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.

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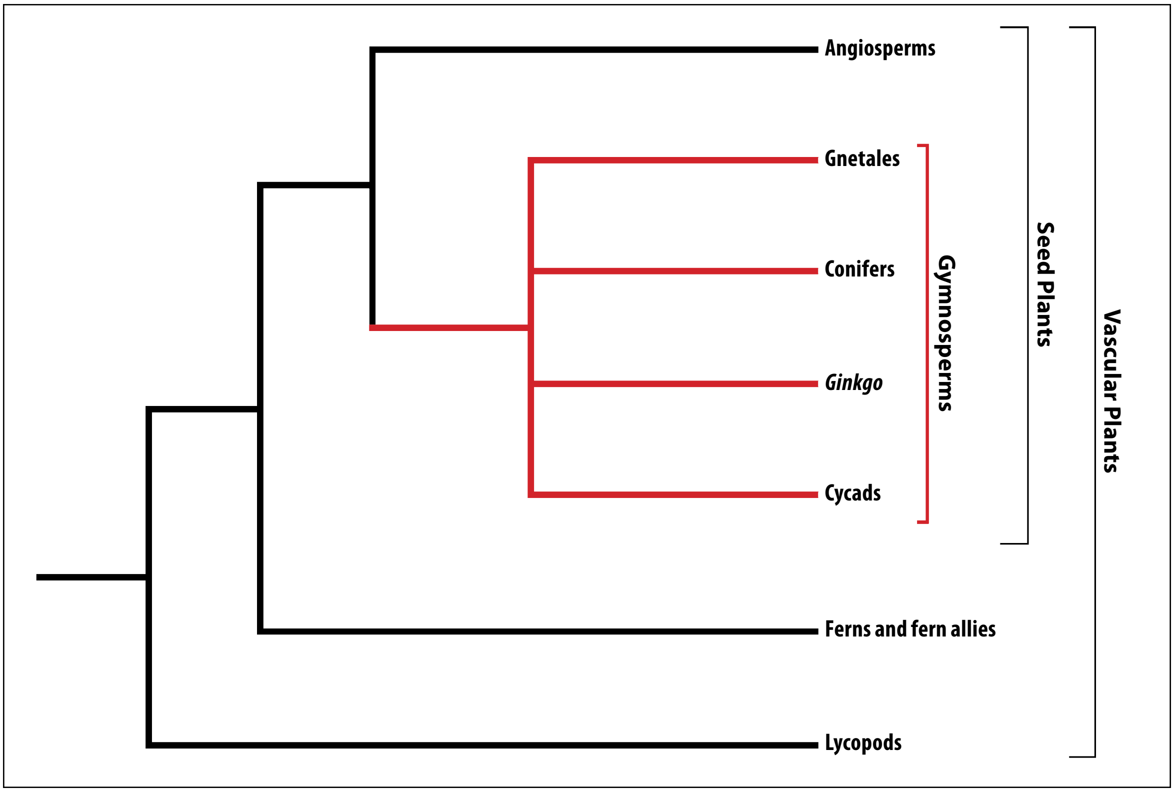
Pine cones are perhaps the most familiar gymnosperm cone type. A mature eastern white pine (*Pinus strobus*) cone is seen here.

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



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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 CALONJE, 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 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 born 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 born on the lower surface of scalelike structures.

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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.

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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_ sprorophylls.

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

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

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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.

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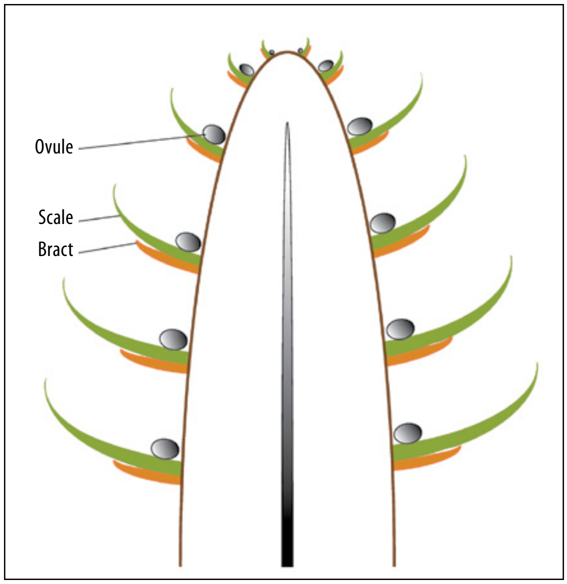
Male ginkgo cones (strobili) bear many pollen-producing organs along a central stalk.

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 gingko is still not entirely settled, the interpretation is important because it will direct our understanding on the relationships of all seed plants.



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The bract–scale structure of a pine cone.

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 variable 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-

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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.

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 remaing 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-

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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.

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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.

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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.

DENNIS STEVENSON, NEW YORK BOTANICAL GARDEN

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

NANCY ROSE

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.

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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.

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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.**

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Ephedra sinica **female cone with ovules in the upper most 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

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

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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 scalelike, 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.

DONNA TREMONTE

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

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

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.

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-

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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.

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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.

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