Wake Up and Smell the Ginkgos

Peter Del Tredici

Ginkgo biloba is one tree that most Americans—even those with little knowledge of botany—can recognize. There are two reasons for this: first, its fan-shaped leaves are highly distinctive and impossible to confuse with any other tree; and second, it is widely cultivated as a street tree in many urban areas throughout much of the United States. Because of its environmental adaptability, its resistance to pests and diseases, and its general tolerance of inhospitable growing conditions, ginkgo is experiencing a spike in popularity as evidenced by the long rows of them that are showing up in commercial and municipal landscape projects across the country. In this regard, Americans are following the pattern set in Japan where ginkgo accounts for 11.5% of all the street trees growing in that country—more than any other single species (Handa et al. 1997).

As well as gaining in popularity, ginkgo has also been experiencing a surge in attention from the scientific community, particularly from the Chinese, for whom the tree has become a national symbol of their botanical heritage. The pur-

An allée of ginkgos, about 100 years old, on the campus of Tokyo University.

Ginkgo has unmistakable fan-shaped leaves.

One of the old ginkgos at Bai Yuan village in Wuchuan County, Guizhou Province. Note the epiphytic ferns growing on its trunk.

pose of this article is to acquaint the reader with some of this new information about the plant's unique evolutionary history as well as its ecological role as a plant teetering on the brink of extinction in the wild.

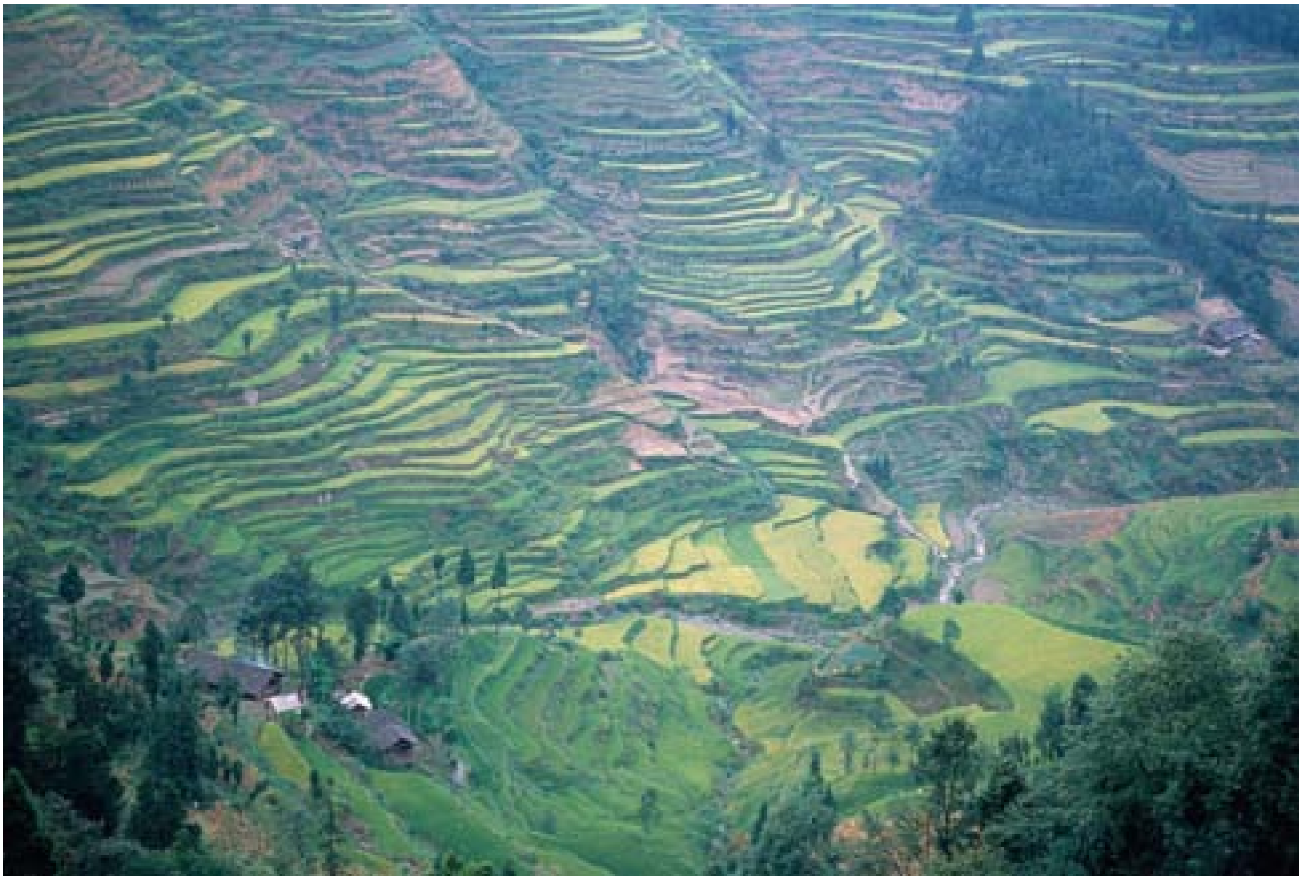
Ginkgo's Homeland

Questions about the extent of *Ginkgo biloba*'s native range in China—or if native populations even exist at all—have been the subject of debate among botanists for well over a hundred years (Del Tredici et al. 1992, Li et al. 1999). The conflict has only recently been resolved with the help of DNA analyses (Fan et al. 2004, Shen et al. 2005, Wei et al. 2008) which have demonstrated that isolated ginkgo populations located in southwest China, especially around the southern slopes of Jinfo (or Golden Buddha) Mountain in Chongqing Province (28°53' N; 107°27' E), possess a significantly higher degree of genetic diversity than populations in other parts of the country, indicating native status. The area has a mesic, warm-temperate climate with a mean annual temperature of 16.6°C (62°F), and a mean annual precipitation of 1,185 millimeters (47 inches), with ginkgos growing mainly between 800 and 1,300 meters (2,625 and 4,265 feet) elevation (Li et al. 1999).

In addition to the genetic evidence, there is ecological and cultural evidence which suggests that these populations are wild. Ecological work in Chongqing Province, as well as in adjacent parts of Guizhou Province (Xiang et al. 2006), has identified dozens of small populations of ginkgos which can be considered either to be wild trees growing in the midst of native forest or the remnants of wild populations that have lost their forest context. These ginkgo populations occupy land that usually measures a few hectares at most, and they are surrounded by small villages whose residents practice subsistence agriculture. In areas where livestock has been excluded, spontaneous ginkgo seedlings and saplings are common in the forest understory.

In the cultural realm, much of northern Guizhou Province has been settled over the past three hundred years or so by people of Miao descent who, unlike the Chinese of Han descent, have no tradition of consuming ginkgo nuts and therefore have no history of cultivating the tree. While this situation began to change around 1980, cultivation by humans cannot explain the many large ginkgos scattered throughout the area that are *not* growing near temples. (Ginkgos found near temples are usually human cultivated.) From the ecological/botanical perspective, wild populations of ginkgo tend to show a number of characteristics which distinguish them from populations of cultivated trees. These differences are summarized in Table 1 (page 14).

In addition to the populations around Jinfo Shan, a second area of high genetic diversity for ginkgo occurs in eastern China, in Zhejiang Province, primarily on the slopes of Tian Mu Shan, a sacred mountain with many Buddhist shrines and temples, located about 100 kilo-



The agricultural terraces in the vicinity of Shan Jiang village in Wuchuan County, Guizhou Province. Over the past several hundred years, these have replaced the mixed conifer–broadleaf evergreen–deciduous forest that originally grew there.

meters (62 miles) west of the city of Hangzhou. This area, which was the site of one of the first nature reserves in modern China, has long been considered by botanists to be one of ginkgo's wild locations, but only recently—through the work of Wei Gong and her colleagues (2008) at Zhejiang University—has the distinct genetic ancestry of this population been established.

In contrast to its very limited distribution as a wild plant in China, ginkgo is widely cultivated throughout the temperate world, across a broad range of moisture, temperature, and topographic gradients. In China, the tree can be cultivated between 25° and 42° N latitude where minimum winter temperatures can reach -32°C (-26°F) and maximum summer temperatures 42°C (108°F) (He et al. 1997). Detailed phenological studies in Japan over a fifty year period by Matsumoto and his colleagues (2003) have determined that spring bud break in ginkgo occurs 40 days earlier in the extreme south of the country (30° N latitude) than it does in the far north (43° N latitude) and that autumnal leaf drop happens about 40 days later, making for an effective vegetative growing season range of 170 to 260 days across 13° of latitude. It's no wonder that ginkgo is touted as a paragon of environmental adaptability.

Ginkgo Sexuality

Ginkgo biloba is a dioecious species, with separate male and female trees occurring at roughly a 1:1 ratio. Ginkgo shows a long juvenile period, typically not reaching sexual maturity until approximately 20 years of age. Male (microsporangeate) and female (ovulate) sex organs are produced on short shoots in the axils of bud scales and leaves. The male catkins emerge before the leaves and fall off immediately after shedding their pollen to the wind. Pollination

(Left) A portion of the stand of wild ginkgos at Bai Yuan village in Wuchuan County, Guizhou Province. Note the tall, straight form of the trees indicting that they grew from seed. (Below) Cultivated ginkgos in this orchard show the typical shorter, wide-spreading form.

Table 1. The botanical and ecological characteristics of remnant natural ginkgo populations versus cultivated ginkgo populations in China

Remnant natural ginkgo populations	Cultivated ginkgo populations
Sex ratio should be more or less balanced with males at a 1:1 or greater ratio than females.	Skewed sex ratio—overwhelmingly female.
Trees are growing mixed in with numerous other species that are native to the surrounding forest.	Few other species growing with ginkgo; if other trees are present, they are typically cultivated for some specific purpose.
The growth form of most of the trees is single stemmed with relatively few lower branches (indicative of having grown up from seed).	Low-branched growth form of female trees (indicative of vegetative propagation by cuttings or grafts).

typically occurs anywhere from mid-March in areas with mild winters to late May in areas with severe winters.

The ovules on female trees are 2 to 3 millimeters (about .1 inch) long at the time of pollination, and are produced mostly in pairs at the ends of long stalks. When the ovule is receptive, it secretes a small droplet of mucilaginous fluid from its apical tip which functions to capture airborne pollen. Retraction of this droplet at the end of the day brings the pollen into the pollen chamber. Once inside the ovule, the pollen grain germinates to release the male gametophyte which attaches itself to the inside wall of the ovule. Here it undergoes a four- to five-month-long period of growth and development which is supported by the tissues of the expanding ovule (Friedman and Gifford 1997).

Ginkgo ovule with pollination drop at tip.

Sometime in September or October, depending on the latitude, the development of the male gametophyte culminates with the production of a pair of multiflagellated spermatozoids. In one of nature's most dramatic moments—first described by the Japanese botanist Hirase in 1896—the two microscopic sperm cells must swim, propelled by about one thousand tiny flagella, a full millimeter across a fluid-filled channel to reach the waiting egg cell, where only one can claim the prize. Contrary to what has often been written, fertilization takes place while the ovules are still on the tree and embryo development begins posthaste. The embryo length may range from less than 1 millimeter to 5 millimeters (.04 to .2 inch) at the time of seed drop, which can occur anywhere between September and November, depending on local weather conditions. Once the seeds fall to the ground, the embryo continues to develop until the arrival of cold temperatures (below 10°C [50°F]), at which point elongation stops. With the onset of warm weather in the spring, the embryo resumes its growth, which culminates in germination in late spring or early summer.

Ginkgo Nuts

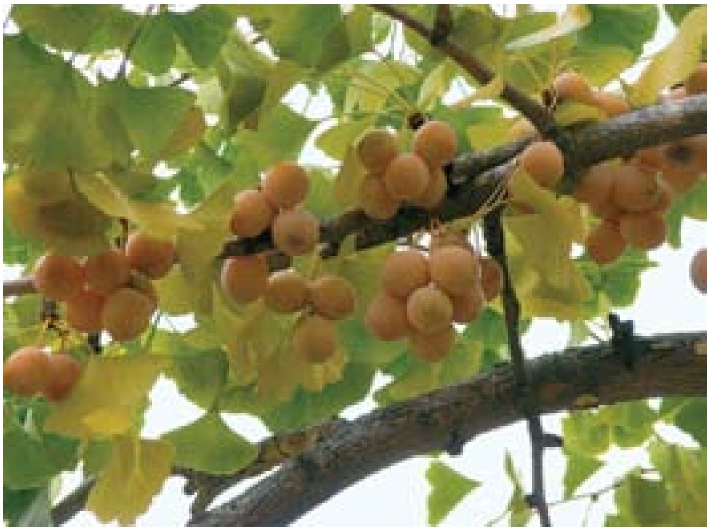
It is now generally accepted that ginkgo was first cultivated by the Chinese not for religious purposes but rather for its edible seeds, which at maturity are relatively large and nutritious. The seed, as it falls from the tree, consists of an embryo embedded in the tissue of the female gametophyte surrounded by a thick seed coat. The intact seed coat consists of a soft, fleshy outer layer (the sarcotesta), a hard, stony middle layer (the sclerotesta), and a thin, membranous inner layer (the endotesta).

The seed, devoid of the famously smelly sarcotesta, is generally referred to as the "nut" with dimensions that range from 19 to 30 millimeters by 11 to 14 mm (approximately 1 by .5 inch). Over the past several hundred years, Chinese horticulturists have selected scores of cultivars which produce large and/or distinctively shaped nuts. Large plantations of these select ginkgo cultivars are common throughout eastern and central China.

The putrid odor often associated with ginkgo seeds typically develops only after they have lain on the ground for several days and have begun to rot. The smell is due to the presence of two volatile compounds in the sarcotesta—butanoic and hexanoic acids (Parliament 1995). The sarcotesta also contains numerous fatty acids and phenolics, one of which, ginkgoic acid, is known to cause allergic contact dermatitis in some people (Kochibe 1997).

A Common-Garden Experiment

The timing of pollination, fertilization, seed abscission, and germination in ginkgo are strongly affected by the latitude of cultivation as well as by local climate conditions. In the



Mature ginkgo seeds on a tree at Forest Hills in Boston, Massachusetts.

fall of 2002, I undertook a series of common-garden experiments to explore the relationship between the timing of pollination and the timing of germination in ginkgo by cultivating in a common location seeds produced by trees from two different latitudes. One lot consisted of about 500 cleaned seeds from trees that were being cultivated for nut production, which I purchased on September 22, 2002 at Tuo Le Village, Panxian, in southern Guizhou Province, China, (25°36' N). For comparative purposes, I collected ginkgo seeds on October 31, 2002 from beneath a number of trees growing at the Forest Hills Cemetery in Boston, Massachusetts (42°17' N).

When sown in the Arnold Arboretum's heated greenhouse (20°C [68°F]), the Guizhou seed began germinating on November 12—approximately 58 days after abscission—while the Boston seed did not begin germinating until January 6—some 67 days after abscission. Assuming approximate pollination dates of March 24 for the Guizhou seed and May 17 for the Boston seed, the total time elapsed from pollination to germination under continuously warm greenhouse conditions was 233 days and 234 days respectively, a remarkably confluent result given their different latitudinal origins.

A second striking result of the experiment was that only 15% of the uncleaned, outdoor-sown Boston seed germinated versus 72% germination for a replicate lot of one hundred seeds washed clean of their smelly sarcotesta. The fact that cleaned ginkgo seeds germinated at statistically significantly higher percentages than those with their sarcotesta intact suggests that animals which consume the seeds—provided they do not crush the thin-shelled nut—might play a role in promoting successful seedling germination (Rothwell and Holt 1997, Del Tredici 2000). The specific mechanism whereby the sarcotesta reduces the germination capacity of ginkgo seed is currently unknown, but the exclusion of light is probably not an explanation given that William Friedman (1986) has shown that female gametophytes with all their seed coats intact are capable of photosynthesis.

Ecological Implications

The results of my experiment indicate that aspects of ginkgo's sexual reproduction cycle are strongly influenced by temperature (Del Tredici 2007). For seeds left outdoors immediately following seed drop, the timing of their pollination influences the timing of their germination the following spring which, in turn, influences their chances of surviving the following winter. In warm-temperate climates—such as Guizhou Province—ginkgo seeds are shed in late summer or early fall, and the embryo is able to make considerable growth during the mild weather that follows. In cold-temperate climates—such as Massachusetts—seeds are shed much later in the season and the cooler temperatures of mid to late fall delay embryo development until warm weather arrives the following spring. This differential timing of embryo maturation means that seeds produced by trees growing in warm-temperate climates will be ready to germinate during the favorable conditions of

Table 2. A comparison of the phenology of the sexual reproduction cycle of *Ginkgo biloba* growing in Guizhou Province, China versus Massachusetts, USA.

Location	Pollination	Seed Abscission	Outdoor Germination
Guizhou, China (25° North latitude)	mid-March to early April	mid-September	mid-March
Massachusetts, USA (42° North latitude)	mid-May	late October to early November	mid- to late June

mid to late spring (March through early June), while those in cold climates will not germinate until later in the summer (late June through early August), when conditions for establishment are less favorable and the seedlings have less time to accumulate carbohydrates before going into winter dormancy.

In this regard, it is worth noting that in Tuo Le Village in Guizhou Province, ginkgo seeds sown outdoors would typically germinate in March, while the same seed sown outdoors in Boston did not germinate until May 29, approximately two months later. From an ecological perspective, the complex phenology of ginkgo's sexual reproduction cycle may well have constrained the species' ability to migrate, independently of humans, into cold-temperate regions with short growing seasons, and probably accounts for its limited warm-temperate distribution as a wild or semi-wild tree in the mountains of central and eastern China (Li et al. 1999, Xiang et al. 2006, Wei et al. 2008). Table 2 presents a comparison of the phenology of *Ginkgo biloba*'s sexual reproduction cycle in Guizhou Province, China versus Massachusetts, USA.

NANCY ROSE

A fossilized leaf of *Ginkgo yimaensis*.

Evolutionary Implications

The fossil species *Ginkgo adiantoides* existed in the northern hemisphere from the Upper Cretaceous through the Middle Miocene (roughly 70 to 12 million years ago) and is considered by paleobotanists to be morphologically indistinguishable from the modern *G. biloba* (Tralau 1968). Most of the ginkgo fossils from this time period in Europe and North America come from sites above 40° N latitude that were originally disturbed stream margins and levee environments, and typically occurred in association with a consistent set of riparian plants, including *Cercidiphyllum, Metasequoia, Platanus,* and *Glyptostrobus* (Royer et al. 2003).

Fossils of a new *Ginkgo* species (*G. yimaensis*) from Liaoning Province, China, recently described by Chinese paleobotanists Zhou and Zheng (2003), have pushed the lineage of *G. biloba*-type ovules back to the Lower Cretaceous, about 120 million years ago. This suggests the possibility that the seeds of *G. yimaensis* could have possessed a temperature-sensitive, developmental-delay mechanism similar to that of *G. biloba.* Such a trait would have allowed this species to reproduce successfully in regions of the northern hemisphere that were undergoing dramatic cooling after a long period of warm conditions. Indeed, Zheng and Zhou (2004) have proposed that "the drastic climatic changes during the Upper Jurassic and Lower Cretaceous, around 140 to 150 million years ago, were responsible for the transformation of the ovulate organs of the *G. yimaensis* type into the modern *G. biloba* type," including the development of short shoots, the reduction and protection of ovulate organs, and the production of larger seeds. *Ginkgo biloba*'s temperature-sensitive, embryo-development-delay mechanism could well have been another climate-induced Cretaceous innovation—an evolutionarily primitive but ecologically functional form of seed dormancy.

Ginkgo Seed Dispersal

Researchers studying various ginkgo populations in Asia have reported a number of animals feeding on, and presumably dispersing, the malodorous, nutrient-rich seeds. In China, dispersal agents include two members of the order Carnivora: the leopard cat (*Felis bengalensis,* family Felidae) in Hubei Province and the masked palm civet (*Paguma larvata,* family Viveridae) in Zhejiang Province (Del Tredici et al. 1992). In Japan, where ginkgo was introduced from China some 1,200 years ago, another member of the order Carnivora, the raccoon dog (*Nyctereutes procyonoides,* family Canidae), has been documented feeding on ginkgo seeds, and its droppings have been found to contain intact seeds which germinated the following spring (Rothwell and Holt 1997).

The existence of three reports of omnivorous members of the Carnivora consuming whole ginkgo seeds suggests that the rancid smelling sarcotesta may be attracting primarily nocturnal scavengers by mimicking the smell of rotting flesh—in essence acting as a carrion-mimic (Del Tredici et al. 1992). The fact that ginkgo seed germination percentage is enhanced by removal of the sarcotesta lends further credence to this theory.

Ancient Dispersal Agents

In 2002, Zhou and Zhang reported the discovery in China of a long-tailed bird (*Jeholornis* sp.) from the Early Cretaceous with a large number of ginkgo-like seeds in its crop. This provides direct evidence that early birds potentially *could* have been involved in seed dispersal activities, although the seeds' intact nature suggests they were destined for digestion in the gizzard. In general, *Ginkgo biloba* seeds do not fit the typical profile of a fruit dispersed by modern birds (van der Pijl 1982).

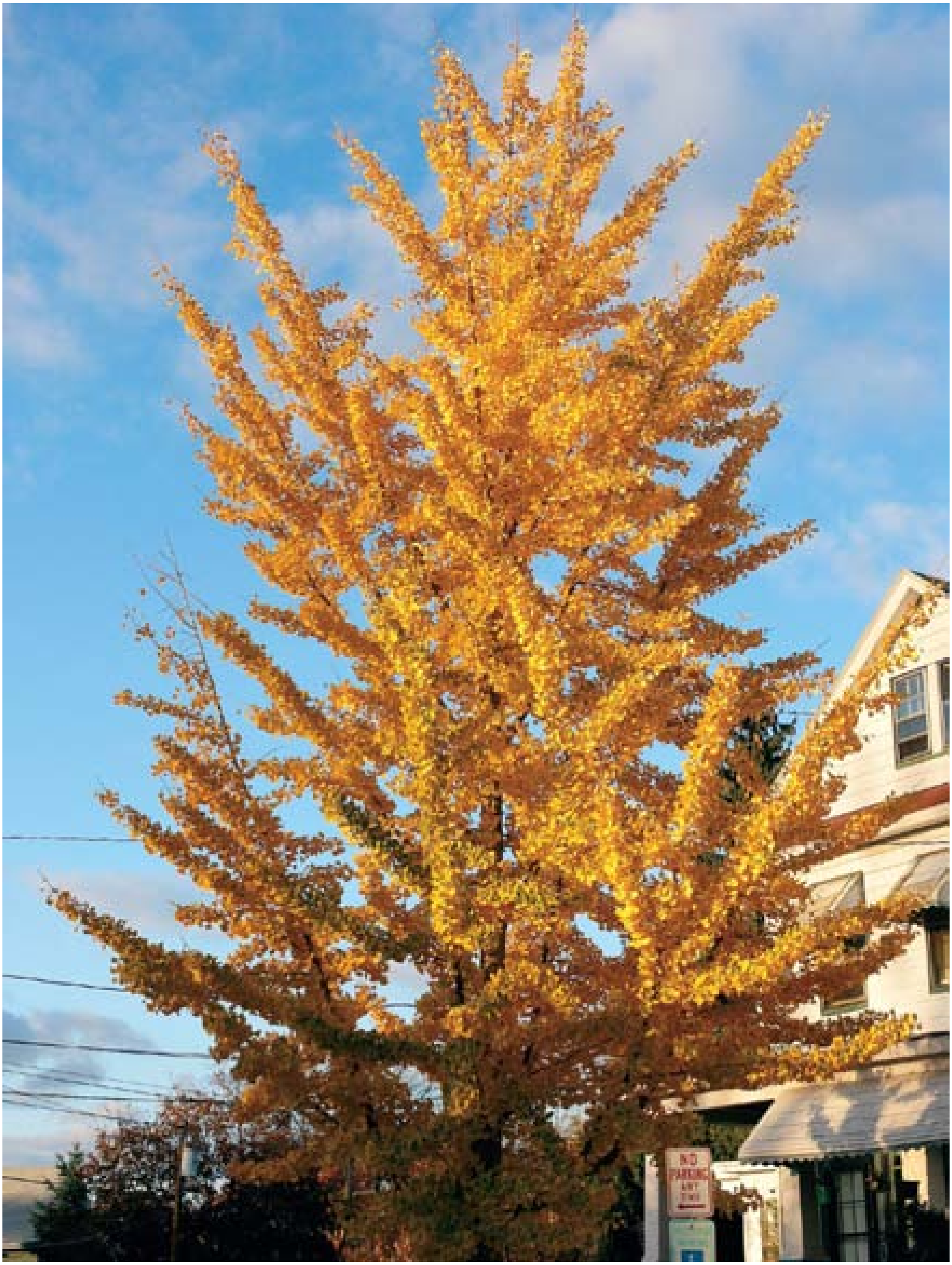
Prior to the discovery of *Jeholornis,* most of the speculation about Cretaceous ginkgo dispersal agents centered on dinosaurs, based primarily on their temporal overlap. If dinosaurs were involved with the dispersal of ginkgo seeds, it probably would have been carrion feeding scavengers, with teeth adapted to tearing and swallowing flesh, rather than herbivores with grinding dentition that would have

A spontaneous ginkgo sapling growing out of a karst rock formation at Niu Tang village in Wuchuan County, Guizhou Province.

crushed the thin-shelled seeds. At any rate, any connection between dinosaurs and ginkgo seed dispersal is, at best, conjecture based on circumstantial evidence.

Ginkgo's Future

By rights, *Ginkgo biloba* should have gone extinct long ago along with all of its close relatives. The fact that it did not provides botanists with a unique window on the past—sort of like having a living dinosaur available to study. As remarkable as ginkgo's evolutionary survival is, the fact that it grows vigorously in the modern urban environment is no less dramatic. Having survived the climatic vicissitudes of the past 120 million years, ginkgo is clearly well prepared—or, more precisely, preadapted—to handle the climatic uncertainties that seem to be looming in the not too distant future. Indeed, should the human race succeed in wiping itself out over the course of the next few centuries, we can take some comfort in the knowledge that the ginkgo tree will survive.



This ginkgo, growing as a street tree in New Brunswick, New Jersey, shows the species' outstanding yellow fall color.

True survivors, these severely pruned ginkgos on a Tokyo street are growing in spite of cramped planting spaces and air pollution.

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