

arnoldia

The Magazine of the Arnold Arboretum
VOLUME 70 • NUMBER 4



arnoldia

The Magazine of the Arnold Arboretum

VOLUME 70 • NUMBER 4 • 2013

Arnoldia (ISSN 0004-2633; USPS 866-100) is published quarterly by the Arnold Arboretum of Harvard University. Periodicals postage paid at Boston, Massachusetts.

Subscriptions are \$20.00 per calendar year domestic, \$25.00 foreign, payable in advance. Remittances may be made in U.S. dollars, by check drawn on a U.S. bank; by international money order; or by Visa, Mastercard, or American Express. Send orders, remittances, requests to purchase back issues, change-of-address notices, and all other subscription-related communications to Circulation Manager, *Arnoldia*, Arnold Arboretum, 125 Arborway, Boston, MA 02130-3500. Telephone 617.524.1718; fax 617.524.1418; e-mail arnoldia@arnarb.harvard.edu

Arnold Arboretum members receive a subscription to *Arnoldia* as a membership benefit. To become a member or receive more information, please call Wendy Krauss at 617.384.5766 or email wendy_krauss@harvard.edu

Postmaster: Send address changes to

Arnoldia Circulation Manager
The Arnold Arboretum
125 Arborway
Boston, MA 02130-3500

Nancy Rose, *Editor*
Andy Winther, *Designer*

Editorial Committee
Phyllis Andersen
Peter Del Tredici
Michael S. Dosmann
William (Ned) Friedman
Kanchi N. Gandhi

Copyright © 2013. The President and
Fellows of Harvard College



The ARNOLD
ARBORETUM
of HARVARD UNIVERSITY

CONTENTS

- 2 **Beyond Pine Cones: An Introduction to Gymnosperms**
Stephanie Conway
- 15 **Rediscovering Rhododendron Dell, Part 1**
Kyle Port
- 19 **BOOK EXCERPT: *Ginkgo: The Tree That Time Forgot***
Peter Crane
- 28 **GINKGOPALOOZA**
- 31 **2012 Weather Summary**
Sue A. Pfeiffer
- 36 **The Sweet Smell of Spring: *Abelia mosanensis***
Nancy Rose

Front cover: Rhododendron Dell at the Arnold Arboretum. Photo by Nancy Rose.

Inside front cover: Gymnosperms all bear reproductive structures known as cones, but the cones vary greatly within the group. Seen here is the female cone of *Encephalartos ferox*, a cycad in the Zamiaceae. Photo by Michael Calonje, Montgomery Botanical Center.

Inside back cover: Fragrant abelia (*Abelia mosanensis*), accession 591-2003, growing in the Arboretum's Leventritt Shrub and Vine Garden. Photo by Nancy Rose.

Back cover: Illustration of *Ginkgo biloba* (then better known as *Salisburia adiant[h]ifolia*) from Siebold and Zuccarini's *Flora Japonica*. The first plates for the book were published in 1835 but the full publication was not finished until 1870. From the Archives of the Arnold Arboretum.

Beyond Pine Cones: An Introduction to Gymnosperms

Stephanie Conway

Gymnosperms are an intriguing group of plants, yet in many ways they are not well known. Most people can recognize a pine, with its familiar woody cones, but they may not know that this and other conifers are gymnosperms. Or, they may think that conifers are the *only* plants in the gymnosperm group. Undoubtedly the often large-flowered angiosperms (flowering plants) are the better known group within the seed plants, but gymnosperms are well worth a look.

So what are gymnosperms and what makes them so intriguing? There are four groups of plants that make up the gymnosperms: the well-known conifers, plus the lesser known cycads, ginkgo, and the order Gnetales. These groups

are so different from each other that it would be hard to immediately recognize them as related. In fact, exactly how they are related to each other is not entirely clear, but most studies put cycads and ginkgo at the base of a gymnosperm evolutionary tree (meaning that they are the simplest, evolutionarily), and conifers and Gnetales as more evolutionarily advanced.

What does it mean to be a gymnosperm? The most common feature across all four groups is that the ovule (which becomes the seed) is naked (unprotected) prior to fertilization. In comparison, the angiosperms have ovules that are protected by a layer of tissue called a carpel. The word gymnosperm comes from ancient Greek and means “naked seed.” This naked state of the ovule is a unifying feature of the gymnosperms (there are also some shared vegetative features such as wood anatomy), but often these ovules are not visible to the naked eye. This is perhaps what makes them so intriguing: How does this translate to the more common feature that we can see, the cone? How did these evolve? And how does the cone tell the story of the evolution of the gymnosperms?

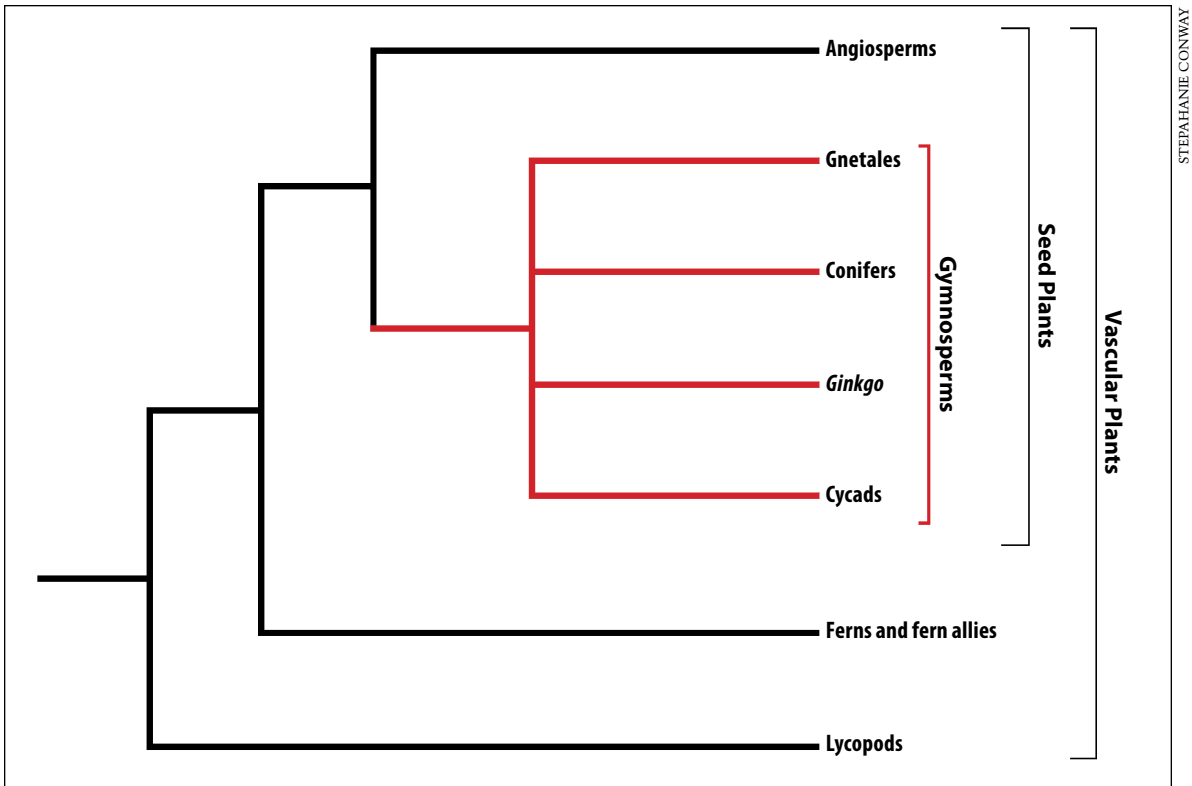
GYMNOSPERM ROOTS

The ancestors of gymnosperms most likely evolved from a group of plants called the seed ferns (pteridosperms), which are known only from the fossil record. These were the first plants to reproduce by seeds, despite looking deceptively like ferns. (True ferns reproduce from spores rather than seeds.) Early seed plants bore their seeds directly on leaves or branches, without any specialized structures like cones. From this starting point we can begin to see how the naked ovules and cones of living gymnosperms evolved. The four lineages of gymnosperms each have a unique set of cone characteristics, and comparisons with the naked eye are extremely difficult. In fact, even comparisons between well-known conifer groups are challenging. To understand



KEITH KANOTI, MAINE FOREST SERVICE, BUGWOOD.ORG

Pine cones are perhaps the most familiar gymnosperm cone type. A mature eastern white pine (*Pinus strobus*) cone is seen here.



STEPHANIE CONWAY

Phylogeny chart showing the relationship of gymnosperms to other plant groups.

the elusive relationship between these cone types, it helps to examine the distinct paths of evolution that each gymnosperm lineage took from the seed fern ancestral condition, how all retained the character of a naked ovule and yet ended up with very different looking reproductive structures.

CYCADS

Cycads are a very ancient lineage of plants with a fossil record that extends back at least 280 million years. They were once very common across most of the planet and were a prominent plant group in the age of the dinosaurs, but they have since retreated to the tropics and sub-tropics. As is the case for all the gymnosperm lineages, it's important to remember that when we look at the cycad taxa growing today we are seeing the survivors of a once very successful plant group. These "leftovers" include 3 families of cycads: Cycadaceae, Zamiaceae, and Stangeriaceae, which contain about 11 genera and 250 species in total.

Cycads have unique characteristics that set them apart from the rest of the gymnosperms

and make them unique among all seed plants. They have a single, typically unbranched trunk with the leaves all bunched together in a crown at the top of the plant. This features makes them look superficially like palm trees, a fact reflected in the common name of one cycad that is often grown as a house plant, sago palm



MICHAEL CALONIE, MONTGOMERY BOTANICAL CENTER

The female cone of *Cycas revoluta*. Note that the sporophylls resemble leaves and are all bunched together at the crown, similar to the leaves. Young ovules are formed on the lower portion of the sporophylls and are very exposed or naked.

(*Cycas revoluta*). Some cycads have trunks that can grow partially or fully underground, others have long, straight trunks and can grow quite tall—up to 18 meters (59 feet) in the Australian cycad *Lepidozamia hopei*. The leaves of cycads are pinnate, with leaflets arrayed in two rows on either side of the rachis. This pinnate leaf form is not found in any other gymnosperms.

Cycads are dioecious, meaning that there are separate male plants that produce pollen cones and female plants that produce seed cones. The cones of cycads are typically large, with many fertile, leaflike organs (sporophylls) that are aggregated into cones. Both cone types are simple, which in botanical terms means the sporophylls are attached directly to the cone axis or column and have no other leaves or bracts associated with them. The simple nature of both the seed and pollen cones is important to the interpretation of the evolution of the cone in cycads. Many botanists believe this shows that the cycads represent an early line of evolution that took a different path from the rest



Cycas maconochiei cones have leaflike sporophylls with green ovules along the margins. Note that in this species the sporophylls are less leaflike than in *Cycas revoluta* but are still bunched together in the crown.



Zamia furfuracea female cones with bright red seeds attached to scalelike sporophylls. Note the lack of leaflike portion of the scale, as compared to *Cycas* sporophylls.

of the gymnosperms. The morphology of the seed cone is quite variable within the cycads, but the *Cycas* type of cone is considered primitive within the cycad group. In this genus, the ovules are borne on the edges of sporophylls, and these sporophylls form in a crown at the top of the plant, similar to the leaves. The sporophylls do in fact resemble young leaves, only these “leaves” have ovules along their edges. Before pollination, the *Cycas* cone represents the best example of a naked ovule within the gymnosperms, as the ovules are very much exposed to the air. The rest of the cycads have ovules borne on scalelike structures, some with leaflike structures along the margin, but many without any leaflike morphology at all. The pollen cones of cycads are similar to seed cones, and pollen is borne on the lower surface of scalelike structures.

It is generally believed that in the ancestral type, cycads bore ovules directly on leaves. Over time, these fertile leaves evolved into a condensed and simplified form—the cycad cone. In *Cycas*, the leaflike structure was somewhat retained, but in more advanced cycads there was further reduction and elimination of the leafy parts, resulting in the scale-type cones found in *Zamia* and other cycads. The fact that the cones are “simple” is important to this interpretation since it means that we can recognize the evolution of the cycad cone from a *leaf* with ovules rather than a *branch* with ovules. This distinction is important

and, as we'll see, shows that the cycad cone and the conifer cone had quite different evolutionary beginnings. But first, let's look at the fascinating *Ginkgo biloba*, which, in terms of cone morphology, is often considered an intermediate between cycads and conifers.

GINKGO

Ginkgo biloba is the sole living species of the once widely distributed order Ginkgoales and is often called a "living fossil." This plant has fascinated botanist for centuries because it represents a unique set of characteristics that alludes to both the cycads and conifers but which represents a unique lineage within the gymnosperms. Ginkgo's flat, fan-shaped leaves are its most distinctive feature; the leaves on the plant's long shoots are typically two-lobed, hence the specific epithet *biloba*. Unlike the cycads, adult trees are heavily branched and have a broad crown.

The fertile structures in ginkgo are unique as well, with little to make a comparison to either the cones of cycads or conifers easy. The male



PETER DEL TREDICI

A *Ginkgo biloba* tree in fall color at Forest Hills Cemetary in Boston.



PETER DEL TREDICI

The female cones of *Ginkgo biloba* are generally thought to have evolved from a branch, but all that remain are the long stalks with terminal ovules (seeds) with a thin fleshy covering.



KEVIN NIXON

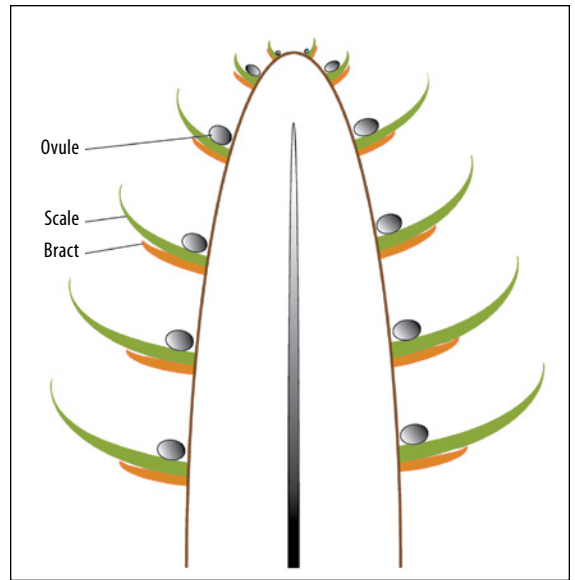
Male ginkgo cones (strobili) bear many pollen-producing organs along a central stalk.

pollen cones (strobili) are simple structures that arise at the base of leaves on the short shoots. They have longish stalks with lots of pollen-producing organs attached directly to the stalk. Female cones (strobili) also arise at the base of leaves on the short shoots and consist of a stalk and two terminal ovules.

The fossil record is large and variable for Ginkgoales, so there is much debate about the ancestor of ginkgo. This makes the interpretation of the cone difficult. However, the most common interpretation of the female reproductive structure of ginkgo is that it is an extremely reduced and modified branch, so highly reduced that only the stalk and the two terminal ovules remain. While the entire evolutionary history of ginkgo is still not entirely settled, the interpretation is important because it will direct our understanding on the relationships of all seed plants.

CONIFERS

Conifers are the most conspicuous group of gymnosperms, containing 7 families and more than 600 species. They tend to dominate forests in the Northern Hemisphere and have a rich and diverse existence in the Southern Hemisphere, but are reduced in numbers in most tropical environments. Conifers are such a highly vari-



The bract-scale structure of a pine cone.

able group that this whole article could be spent summarizing their general characters. Instead we shall just look at a few interesting examples.

The pollen cones of conifers are always simple, that is, the organs that produce pollen are attached directly to the cone axis without other associated leaves or bracts. The story of the female seed cones is much more complicated and a curious person only needs to go outside and look at various conifer cones to sense the issues at hand. For example, how does the cone of a juniper (*Juniperus*) compare to that of a fir (*Abies*)? How about *Calocedrus* compared to *Cephalotaxus*? And what about *Taxus*, is that even a cone?

Our current understanding of the conifer cone comes mostly from a Swedish paleobotanist named Rudolf Florin. Prior to Florin (and many others who also contributed), there was no cohesive interpretation of the different parts of the cone in different families and how they could have evolved from a single ancestor. Florin's theory is centered on the fact that the female cone of *Pinus* is a compound structure. This means that each cone has a single, central column or axis, to which other "col-



The large, attractive cones of this Korean fir cultivar (*Abies koreana* 'Silberlocke') have long yellow bracts with pointed tips. These bracts can be seen protruding from below the brown scales.

umns" are attached. Each of these attached columns has its own set of organs attached to it. In other words, you can break up a cone into a number of individual units, and each unit has a complete, replicate set of organs. Each one of those units is made up of a bract, a scale, and ovules. The bract is on the outside, and the scale is on the inside. This scale is sometimes called the ovuliferous scale because it is where the ovules are formed and where eventually the seed develops. The fact that the scale where the ovules are formed sits at the base of the bract is important because therein lies the fundamental compound nature of the cone.

PETER DEL TREDICI



Young female Douglas-fir (*Pseudotsuga menziesii*) cones sit upright on the branch and display prominent pink bracts (at this stage the scale cannot be seen). The more mature male pollen cones (hanging downward) have pollen organs attached directly to the cone axis.

PETER DEL TREDICI



Young cone of northern Japanese hemlock (*Tsuga diversifolia*) with large green and purple scales. The much smaller bracts (white with brown tips) can be seen on the scales closest to the stem.

Florin proposed that in the ancestor of the conifers, seeds were formed on widely spaced branches, each branch with a number of fertile scales that bore stalked ovules. Each branch formed at the base of a bract. He proposed that over evolutionary time these branches transformed to have fewer and fewer scales until there was only one, that the ovules lost their stalks, and that the single remaining scale became more and more fused to the bract. So the interpretation is that each unit (an individual bract-scale complex) that we break off a cone is all that remains of a once large branch.

Most of the other genera in the pine family (Pinaceae) have fundamentally the same bract-scale complex but with different shapes and sizes of the bracts and scale. In *Pinus* for example, the bracts are small and inconspicuous compared to the scales, whereas in Douglas-

PETER DEL TREDICI



The most prominent feature of this young *Sciadopitys verticillata* cone is the large white scales, with the smaller brown bracts hidden underneath.

firs (*Pseudotsuga*), as well as certain species of *Abies* and hemlock (*Tsuga*), the bracts are long and conspicuous, often forked, and the scales are small. In cases where the bracts or scales are small and inconspicuous, it is very difficult to see them at all, except in early stages of development, and sometimes only with a microscope.

In umbrella pine (*Sciadopitys verticillata*, the sole species in *Sciadopityaceae*) the scales are the main feature of the mature cone. The bract is only apparent early in development and becomes fused with the scale during further growth, becoming almost indistinguishable. However, in *Araucariaceae*, a Southern Hemisphere family, there is no apparent ovuliferous scale at any time during development; instead, the ovules are borne directly on the bracts. In such groups where there is no ovuliferous scale, this scale is considered to have been lost over evolutionary time. In other families of conifers the story is more complicated, and comparisons between adult cones of different groups stretches Florin's model to its limits.

The cypress family (*Cupressaceae*) is a large and diverse group that also shows great diversity in cone types within the family. In *Sequoia*, *Sequoiadendron*, and *Metasequoia*, the ovuliferous scale only appears as a small mound of tissue at the base of the ovules very early in development. The cones of *Cupressus* and *Chamaecyparis* are similar to each other, with four or more opposite pairs of woody bracts and nothing that resembles an ovuliferous scale. *Juniperus* forms what looks like a berry, but in fact the "berry" is the completely fused, swollen bracts that have become soft and pulpy after fertilization. Before full ripening the seamlike outlines of the bracts can often be seen in the flesh. Again, no traces of an ovuliferous scale can be found. In some juniper species the cones are reduced to a single seed per cone. This extreme level of reductions is often associated with reproductive advantage since the single ovule occupies the prime position for fertilization and the colored bracts serve to attract birds and other animal dispersers. Thus, this simplified cone with a minimal number of organs is considered evolutionarily advanced.



Cupressus tonkinensis has a female cone with woody bracts that open to release the seeds.



The purple bracts of the berrylike cones of Eastern red cedar (*Juniperus virginiana*) swell and become fleshy. A glaucous waxy coating gives the cones a blue cast.



The female cones of *Podocarpus macrophyllus* have a single seed covered in a fleshy bract and scale; the receptacle below it will swell and become red when mature.

PETER DEL TREDICI



The fleshy olive-shaped female cones of *Cephalotaxus fortunei*.

ROBERT VIDEKI, DORONICUM.KFT., BUGWOOD.ORG



Cones of *Taxus* (*T. baccata* is seen here) are so different that they are hard to compare to other conifers. In this species, the seeds are formed terminally on the end of short stems, and a swelling at the base of the ovule develops into a fleshy red aril that covers the seed and also attracts seed dispersers. On the younger green cone the single terminal seed can be seen with the fleshy aril just starting to develop.

The large Southern Hemisphere family Podocarpaceae also developed a berrylike cone, with fleshy parts to aid dispersal and minimal numbers of seeds per cone. However, this family has a unique cone type that looks nothing like the cones of *Juniperus*. The cones typically consist of a number of sterile bracts and one fertile bract on which the ovule arises on a structure called the epimatium, which is considered the evolutionary equivalent to the ovuliferous scale. In *Podocarpus*, the bracts at the base of the cone also swell into an often colorful “receptacle” that, as in *Juniperus*, probably serves in attracting animals for dispersal.

Plum yew (*Cephalotaxus*) also has fleshy, single-seeded cones that look suspiciously like olives. The early development of *Cephalotaxus* shows a lack of ovuliferous scales, and instead the ovules form on the bracts in a manner similar to other conifers. However, the bracts grow out to cover the seed in a fleshy covering that, as seen in *Podocarpus*, presumably aids in animal dispersal of the seed.

Taxus is the final example of a female conifer cone and it's one that does not fit within Florin's theory of conifer cone evolution. The female reproductive structure of *Taxus* does not have ovules on bracts or scales; instead, it has a single terminal ovule. This ovule sits at the end of a short branch, and an outgrowth at the base of the seed becomes a fleshy red aril that partly covers the seed. Florin himself was so convinced of the fundamentally different nature of the cone structure in Taxaceae that he placed the family in a different order, the Taxales. This implied that Taxales had different ancestors than the rest of the conifers, therefore making the conifers not a natural group. This was a controversial theory, and other researchers have since shown it to be unlikely. Instead, researchers have proposed that the terminal cone may be related to the more advanced cones of the Cupressaceae, including various species of *Juniperus* with single terminal ovules. However, how and from where the *Taxus* type of cone evolved (if considering the conifers as a monophyletic group) has not yet been satisfactorily resolved and remains something of a mystery.

USDA-BLM, USDA-NRCS PLANTS DATABASE



Ephedra viridis, commonly known as green ephedra or Mormon tea, grows in the southwestern United States. It is very drought tolerant and often grows in association with creosote bush and sagebrush.

KEVIN NIXON



Ephedra sinica female cone with ovules in the uppermost fertile bracts. The ovules are secreting a pollination drop, the pollen capturing mechanism of gymnosperms.

GNETALES

The Gnetales are perhaps the most enigmatic group of the gymnosperms, which, considering the mysteries we have already encountered, is no minor statement. Their phylogenetic position within the seed plants remains unresolved and their morphology is puzzling. This order of plants is made up of 3 families—Ephedraceae, Gnetaceae, and Welwitschiaceae—each with a single genus. Many features of these plants are so different that at first glance it is hard to believe they are related, but a few shared features do keep these plants united as a group. These features include an advanced type of water conducting cell called a vessel, which is similar to the type found in flowering plants, as well as the compound and complex nature of both the pollen and the seed cones.

Ephedraceae comprises about 35 species of *Ephedra* and is found mostly in dry, desert-type climates. Almost all species are small, spindly shrubs, although a few grow like vines and one species in Brazil is a small tree. The leaves of

KEVIN NIXON



A male cone of *Gnetum gnemon* with rings of pollen organs below rings of sterile female ovules, some with pollination drops present.

DENNIS STEVENSON, NEW YORK BOTANICAL GARDEN



The seed cones on this female *Gnetum urens* have matured and only one red, fleshy seed has developed from each cone. Above the seed on the right you can see the nodes where the other ovules would have formed, but have failed to develop.

Ephedra are generally scaplike, or occasionally longer and needlelike, and all are joined at the base to form a sheath around the stem. Most species of *Ephedra* are dioecious (separate male and female plants). The pollen cones of *Ephedra* have a pair of bracts at the base of the cones, and the cones themselves are made up of a series of bracts, each with its own fertile shoot. This makes these cones compound structures in the same fashion as the seed cones of

conifers. The female cones are also compound. The cones have a pair of bracts at their base, and the cones themselves are also made up of a series of bracts. The uppermost bracts have ovules in their axes, although often only one develops into a seed.

Gnetaceae has only one genus, *Gnetum*. Most *Gnetum* species are tropical vines, though one of the most widely studied species, *Gnetum gnemon*, is a tree. *Gnetum* species occur in parts of Asia, South America, and Africa as well as some Pacific Islands. If you were to walk past one in the tropics you would be hard pressed to recognize it as a gymnosperm because the leaves are broad, flat, and have netlike veins, making it look much more like a flowering plant (angiosperm). *Gnetum* cones are also very distinct from typical conifer cones and they form fleshy seeds that look like berries. Both the cones that produce pollen and those that produce seeds are compound structures and unique among gymnosperms. In *Gnetum gnemon* they are long and have distinct nodes where the fertile structures are formed. The pollen cones have bracts that cover the nodes, and underneath these a number of pollen organs are enclosed within two fused structures. Above this ring of pollen organs there are often aborted female ovules, which has lead many botanists to consider the cone of *Gnetum* to be primitively flowerlike. The seed cone also is on a long axis, with the fertile structures occurring on the nodes. There are bracts that cover a ring of 8 to 10 ovules. Each ovule is surrounded by 3 bractlike structures that form envelopes around the ovule.

Welwitschiaceae consists of only one species, *Welwitschia mirabilis*, which may be one of the strangest plants on the planet. It grows only in the Namib Desert of Angola and Namibia and produces just two huge leaves from a short, woody, unbranched stem. The leaves grow an average of 8 to 15 centimeters (3 to 6 inches) per year, and often are split and twisted at their ends, forming a tangled mass. Some *Welwitschia* leaves have been measured at up to 6 meters (19.7 feet) long. The plants survive in the desert by developing a huge taproot that may extend down nearly 2 meters (6.6 feet). A few plants have been estimated to be close to

2,000 years old. The cones of this odd plant develop from buds on the woody crown between the two leaves. Both the pollen cones and seed cones are compound and consist of two rows of opposite bracts. In the base of these bracts the fertile shoot emerges. Pollen cones bear 6 pollen organs that have fused bases. These are enclosed by 2 sets of bractlike structures. There is an aborted ovule in the middle of the apex. The seed cones are similar in design to the pollen cone; the outer bracts are not fused and inner bracts are long and fused and form an envelope over the ovule.

The Gnetales are particularly challenging to botanists because they seem to jump around within the phylogeny of seed plants depending on the type of study being carried out. This makes it difficult to confirm theories about the evolution of their cones. They have at various times been aligned with angiosperms, in part due to the organization of the cones; *Gnetum* and *Welwitschia* especially lend themselves to comparison with flowers because of the organization of their pollen and seed strobili. Also, the presence of bracts that envelope the ovule means that the ovule is not necessarily naked, as in the rest of the gymnosperms. However, an equally valid interpretation is the placement of Gnetales within the gymnosperms as sister to the conifers, which makes comparisons of the bracts and scales of conifers relevant. Where Gnetales sits in the phylogeny of seed plants is significant because their placement affects the evolutionary concepts for all of the shared features of the gymnosperm cone. A resolution of their evolutionary position would likely come from the fossil record, but the fossil record for the Gnetales is poor, or at least very few fossils have been correctly identified as belonging to this group. Taken altogether, the most recent evidence from fossils, morphology, and genet-



DONNA TREMONTE

Male cones of *Welwitschia mirabilis* are composed of numerous bracts, each with protruding pollen organs.



GILLIAN COOPER-DRIVER

Female cones of *Welwitschia mirabilis* form on the woody crown and are made up by a number of bracts with enclosed ovules.

ics places the Gnetales as nested within the gymnosperms, but just where exactly within this group remains controversial.

GYMNOSPERM EVOLUTION

As a group, the gymnosperms present a diverse and beautiful lineage of plants whose morphology tells a superb, if not fully understood, evolutionary story. The structure and function of the cone has only been briefly covered here,



GILLIAN COOPER-DRIVER

An adult *Welwitschia mirabilis* plant growing in the Messum River area in Namibia.

but the common theme across all the lineages has been an evolution towards simplifying the reproductive structure. This has been achieved in a variety of ways and with different results. Cycads reduced the leafy portion of their cones down to a scale. Ginkgo reduced a large branch to a single stalk with two ovules. Conifers tended towards simplifying the branch complex to just a bract, or getting rid of the traditional cone altogether, and 4 out of the 7 conifer families developed a fruitlike structure as well as reducing the seed number. Gnetales began experimenting with having both seed and pollen structures within a single cone.

While a pine cone may be the best known representative of gymnosperm reproductive structures, it is in fact only a small part of the gymnosperm story. The current, living assemblages of gymnosperm groups are really only relicts of what once was a gymnosperm dominated world, so the task for us is to understand the whole narrative of dominance and decline. The gymnosperms of today are incredibly important since they represent 4 out of the 5 extant lineages of seed plants (angiosperms are the fifth lineage) and botanists continue to study exactly what gymnosperms are and how they evolved. Current research includes phylogenetic stud-



PETER DEL TREDICI

Male cones of *Pinus muricata* are simple, with a bract at the base of each cone and the pollen organs attached directly to the cone axis.



The young female cones of *Pinus longaeva* have long pink scales above smaller bracts.

ies using data sets from thousands of species and multiple genes to tease apart relationships both at the species level and between distant lineages. Genetic studies of, for example, how the genes that determine flowering in angiosperms are related to the genes that determine cone formation in gymnosperms, and morphological studies on the evolution of the different parts of the gymnosperm cone continue with modern techniques. Such mysteries of the gymnosperms have fascinated botanists for centuries and will continue to do so for many years to come.

Resources

- Beck, C. B. 1988. *Origin and evolution of gymnosperms*. New York: Columbia University Press.
- Esau, K. 1977. *Anatomy of Seed Plants*, Second Edition. New York: John Wiley and Sons.
- Farjon, A. 2008 *A natural history of conifers*. Portland, Oregon: Timber Press.
- Farjon, A. and S. Ortiz Garcia. 2002. Towards the minimal conifer cone: ontogeny and trends in *Cupressus*,

Juniperus and *Microbiota* (*Cupressaceae* s. s.). *Botanische Jahrbücher für Systematik Pflanzengeschichte und Pflanzengeographie* 124: 129–147.

- Florin, R. 1948. On the morphology and relationships of the Taxaceae. *Botanical Gazette* 110: 31–39.
- Gifford, E. M. and A. S. Foster. 1989. *Morphology and Evolution of Vascular Plants*, Third Edition. New York: W. H. Freeman and Company.
- Matthews, S., M. D. Clements, and M. A. Beilstein. 2010. A duplicate gene rooting of seed plants and the phylogenetic position of flowering plants. *Philosophical Transactions of the Royal Society B* 365: 383–395.
- Stewart, W. N. and G. W. Rothwell. 1993. *Paleobotany and the Evolution of Plants*. New York: Cambridge University Press.
- Tomlinson, P. B. and T. Takaso. 2002. Seed cone structure in conifers in relation to development and pollination: a biological approach. *Canadian Journal of Botany* 80: 1250–1273.

Stephanie Conway is a PhD student from the University of Melbourne and a Visiting Research Fellow in the Friedman Lab at the Arnold Arboretum.

Rediscovering Rhododendron Dell, Part 1

Kyle Port

A pile of plant record labels, mysteriously stripped from accessioned plants in the Arboretum's Rhododendron Dell, sent Manager of Plant Records Kyle Port on a mission to assess, verify, and relabel the collection

In this issue, Kyle reports on the early history of Rhododendron Dell, and in the next issue he will write about the multi-layered curatorial process involved in the Rhododendron Dell project.

One hundred forty years ago, a triumphant rhododendron show bloomed on the Boston Common. For a nominal fee, attendees were ushered under tents where plants from private collections, including those of Arnold Arboretum director Charles S. Sargent and the event's sponsor, H. H. Hunnewell, were arranged. Rhododendron hybrids imported from Anthony Waterer (Knap Hill Nursery, Woking, England) garnered considerable attention. The revelation that *R. 'Album Elegans'* and a few other cultivars were hardy outdoors in the Boston area soon fostered planting trials beyond conservatory walls, specifically in the bur-



EDITORIAL NOTES Rhododendron Show at Boston

The Rhododendron show on the Boston Common was a sight never to be forgotten—the finest in colors and display of choice varieties this country has ever beheld. It was with considerable difficulty the bare privilege was secured from the common council, to exhibit upon the Common; and next, it was believed to be almost impossible to transport and successfully flower so many plants as would be needed to produce the desired effect. Thanks, however, to the untiring energy of Mr. H. H. Hunnewell, Charles S. Sargent and E. S. Rand, jr., every difficulty was surmounted, and for the entire month of June the denizens of that city saw a collection of Azaleas and Rhododendrons of rare value and great beauty ...

Two large tents were erected, one about 60 by 100 feet, the other 100 by 300 feet, and the plants transplanted from their native home and conservatories of Mr. Hunnewell and Mr. Sargent, and placed in the natural soil of the Common. Within the tents were laid out, first, an avenue of 100 feet in length, bordered with Palms and rare Ferns; this led to the Rhododendron beds and walks. In the center of the large tent were three raised beds; the first, 15 by 30 feet; the second, 50 by 80 feet; the third, 15 feet in diameter. Walks also surrounded all the beds, which were lined with specimen plants. Imagine all this space and beds filled solidly with masses of Rhododendrons in full bloom, bearing flowers of most royal size, and delicate as well as glowing and brilliant colors, and it would seem to be but a vision of the garden of Paradise.

... most of them [rhododendrons] are fit for in-door greenhouse culture only, many being but just imported from the Knapp [Knap] Hill nursery of Anthony Waterer, Woking England.

Luther Tucker

The Horticulturist, and Journal of Rural Art and Rural Taste,
Volume 28, August 1873

ARCHIVES OF THE ARNOLD ARBORETUM



The alluring white-flowered *R.* 'Album Elegans' (hybridized by Waterer, pre-1847) was one of the first large-leaved, evergreen rhododendrons proved hardy in Massachusetts. This Arboretum accession of the cultivar was photographed by Ralph W. Curtis in June 1932.

ARCHIVES OF THE ARNOLD ARBORETUM



The burgeoning Rhododendron Dell is seen in this Autochrome glass slide from 1934.

geoning landscapes of the Arnold Arboretum, which had been established just the year before. More importantly, the friendships forged at the Boston show guaranteed that the most sought after rhododendron hybrids of the day would become accessible for viewing and study, free of

the existing soils—Hinckley sandy loam and Scio very fine sandy loam—proved adequate. Stands of eastern hemlock (*Tsuga canadensis*), intentionally left by the previous land owner Benjamin Bussey (1757–1842), provided an ideal amount of shade. And above all, the site



Staff members of the Arnold Arboretum have collected, researched, and written extensively about *Rhododendron*, covering a myriad of species and hybrids. So prolific were early Arboretum contributors that the Royal Horticultural Society bestowed the Loder Rhododendron Cup on C. S. Sargent in 1924, E. H. Wilson in 1927, and Alfred Rehder in 1936.

charge, to anyone who journeyed to the Arboretum.

A suitable location for cultivating these large-leaved rhododendrons was found in a wind sheltered two-acre area between the northern contours of Hemlock Hill and Valley Road, through which Bussey Brook flows. Eventually named Rhododendron Dell,

ARCHIVES OF THE ARNOLD ARBORETUM

allowed for cold air to sink away toward low-lying Bussey Brook Meadow.

The new hybrids were not immediately planted in Rhododendron Dell; instead, the first plantings on the site were of the hybrids' North American parent species, which included *R. catawbiense*, *R. maximum*, and *R. minus*. It is likely that the only remaining plants from these early plantings exist in a mass planting of *R. maximum* accessions 23020 and 23021. These accessions actually comprise a number of accessions that were interplanted over the years and became indistinguishable from each other. The oldest of these *R. maximum* accessions was obtained as seeds in 1880 from Benjamin Marston Watson's Old Colony Nurseries and Seed Warehouse in Plymouth, Massachusetts.

In 1886, the first *R. catawbiense* hybrids from Anthony Waterer were planted in Rhododendron Dell. Some of these hybrid cultivars had been featured in the tents of the 1873 rhododendron show on Boston Common, but now they were being planted outdoors to see how they would fare. Among these inaugural cultivars, *R.* 'Purpureum Grandiflorum' (accession 2804) and *R.* 'Album Grandiflorum' (accession 2805-A) survive to this day. Subsequent introductions such as *R.* 'Mrs. Harry Ingersoll' (accession 6202-C, acquired in 1891) epitomize the allure these hybrid rhododendrons had upon so many. Their survival at the Arboretum solidified a resolve to develop, evaluate, and maintain a collection for the ages. As Sargent wrote to Anthony Waterer in February 1911, "I think that we should have here a correctly named standard set of the hardy hybrid Rhododendrons as so many people depend on the Arboretum for information on such a subject."

While the majority of the early acquisitions of hybrids in Rhododendron Dell were those of Anthony Waterer and his cousin, John Waterer, a number of other international hybridizers are also represented. Fel-



Rhododendron catawbiense 'Grandiflorum'



Rhododendron 'Mrs. Harry Ingersoll'



Rhododendron 'Echse I'



Rhododendron 'Duke of York'

low Englishman G. Paul provided *R.* 'Duke of York' (accession 22616-A, 1921 lineage from a 1915 introduction), and in 1908 German T. J. Rudolf Seidel sent, among others, *R.* 'Echse I' (accession 6175-B), which has bright reddish purple flowers with wavy-edged petals.

In 1919, the federal government's passage of Quarantine No. 37 governing the importation of nursery stock halted shipments of plants by steamer directly to Boston. The Arboretum had

a nearly exclusive reliance on overseas suppliers at the time, but this quarantine forced relationship-building closer to home. North American nurseries, hybridizers, and hobbyists stepped up to meet the challenge and became reliable allies in the development of the *Rhododendron* Dell collections.

Kyle Port is Manager of Plant Records at the Arnold Arboretum.

For a great opportunity to explore the Rhododendron Dell in bloom, join us there for

COLLECTIONS UP CLOSE: RHODODENDRON RAMBLE

on Sunday, June 2, 1:00 to 3:00 p.m.

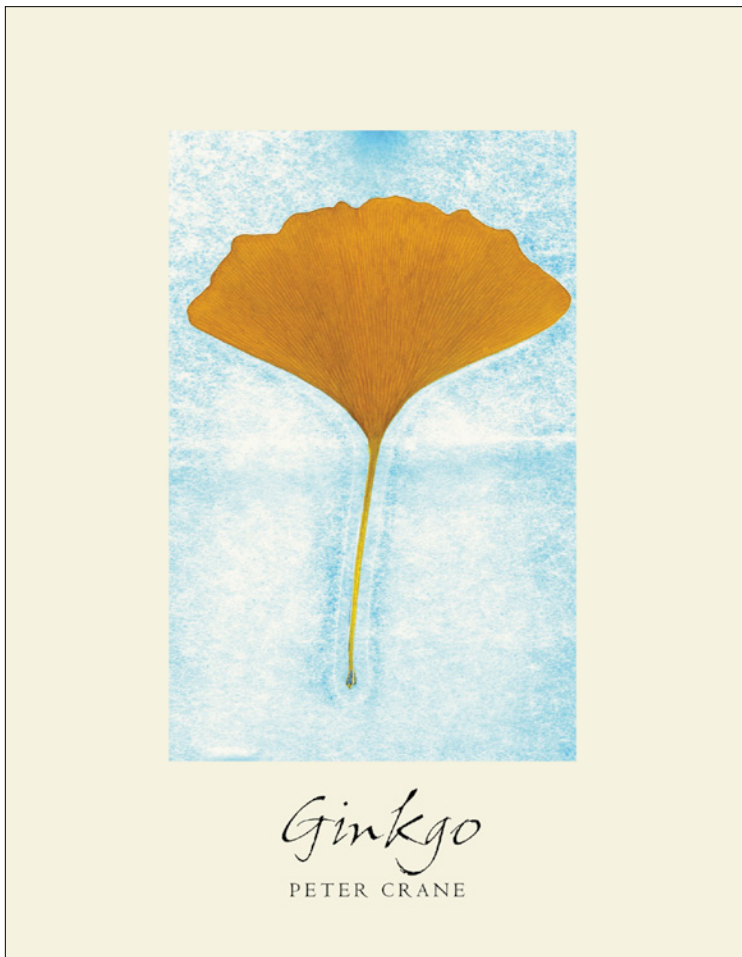
This free event includes walking tours with knowledgeable Arboretum staff and fun science activities for kids.

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

21

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 than now. For example, fossils from the fill of an ancient sinkhole at Willershausen near

EXTINCTION

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

DECLINE AND SURVIVAL

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

EXTINCTION

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,

DECLINE AND SURVIVAL

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

EXTINCTION

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

21. Extinction

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

NOTES TO PAGES 161–165

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.

GINKGOPALOOZA

Peter Crane's book inspired us to gather a few ginkgo images. These pages show just a few of the aspects that make ginkgo such a fascinating plant.

AN ARTFULLY ESPALIERS GINKGO graces a wall of the Sterling Morton Library at the Morton Arboretum (right). At about 55 years old, this ginkgo is a youngster compared to the "Old Lion" ginkgo at the Royal Botanic Gardens, Kew. That venerable tree was planted in 1762 and is seen here in an engraving that originally appeared in the British publication *Gardeners' Chronicle* in March 1889 (lower left), and in a photograph from May 2010 (lower right).

Credit photos, clockwise from upper right: Kris Bachtell, Tony Kirkham, Archives of the Arnold Arboretum



Ginkgo biloba in the Royal Gardens at Kew.
(From the *Gardeners' Chronicle*.)





PEOPLE LOVE GINKGOS. Clockwise from upper left: This wonderful 1921 E. H. Wilson photograph shows a woman hugging an enormous ginkgo at the Temple of the Yellow Dragon, Kuling (Su-shan), China (Wilson recorded the tree at 100 feet tall and with a trunk circumference of 19.5 feet, measured at 3 feet above ground level). Ginkgos stand behind a Buddha statue at the Sensō-ji temple in Tokyo. Over 100 (possibly 200) ginkgo cultivars have been selected, including those with dwarf, fastigiata, weeping, and globe-shaped habits as well as different leaf forms ('Variegata' is seen here). Ginkgophiles enjoy the golden glow under a ginkgo alleé along Ichō Namiki (Ginkgo Avenue) in Tokyo.



Credit photos, clockwise from upper left: Archives of the Arnold Arboretum, Peter Del Tredici, Nancy Rose, Peter Del Tredici





THE GINKGO LEAF'S simple but elegant shape and unique dichotomous venation make it a work of art in itself. Over many centuries its iconic form has appeared on everything from street signs to silverware to shampoo bottles. Shown here (clockwise from upper left) are a live leaf, a plate from Japan, the 1916 woodblock print *Crow and Ginkgo Leaves* by Japanese artist Watanabe Seitei, a pair of silver sugar tongs, and a decorative wall tile.

Credit photos, clockwise from upper left: Peter Del Tredici, Peter Del Tredici, Smithsonian Institution, Nancy Rose, Kris Bachtell



2012 Weather Summary

Sue A. Pfeiffer

Temperatures were again above average in 2012; this was the first year in local recorded weather history that all 12 months had above average temperatures (in 2011, all months except for November were above average in temperature).

JANUARY began with warm temperatures, but a cold front moved in on the 4th and 5th, dropping the low to 10°F. Temperatures rebounded until a second cold front passed through on the 15th and 16th; the low of 6°F, which occurred on both nights, was the low temperature for the year. Overall the month was warm with an average temperature above freezing, almost 8°F warmer than the previous year. Snowfall was well below average—only 4.8 inches accumulated. Most of this snow fell between the 17th and the 22nd, and by the 26th, the snowpack had completely melted. Despite the lack of significant snow accumulation, January was damp and dreary as we received some type of precipitation on 16 out of 31 days.

FEBRUARY was warm and extremely dry. High temperatures in the 40s and 50s occurred on 24 of 29 days and on only one occasion was a high below freezing recorded (28°F on the 13th). Only trace amounts of snowfall were recorded and the ground remained bare for the entire month. February was pleasant and calm except for one storm that passed through on the 25th, dropping 0.52 inches of rain and bringing along wind gusts over 50 mph. This storm provided most of the precipitation for the month as only 0.68 inches fell, well below the 30-year historical average of 4.24 inches. These warm temperatures and dry conditions allowed the horticulturists and arborists access to the collections to prune and mulch.

MARCH began with 4 days of precipitation that fell as a rain-snow mix, delivering some much-needed moisture to soils. This storm brought 1.73 inches of rain equivalence, including 1.8 inches of snow, but by March 6th all snow had melted away. The remainder of the month was dry; the month's total precipitation of 1.99 inches fell far below the 30-year historic average of 5.58 inches. The lack of snowfall in November and December of 2011, coupled with the below average precipitation during February and March and above average temperatures, left soils extremely dry. March was also a month of extreme temperatures—from the 18th to the 23rd we reached temperatures from 75°F to a record high of 82°F, which forced many plants into full



JON HETMAN

An incredibly mild winter led to very early bloom at the Arboretum, including these magnolias in flower on March 22, 2012.

bloom. These extreme highs were followed by extreme lows as temperatures dipped to 25°F and 26°F on March 26th and 27th respectively. These frosty conditions caused visible damage to many plants in full bloom, turning petals brown. The average high temperature for the month was 54°F, 10°F warmer than the 30-year historic average of 44°F. According to NOAA's National Climate Data Center, March 2012 was the warmest month on record in all of the lower 48 states; 15,000 weather related records (7,755 daytime records and 7,517 nighttime records) were broken and at least one record was broken in each of the 50 states.

APRIL was another warm month, with the average high temperature 6°F above the average and a record setting high temperature of 90°F on April 16th. Warm temperatures lead certain plants into early flowering but caused visible stress to others. The lack of moisture during the first three weeks was evident as buds dried up and fell off; twig dieback was observed on young shrubs and plants with shallow root systems. On April 23rd, 2.81 inches of much-needed precipitation fell. Following this rain event, many plants leafed out almost immediately, greening up the landscape. This spring was highly unusual, marked with lack of precipitation and high temperatures.

MAY provided typical spring weather; precipitation was frequent as we received rain 14 out of the first 17 days. This much-needed moisture continued the greening of the landscape as leaves emerged and plants recovered from earlier drought conditions. Warmer temperatures during April allowed many plants to flower earlier than usual, including those in our famous lilac collection. Fortunately, cooler temperatures during early May sustained lilac blooms until Lilac Sunday on May 13th. We reached a high of 85°F on the 27th and a low of 42°F on the 11th. Both temperature and precipitation were slightly above the historic averages.

JUNE began with six straight days of rain, cloudy conditions, and cooler temperatures with highs in the 50s and 60s (far below the mid 70s average for the month) and overnight lows in the 40s. A fast-moving storm came through on the 8th, delivering thunder, lightning, and an additional 0.41 inches of precipitation in a relatively short period of time. Minor damage was reported, with tree limbs down and a lightning strike on a mature white pine, which resulted in its decline and eventual removal. This opening week brought 2.24 inches of rain in total, leaving soils plenty moist. Mid-June saw temperatures return to normal with mostly sunny conditions. Temperatures continued to rise as we experienced a record breaking 3-day heat wave from the 20th to the 22nd with temperatures reaching 95°F. This sudden increase in temperature caused recent transplants to flag. Relief from the heat came on the afternoon of June 22nd as a thunderstorm delivered 0.67 inches of rain. Steady precipitation continued on the 24th and 25th and later that evening a violent thunderstorm delivered 2.43 inches of rain along with minor damage to the collections. Already moist soils could not absorb this rapidly falling rain, resulting in flooding and erosion damage in the collections and on secondary gravel roads. Overall, the cool temperatures early in the month were balanced by the heat wave during the latter part of the month, leaving us with above average temperatures for the month. Rainfall was 6.10 inches, well above the average of 4.31 inches for the month.

JULY was the warmest month of the year with highs mostly in the 80s and 90s. The month started off sunny and warm with minimal precipitation and consistently high temperatures in the 80s. A 6-day heat wave (temperatures 90°F or higher) occurred from July 13th to the 18th, peaking at 95°F on July 17th. Humidity was also high and the heat index reached above 100°F. Both people and plants were stressed; recent transplants, in particular, required vigilant monitoring and supplemental irrigation. A cold front moved in during the afternoon of the 18th bringing an evening of thunderstorms, hail, and a spectacular lightning show. The system dropped 1.53 inches of rain and brought with it more bearable temperatures in the 70s and low 80s. Storms on the 24th and 29th provided additional precipitation.

AUGUST was sunny, hot, and humid. Rain on the 1st and 2nd (1.21 inches total) and the monthly high temperature (92°F) on the 3rd led to very high humidity—98%—during the first week. Several thunderstorms with intermittent rainfall from the 11th through the 18th delivered an additional 1.6 inches of precipitation. The remainder of the month provided ideal summer conditions—sunny days with high temperatures in the mid 80s and lows in the 60s. Arboretum visitation increased as these comfortable conditions set in. Overall it was a fairly typical August, with average high temperatures 5°F warmer than normal and below average precipitation.

SEPTEMBER rainfall was slightly below average and temperatures were slightly above average. We received 3.90 inches of rainfall this month, most of which fell during four well-spaced events on the 5th, 9th, 18th–19th, and 29th, providing consistent moisture to plants throughout the month. The storm that passed through on the evening of the 18th and into the 19th brought strong winds, with gusts of over 30 mph recorded. Temperatures were slightly above average; the high of the month was 85°F on the 8th and the low was 41°F on the 24th. The grounds continued to look lush and showed no signs that fall was on the way.



A large sugar maple (*Acer saccharum*) limb broke and fell near the Centre Street Gate on September 8, 2012, a windy day with gusts over 20 mph.

OCTOBER started off with consistent rain events during 13 of the first 16 days but provided only 0.96 inches of rain in total. The first frost occurred on the 12th, ending the growing season at 194 days. The monthly high was 80°F on the 16th and the low was 31°F on the 12th. The main weather event of the month was the arrival of Superstorm Sandy, which was initially predicted to hit Boston head on. As the late season hurricane moved up the east coast its path shifted to the south as it swung around and plowed straight into the New Jersey–New York (Long Island) areas during the evening of the 29th. At the Arboretum, the storm arrived



Autumn color was in full swing at the Arboretum on October 24, 2012.

with light rain and increasing winds on the 29th; a maximum wind gust of 25.3 mph was recorded in the early afternoon. On Monday, conditions intensified with wind gusts from 30 mph to a maximum of 50.3 mph (recorded at 2:15 and 2:30 p.m. at the Weld Hill Research Building). Sustained winds ranged from 20 to 23 mph throughout the afternoon. At 8:45 p.m. wind speed and gusts dropped suddenly and the atmospheric pressure and air temperature began to rise. We were very fortunate not to receive a direct hit from Superstorm Sandy, but there was some damage at the Arboretum. About two dozen trees were lost; many of these were older and located in natural areas. Despite the storm's 2.66 inches of rain, precipitation for the month remained below the 30-year historic average of 4.69 inches.

NOVEMBER was a relatively dry month with only 1.46 inches recorded (well below the 4.76 inch average). Half of that rain equivalence came from the winter's first snowfall, 2.5 inches overnight on the 7th–8th. Temperatures in the 50s quickly melted the snow. This storm brought high sustained winds with gusts over 30 mph on both days. A warm front brought temperatures into the mid 60s from the 11th through the 13th, but this warm weather did not last as more seasonal temperatures in the 40s and low 50s set in for the remainder of the month. Overall temperatures were slightly above the historic average. We reached a high of 67°F on November 12th and a low of 26°F on the 29th.

DECEMBER was an extremely wet month with variable temperatures. We received a total of 7.11 inches of precipitation, of which 6.08 inches fell during the second half of the month. Most of the total precipitation arrived as rain except for 4 inches of snow on the 30th. Two large storms passed through bringing high winds and heavy rain; the event of December 21st and 22nd brought wind gusts of 35 mph and 30 mph and 0.8 inches of rain while the storm on the 27th brought gusts of over 40 mph and 2.49 inches of rain. We reached our highest temperature of 60°F on December 10th and the average high temperature for the month was 44.2°F, more than 5°F warmer than average. Daily high temperatures did not dip below the freezing mark until the final day of the year, when we reached only 29°F and had a low of 16°F. What a way to end this unusually warm year—with one of the coldest days of 2012!

Arnold Arboretum Weather Station Data • 2012

	Avg. Max. (°F)	Avg. Min. (°F)	Avg. Temp. (°F)	Max. Temp. (°F)	Min. Temp. (°F)	Precipi- tation (inches)	Snow- fall (inches)
JAN	41.1	24.2	32.7	59	6	3.62	4.80
FEB	44.3	25.9	35.1	57	13	0.68	
MAR	54.0	35.6	44.8	82	19	1.99	1.80
APR	62.3	41.1	51.7	90	29	3.54	
MAY	68.5	52.4	60.5	85	42	4.14	
JUN	74.9	56.9	65.9	95	47	6.10	
JUL	85.2	65.0	75.1	95	56	3.23	
AUG	83.8	64.0	73.9	92	53	2.92	
SEP	74.1	54.3	64.2	89	41	3.90	
OCT	64.4	46.1	55.3	80	31	4.28	
NOV	48.0	33.6	40.8	69	26	1.46	2.50
DEC	44.2	30.3	37.1	60	16	7.11	4.10

Average Maximum Temperature 62.1°F

Average Minimum Temperature 44.1°F

Average Temperature 53.1°F

Total Precipitation 42.97 inches

Total Snowfall in 2012 13.39 inches

Snowfall During Winter 2011–2012 8.79 inches

Warmest Temperature 95°F on June 20,
June 22, and July 17

Coldest Temperature 6°F on January 15 and
January 16

Last Frost Date 29°F on April 1

First Frost Date 31°F on October 13

Growing Season 194 days

Growing Degree Days 3294.5 days

The Sweet Smell of Spring: *Abelia mosanensis*

Nancy Rose

Someday I really want to publish a scratch-and-sniff issue of *Arnoldia*, providing a “by the nose” tour of the Arnold Arboretum. I’d probably skip the less pleasant odors—skunk cabbage, ripe ginkgo cones, the stinkhorn fungi that pop up in mulched planting beds—in favor of the many truly wonderful scents to be found here. While pleasant fragrances occur from winter (e.g., the flowers of *Hamamelis mollis* ‘Princeton Gold’) through autumn (e.g., falling *Cercidiphyllum japonicum* leaves), the floral explosion from mid-spring to early summer brings the peak sniffing season.

Come May, there are plenty of sweet-smelling flowers to stick my nose into but my current favorite is the aptly named fragrant abelia (*Abelia mosanensis*). This deciduous abelia is less well known than glossy abelia (*Abelia × grandiflora*), an evergreen or semi-evergreen hybrid species that, with its many cultivars, is a popular landscape plant, particularly in the southeastern quarter of the United States. Fragrant abelia is a somewhat rangy shrub, forming a loose mound of slender, arching stems and reaching a height of 4 to 6 feet (1.2 to 1.8 meters), possibly taller, with an equal or slightly greater width. Its bright green, ovate leaves often have a bronze or reddish tint when emerging. Some sources claim that fragrant abelia has showy red-orange autumn foliage, but specimens at the Arboretum have turned pinkish brown at best.

Fragrant abelia blooms in May to early June at the Arboretum. Flowers are borne in short terminal panicles. The flower buds are rich reddish pink and open to white, funnellform flowers with 5-lobed corollas. The obovate sepals often have an attractive pink tint and persist long after the flowers fall. The fruit is a leathery achene topped by the persistent sepals. But back to the flowers. They are marvelously fragrant, but it’s difficult to put into words exactly what the fragrance is (this is where I need that scratch-and-sniff feature). References variously

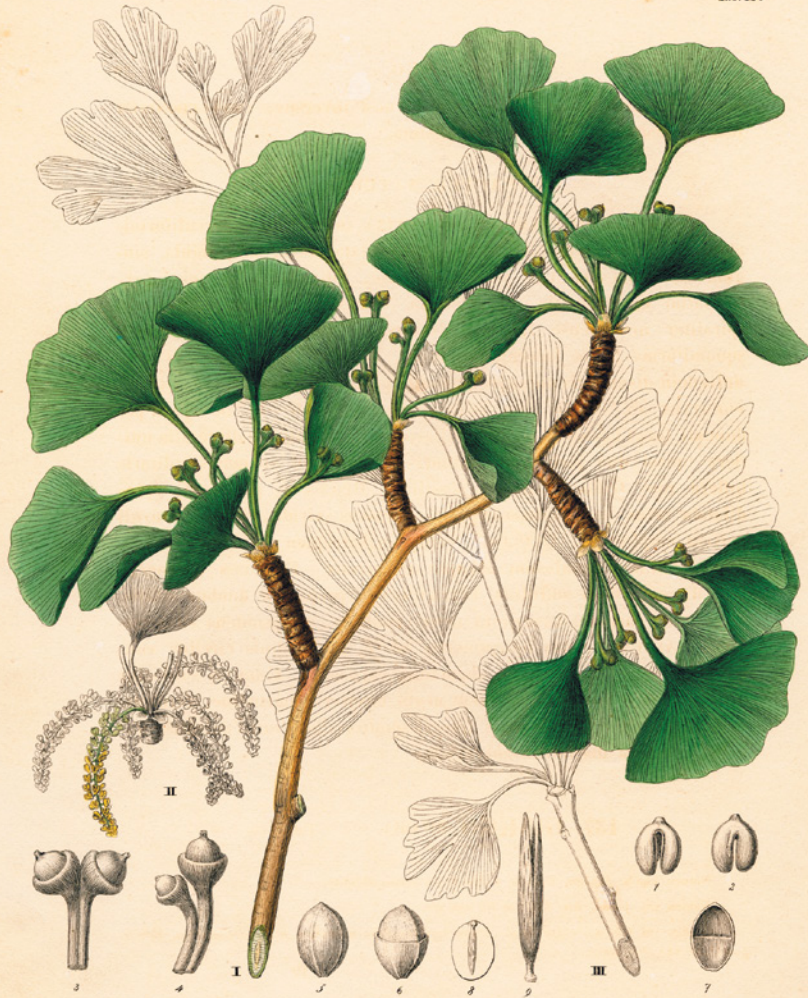
compare the fragrance to lilacs, lilies, hyacinths, and Korean spice viburnum (*Viburnum carlesii*). I think I’d go with the best-scented common lilac (*Syringa vulgaris*), maybe ‘President Lincoln’, plus a hint of orange blossom, a drop of lily-of-the-valley (*Convallaria majalis*), and a shot of tropical fruit.

The Arboretum has a limited history with *Abelia mosanensis*. The species is native to Korea but was not collected by Ernest Henry Wilson on his expeditions there (in fact, the species name was not published until 1926, eight years after Wilson’s last visit to Korea). During an October 1977 plant collecting expedition to South Korea, Arboretum botanists Steven Spongberg and Richard Weaver collected *Abelia mosanensis* seeds in the Seoul National University Forest near Kwangyang in Cholla-Namdo Province. Arboretum greenhouse records indicate that the seeds were sown but there was no germination. We currently have three specimens of fragrant abelia at the Arboretum, all growing in the Leventritt Shrub and Vine Garden. There are two individuals of accession 282-2003, which were purchased as container-grown plants from Spring Meadow Nursery in 2003. There is one plant of accession 591-2003, which was grown from seeds received from the Academy of Science in Salaspils, Latvia. The seeds were offered in the Academy’s Index Seminum (seed exchange list) and were collected from cultivated plants growing at a garden in Latvia.

Fragrant abelia is available from a number of commercial sources. It is considered cold hardy through USDA zone 5 (average annual minimum temperature -20 to -10°F [-28.9 to -23.3°C]) and grows best in full sun or partial shade and moist, fertile, somewhat acidic soil. Though perhaps not the tidiest or most handsome of shrubs, it is worth growing just for the delicious fragrance of its flowers.

Nancy Rose is a horticulturist and the editor of *Arnoldia*.





SALISBURIA adiantifolia.