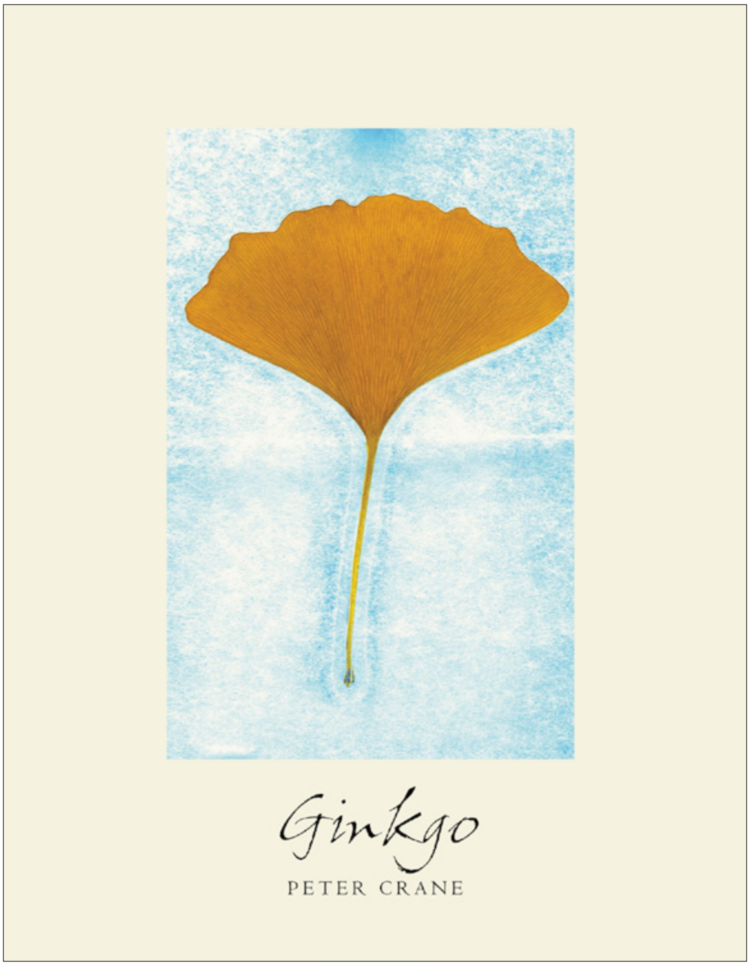
BOOK EXCERPT

Ginkgo: The Tree That Time Forgot

Peter Crane

Editor's Note: In his new book, noted botanist Peter Crane has gathered a vast trove of information on the ginkgo, undoubtedly one of the most loved trees in the world. Exploring topics ranging from paleobotany to evolutionary biology, plant exploration, and human culture, the author presents fascinating tales from the ginkgo's very long history on Earth. Printed here by permission of the publisher is Chapter 21, "Extinction." (Don't worry, ginkgophiles—Chapter 22 is "Endurance.")



Ginkgo: The Tree That Time Forgot
Peter Crane
Yale University Press, 2013. 408 pages.
ISBN: 978-0-300-18751-9

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Extinction

Many rivers to cross
But I can't seem to find my way over.
—Jimmy Cliff, "Many Rivers to Cross"

Given its long fossil history, the presence of ancient ginkgo across much of the Northern Hemisphere for most of the past 65 million years is not so surprising. Ginkgo and its extinct relatives were seemingly nearly everywhere on the planet for eons, and despite their clear decline about 100 million years ago, ginkgo managed to persist in many places. However, looking back from today, the fact that ginkgo was growing wild in Bulgaria and Greece just 5 million years ago nonetheless seems strange. It reminds us that not so long ago the world was a very different place. In the grand sweep of geologic time the distribution of animals and plants on our planet has changed rather quickly; where they live and grow now bears a strong imprint of history.[1]

Fossil floras from the Late Miocene and Pliocene provide irrefutable evidence that in addition to ginkgo, there were many other plants in western North America and Europe between about five million and fifteen million years ago that no longer grow there. In terms of the trees the vegetation in these areas was much richer then than now. For example, fossils from the fill of an ancient sinkhole at Willershausen near

Göttingen, Germany, show a mix of broadleaved and coniferous forests. On richer soils broadleaved forest included species of maple, birch, hickory, beech, ash, oak, and elm among about thirty-four tree species. Conifer forest included many trees that no longer occur today in Europe but can be found growing in the warm temperate forests of eastern Asia: the umbrella pine, for example, as well as the Chinese swamp cypress, the katsura, the dawn redwood, and the hardy rubber tree. Like ginkgo, in Europe, they all disappeared relatively recently.

In North America, fossil evidence from Clarkia, Idaho, shows exactly the same pattern. Again, the Chinese swamp cypress and the katsura are both present, along with the dawn redwood and the China fir. All of these plants are today restricted to eastern Asia. At both Clarkia and Willershausen there was also the Cathay silver fir, a rare conifer discovered as a living plant only in 1955. Today it has a scattered and restricted range in southwestern China. After about five million to fifteen million years ago, these plants were never seen in Europe and North America again, but somehow they managed to persist in the East.[2]

It is hard to understand exactly when and how these species were eliminated from Europe and North America because in most cases the fossil record is not sufficiently complete to provide a detailed picture of how their distribution gradually changed from being widespread in the past to being much more restricted today. We can, however, get some idea of how they may have fared by tracing the fate of a few of their associates that have especially distinctive pollen grains. Pollen grains are produced and preserved in the fossil record in vast numbers, and when they are sufficiently diagnostic of a particular tree, and readily recognized in fossil assemblages, they can be used to get a fine-grained look at how that plant fared as global climates deteriorated.

Particularly instructive is the history of the Caucasian wingnut, a tree in the walnut family that has especially distinctive pollen grains. These pollen grains disappear and reappear through successive glacial and interglacial phases in southern Britain. After each of the first few glacial advances up to about 500 thousand years ago, pollen grains of the Caucasian wingnut reappear in the intervening warm interglacials. These plants seem to have been forced south by successive glacial advances, but they evidently migrated back again into Britain, presumably from the south and east, as the climate warmed. However, these distinctive pollen grains are last seen in Britain during the Hoxnian interglacial between about 374 thousand and 424 thousand years ago. For some reason, in the two most recent interglacials, the Eemian, which lasted from about

114 thousand to 130 thousand years ago, and the present Holocene, which began about 10 thousand years ago, the Caucasian wingnut never made it back.[3]

It would be wonderful if we could follow the history of ginkgo in a similarly detailed way, but unfortunately its pollen grains are too easily confused with those of other plants. However, the example of the Caucasian wingnut does raise a potentially important but unanswered question concerning the ecology of ancient ginkgo: having been displaced from particular places by changing climates, did it have the ability to recolonize? Colder and drier climates may have progressively restricted ginkgo's geographic range, but why did it not bounce back? Surely it should have been able to recolonize those places where it obviously grows so well today.

In most plants, the ability to colonize an area depends on the effectiveness with which seeds are dispersed. Seed dispersal provides plants with the ability to emulate an animal and move from one place to another, albeit much more slowly, generation by generation. The fruits and seeds of many plants show specializations to increase the effectiveness of dispersal, from the parachute-like fruits of dandelions that are blown along by the wind to the seeds of blackberries that are gobbled up along with the fleshy fruits in which they develop and are dispersed in the droppings of birds. A key question in the case of ginkgo is whether one of the factors responsible for its decline over the past few million years was a poor system for dispersing its seeds.

In 1982 the tropical ecologist Dan Janzen and the paleontologist Paul Martin published a provocative article with an arresting title: "Neotropical Anachronisms: The Fruits the Gomphotheres Ate." Their central idea flowed from the observation that many of the common plants in Guanacaste National Park in Costa Rica, where Janzen had worked for many years, appeared to have no natural means of dispersing their seeds. They noted that this was particularly the case for some of the plants in which the fruits and seeds were relatively large, such as guanacaste itself and another legume tree, divi-divi. Today, the fruits and seeds of these trees are eaten by horses and cattle, but these animals have been introduced by people from elsewhere only relatively recently. There are no indigenous animals that appear capable of dispersing them. Janzen and Martin argued that this mismatch arose because these plants had been dispersed in the past by animals that are now extinct. The plants had survived, but the animals capable of dispersing their seeds had not.

Janzen and Martin suggested that such plants used to be dispersed by the large mammals that once inhabited South and Central America but disappeared relatively suddenly, perhaps as a result of hunting by humans, climate change, or both factors acting together, about ten thousand years ago. These now-extinct animals would have included the gomphotheres, massive extinct relatives of modern elephants, that were obviously plant eaters and flourished in Central America for most of the past five million years. Living alongside them were other fruit eaters like ground sloths, glyptodonts, extinct horses, extinct bears, giant armadillos, flat-headed peccaries, and others. Janzen and Martin's point was that the gomphotheres, along with other extinct large mammals, probably played an important role in the ecosystems of Central America over the past few hundred thousand years and that their relatively recent extinction has left us trying to understand an ecosystem that is missing some of its most important parts.[4]

What was most important about Janzen and Martin's idea was its focus on the importance of history for interpreting the world around us. The survival of the plants, after the extinction of the gomphotheres and other animals that may have dispersed them, was an accident of history. In effect the evolutionary histories of the plants and their associated animals were now out of phase. With some slight rhetorical license, Janzen and Martin called those plants that had lost their dispersal agents the "living dead." The implication was that without the dispersers with which they had evolved, their days were numbered.[5]

Janzen and Martin's ideas proved hugely influential, and in 1984 my paleobotanical colleague Bruce Tiffney of the University of California, Santa Barbara, suggested that something similar might have happened in the history of ginkgo. Bruce argued that ginkgo, like Janzen and Martin's tropical trees, was also one of the "living dead," a plant that had lost its dispersers. He speculated that the strange and strong-smelling ginkgo seed might have been a specialization for attracting dinosaurs, or perhaps early kinds of mammals that are now extinct.

Of course, an idea like this is hard to prove, but it does begin to hint at another reason, other than local extinction due to climate, as to why living ginkgo very nearly went extinct. The apparent migration around fifteen million to twenty-five million years ago of ginkgo into eastern and southeastern Europe, areas where it was not previously present, seems to suggest that dispersal was still possible long after the demise of dinosaurs and ancient extinct mammals. However, Bruce's point was nevertheless a good one. A lack of effectiveness in the dispersal of ginkgo seeds may have played a part in its progressive restriction, and the fact that this may reflect more recent extinctions, rather than ancient extinctions at the time of the dinosaurs, is in some ways beside the point.

Unfortunately, even though its smelly seeds are one of its most well-known and distinctive features, we know very little about how seed dispersal works in living ginkgo. However, germination does improve after the fleshy seed coat has been removed—for example, by passing through the gut of an animal. In one of the potentially wild ginkgo populations in China it is also documented that the seeds are eaten by a wild cat, and in Japan they are eaten by badgers. Dogs are sometimes attracted to them too. A friend recalls his dog feasting on ginkgo seeds one autumn on the University of Minnesota campus. It would be helpful to have more information on the kinds of animals attracted to ginkgo seeds today, but even if various mammals are known to collect and eat ginkgo seeds, this is not quite the same as knowing that ginkgo has a reliable seed disperser.[6]

If Bruce is broadly correct, and sometime toward the end of the Mesozoic, or more likely during the Cenozoic, ginkgo lost the animals on which it depended for dispersal, then the effects of climatic restriction would have been greatly amplified. It would have meant that ginkgo, unlike the Caucasian wingnut, for example, was not able to easily recolonize areas from which it had been displaced. It would have continually lost ground, and its populations would have become smaller, moving it ever closer to what conservationists sometimes call the extinction vortex. Colder or perhaps drier climates would have eaten away at ginkgo's once widespread geographic range, and limited powers of dispersal would have reduced ginkgo's ability to recolonize. The effect would have worked like a ratchet; once ginkgo lost ground it was unable to take it back. In North America and Europe the impact over the past few million years may have been especially pronounced if, as seems likely from the fossil evidence, the geographic extent of ginkgo in those areas had already been reduced by climatic drying and other vegetational changes. The mountains and valleys of southern and western China may have provided a greater variety of potential refuges.

Whatever the reason, the pattern of regional extinction could not be clearer. Ginkgo has a more or less continuous record in Asia beginning with the early fossils described by Zhou Zhiyan and his colleagues more than 200 million years ago. It continues through the Jurassic and Cretaceous, to the presence of ginkgo in fossil floras from the Pliocene of Japan. However, in Europe and North America the pattern is different. Here the fossil record of ginkgo is also deep but it is abruptly truncated relatively recently.[7]

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These insights provide a clear example of the importance of fossils to fully understand how our modern world came to be. The natural world is full of patterns, some of them completely unexpected, that can be explained only by reference to history, and as I never tire of saying to my students, if you want to understand the way anything is today, whether it is a plant, a person, an ecosystem, an organization, or a country, then you need to understand its history. It is a mantra that is hardly original, but one that is easily forgotten in our modern preoccupation with the here and now. In biology, these kinds of historical complications are the reason why we ignore evolution, and the direct historical evidence that comes from paleontology, at our peril.

In particular, the fossil record of ginkgo and similar plants helps make sense of a somewhat enigmatic observation made by botanists since the time of Linnaeus: that there are surprising similarities between the plants of eastern North America and eastern Asia. Highlighted at the end of the eighteenth century by the Italian botanist Luigi Castiglioni, and then later by the American Thomas Nuttall, the full extent of these similarities did not become clear until the work of the great nineteenth-century American botanist Asa Gray.[8]

Gray and his contemporaries were at a loss to explain how the pattern had come about. For Darwin, writing to Gray at Harvard in 1856, this was one of the "many utterly inexplicable problems" of botanical geography. Darwin was completely puzzled about why there should be stronger similarities between the flora of eastern North America and eastern Asia than between the floras of eastern and western North America. The fossil record shows beyond doubt, just as Gray later inferred, that these seemingly strange and widely separated occurrences are the result of regional extinction, especially in Europe and western North America, of plants that were once much more widespread. In the case of ginkgo regional extinction went even farther; the species was completely eliminated from Europe, from eastern and western North America, and also from Japan. Even in China its extinction was very nearly total.[9]

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1. Epigraph: From Jimmy Cliff's album *Jimmy Cliff,* 1969, Trojan Records. For more information on the Early Pliocene fossil vegetation in southern Europe, see Kovar-Eder et al. (2006).

2. The Willershausen flora is especially rich; more than 130 species have been collected, representing more than one hundred different kinds of plants. See Straus (1967); Ferguson (1967); Ferguson and Knobloch (1998).

3. Like ginkgo, the Caucasian wingnut has been reintroduced by people into many of the places where it once grew; there are large specimens of the Caucasian wingnut at Kew, for example, that date from the late nineteenth century. The nearest native populations are in the Caucasus, with its closest relative, a similar species native to China.

4. The gomphotheres may have persisted until as recently as six thousand years ago in present-day Colombia; see Rodríguez-Flórez et al. (2009). For a complete list of now-extinct large herbivores of Central America, see Janzen and Martin (1982, 21).

5. For a popular discussion and elaboration of Janzen and Martin's idea, see Barlow (2002).

6. Known foragers of the seeds of living ginkgo include the catlike *Paguma larvata* in China and the Japanese badger *Nyctereutes procyonoides.* Rothwell and Holt (1997) note the improved germination rates of seeds scarified by passing through the digestive tract of badgers.

7. By the end of the Pliocene, ginkgo had disappeared from the fossil record everywhere except perhaps for a small area of southern Japan; see Uemura (1997).

8. Castiglioni had visited North America between 1785 and 1787, and also had consulted *Flora Virginica,* published by Gronovius in 1739 and 1743, and Thunberg's *Flora Japonica* published in 1784: see Spongberg (1993). Asa Gray at Harvard was a frequent correspondent and staunch supporter of Darwin in North America. Darwin's letter to him on "botanical geography" was written on October 12, 1856. New information that Gray had at his disposal included Siebold's *Flora Japonica* as well as specimens brought back from the Rodgers-Ringgold Expedition (1853–1856), also known as the

North Pacific Exploring and Surveying Expedition, a United States scientific and exploring project with the broader purpose of finding shorter trade routes for merchant ships in the Pacific; see Cole (1947). Also available were specimens brought back from Japan by Charles Wright.

9. Gray (1859, 422) listed about 580 Japanese species "which have particular relatives in other and distant parts of the northern temperate zone," along with the corresponding plants in the floras of Europe; central and northern Asia; western North America; and eastern North America. To explain the widely separated but highly similar floras of eastern Asia and eastern North America, Gray suggested that before the glacial epoch, the flora of the North Temperate Zone had been relatively homogeneous and that regional extinction during the Ice Ages resulted in greater losses from western North America and Europe. In some cases the impact of regional extinction was less pronounced. The sweet gum, for example, has widely separated remnants not only in eastern Asia and eastern North America, but also in southeastern Europe.