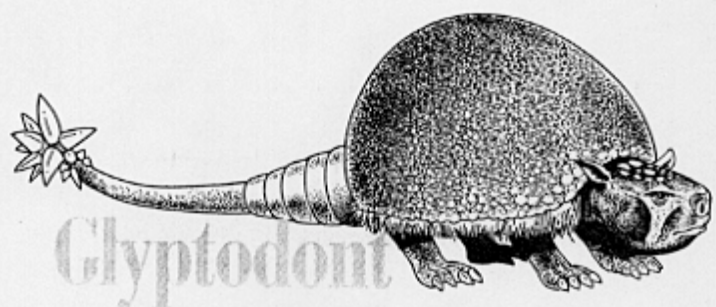
—Paul Martin and David Burney

Grocery stores are excellent places to encounter ghosts. They lurk in the fruit section, feasting on ecological anachronisms. Paul Martin thinks he's spotted ghosts among the bins of apples and pears. Martin is a paleoecologist at the University of Arizona, and he likes to dwell in the Pleistocene. He has been honing his occult skills for a quarter century. I'm a neophyte, so I head straight for the tropical fruits, where ghosts are easier to conjure.

For thirteen thousand years, since the extinction of the massive at the end of the Pleistocene, papaya has been haunted by spectacular ghosts (Janzen and Martin 1982). Most impressive are the gomphotheres and ground sloths, with gapes large enough to take in the soft fruit whole. Originating in Mexico, *Carica papaya* had evolved its fruit form to attract great herbivores. But soon after humans arrived in the New

This essay is adapted from Connie Barlow's forthcoming book, The Ghosts of Evolution: Nonsensical Fruits, Missing Partners, and Other Ecological Anachronisms *(© 2001 by Connie Barlow; all rights reserved), and is used with kind permission of Basic Books.*





World, that strategy for reproduction came to an end. The holocaust of megafaunal extinction deprived papaya of its best seed dispersers.

The avocado bin attracts ghosts of glyptodonts and toxodons as well as gomphotheres and ground sloths. Because almost all fifty species of genus *Persea* are native to the tropics and subtropics of the Americas, one can surmise that the avocado genus developed its single-seeded form in the Western Hemisphere. Not all *Persea* species evolved with megafauna in mind, however. The kind that thrives along the Gulf Coast of the United States bears fruit not much bigger than blueberries.

Like papaya, the species of avocado found in grocery stores (smooth and rough-skinned varieties of *Persea americana*) has been haunted for thirteen thousand years. Many living frugivores, omnivores, and even carnivores are attracted to the oily pulp, but only an animal with a massive gullet will swallow the huge seed along with the flesh. The cultivated varieties of *Persea americana* have far thicker pulps surrounding the seed than does the ancestral stock, but the seed itself is virtually unchanged in girth (Cook 1982). From a functional and evolutionary perspective, avocado *intends* its fruits to be swallowed whole. That's how the species disperses its seed. The oily flesh is simply the lure. A parent tree could wish for no more desirable fate for its offspring than to have its seeds plopped into the world within steaming heaps of dung.

Whether growing in commercial orchards of southern California or forest fragments of the neotropics, domestic and wild avocado trees still expect giant mammals to stop by for the harvest. Wave upon wave of Cenozoic megafauna faithfully harvested avocado fruits, season upon season, for tens of millions of years. The identities of the dispersers shifted every few million years, but from an avocado's perspective, a big mouth is a big mouth and a friendly gut is a friendly gut. The passage of a trifling thirteen thousand years is too soon to exhaust the patience of genus *Persea*. The genes that shape fruits ideal for megafauna retain a powerful memory of an extraordinary mutualistic relationship. Embellished by our own scientific understanding, that memory would look something like this.

THE SCENE IS A TROPICAL FOREST IN CENTRAL AMERICA fifteen thousand years ago, and a giant has just arrived. Perhaps attracted by the scent of ripe pulp, a three-ton mother and her bear-size toddler approach a tree that shed its fruit crop a few days before. The visitors are ground sloths, whose closest living relatives are South American tree sloths,

-ground sloth illustration from *Cenozoic Gravigrade Edentates of Western North America* by Chester Stock, 1925

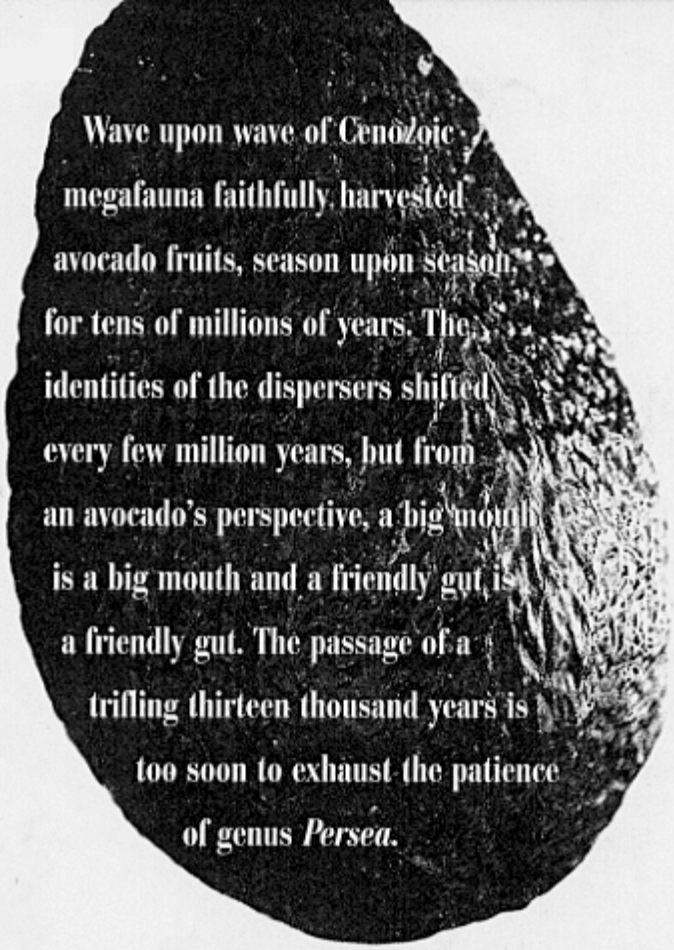
anteaters, and armadillos. *Eremotherium* looks like nothing alive today. Think of a bear crossed with a prairie dog or marmot and endowed with the bulk of an elephant. The adult sloth begins to sniff the carpet of fruits for the ripest specimens. Her agile offspring climbs a nearby tree for safety and also because, at this age, climbing is not only possible but irresistible. In a few years, the young sloth's tree climbing days will be over. By then, an enormous bulk and powerful clawed forelimbs will suffice to ward off all but the most determined predators.

The mother finds a fruit that smells acceptable and tests it for softness between frontally toothless jaws. The whole fruit is then mashed between tongue and palate. The slippery seed slides easily down the animal's gullet, along with the nutritious pulp. Laxatives in the pulp ensure that the seed will complete its dark journey before digestive juices do it harm.

Other seeds follow. Before she is satiated, the sloth and her young depart. The adult sloth will balance the oily meal with leafy browse, thus keeping microbes happy in the vast fermentation vat of her gut. Tomorrow the pair will return to the same tree, dispersing seeds enroute. Or perhaps *Eremotherium* will choose a papaya tree instead. To feed on papaya, the great sloth will sit up on her haunches, using her sturdy tail for a third point of balance. She will choose the ripest pendulous fruit—all of which are borne on the trunk of the small tree. Her reach may exceed four or even five meters.

The sloth's limbs still bear signs of arboreal ancestry. In shuffling from plant to plant, *Eremotherium* walks on the sides of her paws. The awkward gait may owe to phylogenetic inertia—an inability to evolve away from an established form. Perhaps, too, it owes to the survival advantage of in-turned paws. An enhanced ability to climb when young should more than offset an inability to run later on. Or perhaps the anatomical quirk is necessary for the sloth to walk at all. *Eremotherium*'s front feet bear exceptionally long claws, as do the front feet of a relative that will survive the end-Pleistocene extinction: South America's giant anteater. The anteater walks on its knuckles, claws behind and curled skyward.

Meanwhile, in another part of the forest, one that is especially rich in avocado trees, a small herd of gomphotheres (genus *Cuvieronius*) approaches on an ancient trail. The herd has traveled tens of miles in the past three days, munching greenery along the way. The matriarch remembers the route. She remembers this avocado-rich valley and others throughout a vast region, as well as good places and times to find papaya, cherimoya, sapote, *Cassia grandis*, and many other treats. She learned these sites while following the lead of her mother, the former matriarch.



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The gomphotheres arrive at the avocado grove when the fruits are near their prime. A half dozen elephantine trunks probe the carpet of green-brown fruits. This is the first avocado experience for the youngest member of the clan. The pulp tastes as good as it smells, but the seed is too big to be swallowed. Much pulp is lost as the young proboscidean works the seed out and over the edge of his mouth. Then he picks up another fruit, and another. Finally, he manages to crush a slippery seed between cusped molars. The mash is hastily rejected. The bitter toxins are the plant's way of ensuring that dispersers do not become seed predators. Seeds are to be swallowed, not chewed.

Giving up, the young gomphothere nudges a cousin into play while the adults continue to eat. The avocados are soon gone, and the matriarch leads the herd to a forest clearing where browse is abundant. In a day or two, the gomphotheres will begin to deposit in fertile mounds the avocado seeds, along with many smaller seeds of other fruiting species ingested around the same time. Many of the seeds that survived the intestinal voyage will fall prey to seed-eating rodents or parrots, especially after dung beetles have carved the heap into fragments, rolling away the rich matrix to feed their young. Perhaps one seed will become a tree.

Ten years pass. A young avocado tree bears fruit for the first time. The gomphotheres discover it easily and add its location to clan memory. By no coincidence, the tree is near an ancient, well-worn path.

FIFTEEN THOUSAND YEARS PASS. *PERSEA AMERICANA* STILL grows in Central American forests not yet turned into pasture. But the extent and density of the species does not match its former glory. A menagerie of small pulp thieves and seed predators raid the fallen fruits. Those who plunder the pulp leave behind seeds destined to compete with the parent. Seed predators may wait for the molecular transformations of germination to subdue the toxins, or they may gnaw into seeds to extract just the embryos. Now that the migrators are gone, the sheer mass of fruit overwhelms the appetites of locally based thieves and predators. Molds attack the pulp of many overripe fruits. Fungal hyphae work their way into the seeds.

If a tree is very lucky, a jaguar may happen by. The avocado's oily flesh is attractive to this otherwise strict carnivore (Cook 1982). Because jaguar teeth are designed for tearing flesh—not grinding seeds—and because its gullet is adapted for swallowing great chunks of meat, a jaguar is a helpful seed disperser for avocado. But large carnivores were never abundant and are less so today. The avocado lineage may have been saved from extinction by the rare jaguar who takes advantage of an easy meal, and perhaps by agouti rodents that gather and bury avocado seeds just as squirrels gather and bury acorns (Hallwachs 1980). The occasional pulp thief who scampers off with a fruit in its mouth, in order to strip off the pulp in a safer location, has surely helped the lineage as well. Nevertheless, the fruit of avocado was not shaped by millions of years of selection for these underabundant, ill-fitted, or fickle dispersal agents.

Nor was it shaped by the food preferences of bipedal apes, who invaded avocado territory just before the gomphotheres and ground sloths disappeared. Those apes are now doing a better job dispersing one species of the genus than any animal has done before. The dominant habitat for avocado today is in villages and orchards—and its range now wraps around the world.

Fortuitously, avocado was superbly built to attract the new mutualists. Nevertheless, it was not built to the specifications of apes. Rather, the fruit of the avocado (like that of mango, grapefruit, and pomegranate in the Eastern Hemisphere) was the plant kingdom's ingenious response to the pageant of beasts grown big throughout the Cenozoic and throughout the world. The beasts did not become giants in order to consume avocados. Their gigantism owes to millions of years of adaptive change to deter predators, to store energy for lean times, and to overpower rivals in mating jousts. In contrast, the avocado lineage did indeed evolve big-seeded, big fruits with the big beasts in mind. The bigger the seed, the better provisioned the embryo. Big-seeded plants have an advantage over small-seeded plants in mature forests, where sunlight penetrates to the ground only in patches and for maybe an hour or two each day. Big-seeded fruits of the tropical forests can grow for a year entirely on the energy sequestered in the seed. Perhaps during that pivotal year a tree will topple, allowing a shaft of light to penetrate. Or perhaps the seedling itself will reach a height where photosynthesis can begin in earnest.

Avocado's strategy for propagation made a great deal of sense throughout the long life of this lineage—until the present moment. Even after thirteen thousand years, avocado is clueless that the great mammals are gone. For the avocado, gomphotheres and ground sloths are still real possibilities. Pulp thieves like us reap the benefits. *Homo sapiens* will continue to mold the traits of the few species of genus *Persea* it prefers. Ultimately, however, wild breeds will devolve less grandiose fruits, or else follow their animal partners into extinction.

An avocado sitting in a bin at the grocery store is thus biology in a time warp. So too is papaya and cherimoya, sapote and countless other fleshy fruits of the neotropics. In temperate regions of North America, fruits that remember mastodons and mammoths include the long, spiraling pod of honey locust and the great green ball of the osage orange. These reproductive strategies are all suited for a by-gone world. The fruits are ecological anachronisms. Their missing partners are the ghosts of evolution.

These Pleistocene anachronisms are vivid reminders of a time not long ago when the New World megafauna rivaled that of the Old. The avocado is the American version of the elephant- and rhino-alluring mango of Asian forests. Many American anachronisms have already suffered range contractions and become patchy or rare in the wild. As tapirs and monkeys in the West and elephants and rhinos in the East dwindle, more and more fruits will be pushed over the brink, joining the ranks of the ill-suited and sadly bereft. ☾

Connie Barlow, *a science writer and conservation activist, is a founding member of the Epic of Evolution Society. Her books include* From Gaia to Selfish Genes; Evolution Extended; *and* Green Space, Green Time: The Way of Science. *She divides her time between New York City and the Gila country of New Mexico.*

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