

anther; and the two lower fertile stamens have small brownish anthers. The style projects between these two lower stamens. The long stamens and style serve as a landing platform for insects, often resulting in pollen being deposited on the stigma. Pollen from the long anthers contributes to outcrossing, but the pollen from the middle anther is primarily an edible reward for the insects.

A cultivar of *C. communis*, ‘Hortensis,’ with larger blue flowers, is the source of a blue dye used to color awobana paper in Japan. The plant is still cultivated for this use, in which dye from the blue petals is hand painted onto sheets of paper that are then dried in the sun. To reconstitute the dye, the paper is dipped in water. Dye from *Commelina* was also an important colorant for Japanese woodblock prints, producing a blue-gray color, or green or purple when mixed with other colors. However, for the most part awobana dye has been replaced by other, more permanent blue dyes. Awobana is now used to draw patterns on cloth in the art of silk printing and in tie-dyeing.

Recent studies have shown Asiatic dayflower to be an excellent accumulator of heavy metals, particularly copper. Thus, it might prove useful in soil remediation.

Deadly nightshade (*Atropa belladonna*), Solanaceae

A European plant in the tomato family that, as its common name suggests, is highly poisonous, but that also has a long history of medicinal use. Two commonly used alkaloids from the plant are atropine (a mixture of two mirror-image isomers of hyoscyamine), which is effective for dilating the pupils during eye exams

(but because of its long-lasting effect is now generally replaced by a shorter-acting drug, tropicamide); and scopolamine, an ingredient used in skin patches to help prevent motion sickness. Atropine is also found in some other members of the tomato family, including species of *Datura* (jimsonweed), *Hyoscyamus* (henbane), and *Brugmansia* (angel's trumpet). Atropine works by blocking the contraction of the circular muscle that normally adjusts pupil size to accommodate the level of ambient light. These compounds should be used only under a doctor's direction.

Another common name for the plant, "belladonna" (also the specific epithet), means "beautiful woman" in Italian. During Renaissance times, women put drops of the juice of deadly nightshade fruits into their eyes for vanity's sake, thinking that it made them appear more beautiful. This practice dates to the time of Cleopatra, who used extracts of henbane to dilate her pupils for the same purpose, and in fact, atropine is reportedly used today for cosmetic effect by some modern-day fashion models.

So many other plants in the tomato family are noted for their poisonous properties that when tomatoes were first introduced from the New World, Europeans were initially wary of eating them. The poisonous members of the family have been used in folk medicine and as hallucinogens. The particularly toxic mandrake (*Mandragora* spp.) has roots that can sometimes resemble a human form and has a long history of superstitions surrounding it; it is still used in various "witchcraft" rituals today and has been said to shriek when pulled from the ground.

Disks and rays

The names of two types of flowers commonly found in the heads of many species in the daisy family (Asteraceae). Although a daisy may be perceived as a single flower, it is actually a composite head of many flowers of two types: the inner yellow central part of the head comprises multiple tubular disk (sometimes spelled “disc”) flowers, while the white petal-like parts surrounding it are actually individual flowers called rays. Ray flowers are shortly tubular at their bases and usually have three small lobes at their tips. The flowers may be sterile or pistillate (have female reproductive parts). Such arrangements are referred to as radiate heads and are typified by daisies and sunflowers. The result of grouping many small flowers into a single head is that the now showy head is more likely to attract pollinators.

But not all members of the daisy family look like daisies. Some composites have *only* disk flowers and are termed discoid heads (e.g., thistles [*Cirsium*] and ironweed [*Vernonia*]). The flowers may be sterile, male, or bisexual. Disciform heads, on the other hand, may have separate male and female flowers in the same head, or in separate heads comprising all male or all female flowers. In the genus *Antennaria* (pussytoes), the male heads are discoid and the female heads disciform.

There are also composites with heads composed of only strap-like (ligulate) flowers, as exemplified by the heads of dandelions and chicory. Ligulate flowers differ from the similar-looking ray flowers in that they are perfect, meaning that they have both male and female parts, and the apex of the ligule has five terminal teeth that reflect its origin as a five-lobed tubular flower.



Helianthus annuus
Sunflower

Beyond these basic head arrangements, there are many variations—which make a simple daisy family “flower” not so simple anymore.

For general queries contact webmaster@press.princeton.edu.

Doctrine of signatures

A belief that plants, based on their morphology or color, signified what ailments they would be useful in treating. The belief goes back to the early Greeks (and probably much earlier) and was promoted widely in Europe from the sixteenth century until the advent of modern medicine in the twentieth century. Theologians taught that God had made plants for the use of humans and gave the plants a sign that humans could read in order to understand how to use them. Although this concept is still utilized by some practitioners of alternative medicine, the doctrine of signatures is now viewed



Hepatica americana
Hepatica -or- liverleaf

as pseudoscience. No scientific documentation exists for the belief that plants cure illnesses based on their shape or color—although in some cases, once a plant has been found to be efficacious in treating a disease, people have used hindsight to point to some aspect of the plant that resembled the part of the body being treated and claimed that it was a signature. Cultures around the world have all had their own similar beliefs about their local plants.

Many familiar plants have been employed to treat diseases based on their morphology. A common example is a plant that we call hepatica or liverleaf (*Hepatica americana* and *H. acutiloba*—placed in *Anemone* by some taxonomists), an early-flowering spring plant in the forests of eastern North America. The leaves of hepatica are lobed and in winter turn a deep burgundy color—much like a liver. They were thus deemed to be efficacious for treating liver disease. In the 1800s, the demand for the medicinal products made from the dried leaves of hepatica became so great that the hepatica populations in the southern Appalachians were depleted, and leaves had to be imported from Germany, where a European species was harvested. Subsequent analysis of the chemical components of the leaves found no compounds with documented medicinal value.

Other “signature plants” are birthwort (*Aristolochia* spp.), which has a flower thought to resemble a uterus and was therefore used in treating women during childbirth but is now known to be carcinogenic; St. John’s-wort (*Hypericum* spp.), whose tiny holes in the leaves signified that it was meant to treat all diseases or injuries to the skin (which also has tiny

pores)—St. John's-wort *has* been shown to have some antidepressive properties; lungwort (*Pulmonaria* spp.), with white-spotted leaves that were said to resemble diseased lungs and were therefore deemed useful for treating lung ailments; and walnuts (*Juglans* spp.), used for treating head ailments because they resembled a brain.

On the other hand, the investigation of plants having a bitter taste or a strong odor bears merit, as these qualities may indicate bioactive compounds (e.g., alkaloids) with potential medicinal use. Thus, such sensory signals may be viewed as signatures suggesting that a plant's chemicals might be of medicinal interest.

Dodder (*Cuscuta* spp.), Cuscutaceae

An apparently leafless parasitic plant (the leaves are reduced to tiny scales along the stem) that twines its orange or pale yellow, spaghetti-like stems around other plants. The stems attach initially by secreting a glue and then by penetrating the host tissue to form a haustorium that provides an open connection with the host's vascular system. From that point on, dodder is essentially grafted to the host and will obtain all its water and nutrients from that host.

As it searches for a host, the seedling grows upward, spiraling around until it comes into contact with a suitable host. Some species of dodder will parasitize a number of different hosts; others are more specific about their victims. In either case, dodder has been shown to grow toward hosts having high chlorophyll content (this is due to a phototropism toward the light transmitted by the green parts of the plants). Such hosts will provide a richer source of nutrients for the parasite.

A dodder plant is a tangled mass of vines that produces small white flowers along the stems. If untangled and measured, a mature dodder plant can reach a length of nearly a mile, and several dodder plants may completely cover a small tree. An infestation by dodder is very difficult to control.

When one or several dodder plants parasitize multiple adjacent host plants, they form connected bridges among the plants. These bridges can transmit viruses from one host to another, but they can also play a positive role for host plants under attack from herbivores (e.g., insects). The attacked plant sends hormonal signals to other plants throughout the dodder-connected network, thereby stimulating the undamaged plants to produce defensive compounds against the herbivores.

In a striking example of convergent evolution, another parasitic plant belonging to an entirely unrelated family, the Lauraceae (a family of woody shrubs and trees including spicebush and avocado), has evolved a similar lifestyle and appearance to *Cuscuta*. *Cassytha* is a small genus found mainly in the Southern Hemisphere. It differs from *Cuscuta* in that its stems are initially green and photosynthetic until they establish a connection to a host. They then turn yellowish orange. *Cuscuta* and *Cassytha* are difficult to tell apart unless one examines the flowers or fruits.

Dutchman's breeches (*Dicentra cucullaria*), Papaveraceae

An early-blooming northeastern US wildflower (the species has a disjunct distribution in the Pacific Northwest) with both its common and scientific names descriptive



Dicentra cucullaria
Dutchman's breeches

of the flowers. The flowers are reminiscent of the voluminous pants Dutchmen used to wear. They are arranged along a pink stipe, hanging upside down as though the pants were drying on a clothesline. The genus name, *Dicentra*, is derived from the Greek *dis*, meaning “two,” and *kentron*, “spurred,” and *cucullaria* is Latin for “hooded,” a reference to the closed hood that is formed by the two inner petals over the reproductive parts.

Dutchman's breeches is one of the earliest wild-flowers to bloom, well before many insects are active, but it has evolved a tight ecological relationship with bumblebees, specifically the queens. Queen bumblebees are the only bumblebees to overwinter in northern climes, sheltering in logs, underground, or in other

protected places, all other members of the colony having died during the previous fall. The queen mates before seeking a winter refuge, and upon emerging in the early spring, she is eager to find a place to nest and rear her young. Because of her robust body and hairy covering, she is able to fly on days that are too cool for many other insects—just the weather that prevails when Dutchman's breeches flowers.

Queen bees must find a source of nectar to fuel their own energy requirements before they can build and provision a nest. The flowers of Dutchman's breeches hold ample nectar in the tips of their long, pointed spurs. Thus, the nectar is accessible only to an insect having a proboscis long enough to reach up the length of the flower to obtain it. Queen bumblebees have just such a proboscis. As the bee hangs from the flower with its clawed feet and probes for nectar, pollen falls onto her body and gets carried to the next flower she visits, effecting pollination—a win-win situation.

Dye plants

Plants used to produce colors for dyeing fabric, leather, and other materials. Animals, minerals, and other biological organisms such as fungi and lichens also serve as a source of dyes, their use being documented as far back as Neolithic times. Space precludes discussion of those non-plant-derived pigments here.

By the Iron Age (500 BCE), based on textile fragments, botanical dyestuffs were commonly being used to produce reds, blues, and yellows. Because plant dyes were generally easier to obtain and less costly to produce, they supplanted animal-derived dyes for most

uses. One of the earliest was madder (from *Rubria tinctorium* and related species in the coffee family, Rubiaceae; note that the use of a plant for dye purposes is often reflected in its scientific epithet, as in *tinctorium*). The roots of madder were dried and pulverized to produce the pigment alizarin. Fabric found in the tomb of King Tutankhamun was discovered to have been dyed with this plant product. Madder was also the source of the highly guarded secret formula for the prized “turkey red,” a brilliant red made by mixing unusual ingredients (including dung) with the madder.

Blue dye, produced from the leaves of woad (*Isatis tinctoria*), a weedy member of the mustard family (Brassicaceae), involved a lengthy and complicated process that included grinding the leaves to a pulp that was then drained and kneaded into balls, which were dried on racks for one to several weeks before being ground into a powder. The powder was spread on a stone floor, frequently turned, and sprinkled with water until it began to ferment. Eventually, a claylike substance resulted that represented only one-ninth of the bulk of the original leaves. This substance was made into a water-based solution and heated for at least three hours before the fiber or cloth was immersed. The woad trade once enriched the coffers of dye merchants in Toulouse, France, but the dye fell out of favor when it was replaced by the less costly blue dye from indigo (*Indigofera tinctoria*), a legume. (A recent study reports that indigo dye has been isolated in six-thousand-year-old textiles found in an ancient temple in northern Peru.) One of the reasons indigo replaced woad as a source of blue dye was that it required no mordant.

Today, a small company founded near Toulouse is reviving the traditional production and use of woad. Having observed the production process there, I found the most amazing part was watching cloth emerge from the dye vat as a bright green fabric, which when hung to dry rapidly turned to blue as it oxidized.

Mordants cause a dye to permeate the fabric, make it more lightfast, or completely change the resultant color. Common mordants include alum, acidic substances such as lemon juice and vinegar, chrome, lime, aged urine, and even the material of the dye pot (e.g., tin, copper, or iron). Because of the foul smell of these dye baths, they were generally located at the edge of towns. I can attest to the stench, having visited the dyeing souk in Fez, Morocco, where men stood knee deep in dye vats, their legs and arms permanently colored by the chromium-laden dye being used to color the skins of sheep, camels, and goats.

In addition to the leaves and roots mentioned above, other sources of plant dyes include various barks (e.g., black oak); insect galls (a dye from a particular insect gall that forms on the leaves of kermes oaks [*Quercus coccifera*] was used as a permanent ink well into the twentieth century); stems (e.g., dodder); nut husks (e.g., walnuts); and wood (the bright yellow-orange color of the robes of Buddhist monks was originally obtained from the heartwood of the jackfruit tree [*Artocarpus heterophyllus*], in the Moraceae). But flowers also provided dyers with material from which to produce a number of different colors. Among the many used to produce a variety of yellows and golds are lady's bedstraw, Scotch broom, saffron (only the stigmas of

the flowers are used), safflower, marigolds, and mignonne. After the discovery of the Americas, additional sources of red dye were learned from the Aztecs, including poinsettia's floral bracts and the petals of dahlia. The Native American tribes of the Southwest were particularly skilled at dyeing, with 103 vascular plants, two fungi, and three lichens being recorded as dye-stuffs. The Navajo used the greatest number of these and are still renowned for their naturally dyed woven blankets.

Today, there is interest in returning to more natural dyes, which are often prized for their softer, more subtle color variations and absence of synthetic chemicals—though natural dyes are not without their own side effects, especially for the dyers.

E dible flowers

Flowers eaten by people fall into two categories; the first includes those that we may not think of as flowers, like broccoli (*Brassica oleracea*). If you were to let the broccoli plant continue its growth cycle, the tiny green buds that form the head would open to reveal four-petaled yellow flowers. This is true as well of a food we eat as a seasoning or garnish—capers; these are the flower buds of the caper plant (*Capparis spinosa*). The buds are pickled and frequently used to flavor Italian dishes such as chicken piccata or to garnish salmon. They also serve as a principal flavoring in tartar sauce. Another flower bud, that of daylily (*Heemerocallis fulva*), is delicious when lightly sautéed with garlic in butter or oil, or as an ingredient in stir-fried dishes, especially in Chinese cuisine.

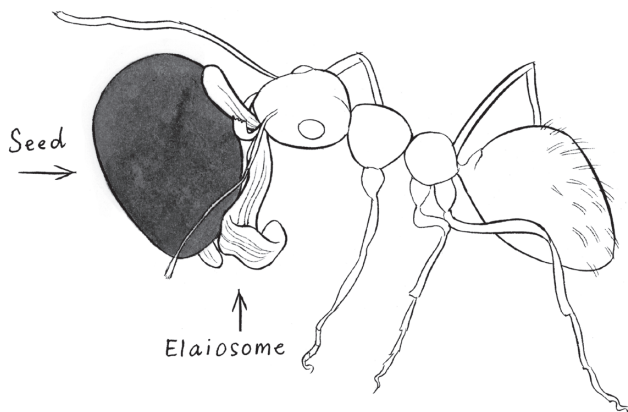
When we enjoy dining on globe artichokes, which are actually the flower buds of the plant (*Cynara scolymus*), we are eating *parts* of a flower head in the aster family: the “leaves,” which are actually floral bracts that surround the flower head, and the “heart,” which is the receptacle to which the flower parts are attached. The fuzzy part that we avoid (the “choke”), if left to mature on the plant, would become a thistle-like flower.

The other category of edible flowers includes those that actually *look* like flowers: some are used as a colorful garnish for salads or desserts (e.g., violets, pansies, nasturtiums, and rose petals); larger flowers, such as squash blossoms or the aforementioned daylilies, when in full bloom may be stuffed with rice, ground meat, and cheese to be served as an appetizer or main course. Squash and daylily flowers can also provide a crispy treat when battered and deep-fried, and dried daylily flowers are sold to be reconstituted in soups.

Elaiosomes

Fleshy appendages attached to the seeds of some plants. They are rich in lipids (oily compounds) and sometimes also contain protein and starch. The term “elaiosome” is derived from the Greek for “oil body.” While elaiosomes have few direct functions for the seed other than perhaps helping to maintain hydration of the seed by absorbing water from the soil, they play an important role in seed dispersal.

Elaiosomes are consumed by ants, which are attracted to them by aromatic compounds produced in the fatty appendage when the seed is ripe. The ants eat the calorie-rich elaiosomes, usually after transporting



the seeds back to their nesting sites, and then discard the seeds. Thus, the plant's seeds are dispersed away from the parent plant to a place that generally has soil enriched by the refuse piles surrounding the ants' nesting site. By providing an enticement for ants to take its seeds, a plant ensures that the seeds will have a chance to grow in other localities where they won't have to compete with the parent plant for resources. The growing conditions in distant sites might prove better suited for the plant's progeny, and such places can provide a safe refuge for the new young plants should a natural or human-made event destroy the original site.

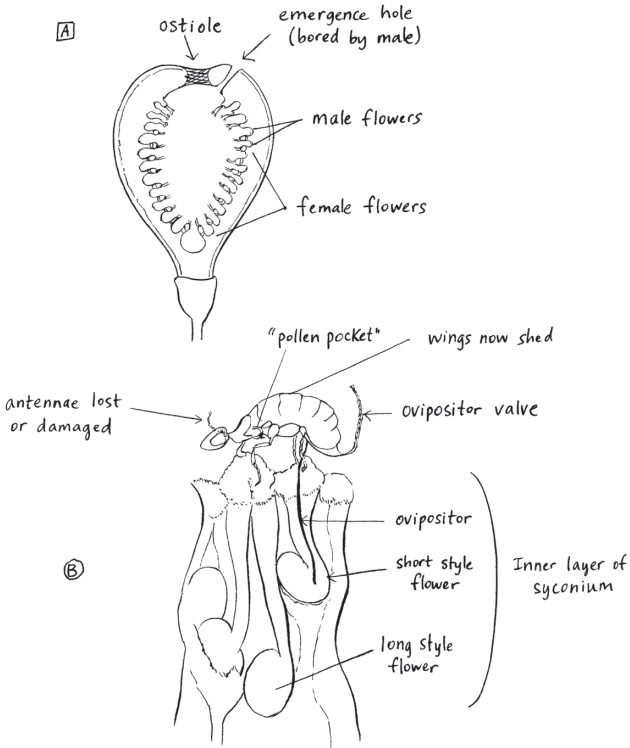
This dispersal system is particularly important in temperate regions where early spring-blooming plants need a means of distributing their seeds to different potentially hospitable sites. It is also of value to early-active ants that need a rich source of food before there is much other food available. Many spring ephemerals in

the northeastern US flora employ this method of seed dispersal, among them trillium (*Trillium* spp.); bloodroot (*Sanguinaria canadensis*); Dutchman's breeches (*Dicentra cucullaria*); celandine poppy (*Stylophorum diphyllum*), which produce their seeds in the spring; and twinleaf (*Jeffersonia diphylla*), which produces and disperses its seeds in the autumn.

Fig flowers (*Ficus* spp.), Moraceae

Simple flowers that occur on a receptacle (as on the disk of a sunflower to which the many central disk flowers and surrounding ray flowers are attached), but in this case the receptacle is folded inward so that the flowers are enclosed *within* an initially hollow structure called a syconium—basically an inside-out inflorescence. Thus, we never see the flowers of a fig plant. It is only after they have been pollinated and the ovaries have begun to develop that we can properly call the fig a fruit.

Yet their pollinators, tiny female wasps with long ovipositors, manage to find the flowers, probably by aromatic cues, and enter the syconium through its sole tiny opening, the ostiole. To give an example of the intricacy of this procedure, I'll describe the process in a fig species familiar to most temperate-zone readers, *Ficus carica*, a native of the Mediterranean region. Early in the season, fig syconia develop that contain many neuter flowers and a few male flowers near the ostiole. A female wasp lays an egg in each of several of the neuter flowers, effectively causing them to swell and become gall-like as the larvae develop within; she then dies within the fig. Male larvae hatch first and seek flower



Ficus carica
Fig

- [A] Basic structure of a typical *Ficus* (fig) Syconium (the fruit) containing male flowers near the top and female flowers basally.
- [B] Female wasp egg-laying, her ovipositor only able to reach into the flowers with shorter styles, while her forelegs unload pollen.

galls containing female wasps, boring into them to fertilize the females. Their mission complete, the males die, never having left the fig. Females then hatch and depart through the ostiole, passing the pollen-bearing male flowers and gathering pollen on their way.

Later-developing syconia have a mixture of neuter flowers and female flowers (or only female flowers). The pollen-carrying female wasps that left the earlier flowers enter these syconia and attempt to lay eggs in the flowers. Because the female flowers have a solid style that is longer than the ovipositor of the wasp, the wasp is able to deposit eggs only in the shorter, open-styled neuter flowers. Thus, receptacles with *only* female flowers produce no wasps. More amazingly, the egg-laying female then takes pollen from the baskets on her legs and deliberately places it onto the receptive stigma of each of the flowers in which she has deposited an egg, thus ensuring pollination.

In this classic but bizarre example of coevolution, figs and certain species of wasps are obligate partners; the figs are dependent solely on the wasps for pollination (sometimes each fig species has its own specific wasp partner), and the wasps in turn are totally reliant on the figs as host plants for their larvae.

It astounds me that researchers have managed to not only puzzle out this most complex mutualistic relationship between figs and wasps but also determine how many variations of this relationship exist between different species pairs in the tropics. Because figs are one of the keystone species in tropical ecosystems, with more than eight hundred species providing food for birds, bats, and primates that eat their fruits and disperse their

seeds, it is important to understand the requirements for perpetuating healthy populations of fig trees, and thus a healthy ecosystem.

The fig-wasp mutualism may be in jeopardy because of climate change. The life span of tropical pollinating fig wasps is very short, ranging from one to two days. This brief life span has been shown to decrease to just a few hours when temperatures increase by 7°F–13°F, thus allowing a shorter window for the wasps to accomplish pollination.

Floral idioms

Idioms that use flowers as a reference to communicate an idea in everyday speech, generally with no need to explain what is meant by the reference. Examples include “gilding the lily,” meaning that it is excessive—and perhaps foolish—to try to enhance something that is already beautiful in its own right; “fresh as a daisy,” meaning to look or feel well rested and energetic; “pushing up daisies,” referring to being dead and buried (under the daisies); “gone to seed,” referring to someone or something that is no longer in its prime state; “a bed of roses,” used as a metaphor for an easy life; “the bloom is off the rose,” used to refer to something that is no longer as new and exciting as it once was; “wallflower,” referring to a person who is shy about interacting with others at social events and would rather blend into the wall than be noticed; “to nip in the bud,” meaning to deal with a problem early before it becomes worse; “stop to smell the roses,” imploring people to take the time in their busy schedules to enjoy the small pleasures of life; “every rose has its thorns,”

indicating that even someone who seems perfect will be found to have flaws; “a late bloomer,” referring to someone who does not reach their potential in talent or other interest until later in life; and “shrinking violet,” describing a person who is shy and avoids the limelight. Other floral idioms are common, both in English and other languages.

**Frost flowers (occur on frostweed
[*Crocianthemum canadense*]), Cistaceae**

A name used for extrusions of sap from the stems of frostweed (*Crocianthemum canadense*) on days with sub-freezing temperatures. “Frost flowers” are not flowers at all, but a weather-induced phenomenon on a small temperate plant commonly called frostweed. You can seek out these “flowers” in winter when the right conditions prevail: a clear, frosty, windless day with a dew point below freezing that follows a frigid night. Usually you must be out before the first rays of sun can strike the plants and warm the air to above freezing. Even the cold winter sun can cause the “flowers” to melt under these conditions.

The small yellow-flowered frostweed, an inhabitant of sandy soils, is not particularly attractive when it blooms in early summer, but in winter it can exhibit a striking phenomenon that is well worth seeking out. Expansion of the supercooled sap in the stems of frostweed on cold, dry nights causes fissures to form along the stem. As the supercooled sap seeps out of the fissures and encounters the first frost crystals, it forms thin, icy ribbons. Additional ice forms at the base of the ribbon, pushing the ribbon farther out and sometimes

causing it to curl upon itself to form flowerlike structures that we refer to as “frost flowers.” Even the forms that are not flowerlike can be quite spectacular.

Some other plants may produce frost flowers in the same manner, among them wild oregano (*Cunila origanoides*) in the mint family, and white crownbeard (*Verbesina virginica*) in the aster family.

Gallé, Émile (1846–1904)

A French glassmaker, renowned for his artful glass vessels featuring designs based on nature, especially plants. Gallé strongly believed that a glass vessel should be not only functional but also decorative. Gallé’s passion for plants began as a child in his family’s gardens in the Alsace-Lorraine region of France. Raised as the son of a successful manufacturer of utilitarian glass and ceramic items, Gallé eventually assumed responsibility for the business and maintained it as a source of income. This gave him the freedom to develop his own workshop, where he could create his artistic and innovative interpretations of nature in glass, ceramics, and eventually cabinetry.

Gallé studied plants as both a scientist and an artist and portrayed them in impressionistic and symbolic ways. He is recognized as a prominent member of the Art Nouveau movement, which dominated the art world of the 1890s and early 1900s, coinciding with the peak of his career. Gallé was strongly patriotic, and when Germany annexed Alsace-Lorraine after the Franco-Prussian War, he began incorporating the flowers representing the villages of that region (e.g., thistles from Nancy, wild white rose from Épinal, etc.),

as well as the symbolic Cross of Lorraine, into his designs as a way of maintaining the French heritage of the region. His pieces featured orchids and magnolias, tree trunks and pine needles, as well as many other plant motifs. He worked initially in enameled glass, then cased glass made of layers of two or more colors fused together, but he is probably most noted for his cameo glass, created by acid etching or carving cased glass to expose the inner color(s).

Gallé achieved international fame within his lifetime, winning prizes at international exhibitions and receiving commissions for works to be presented to royalty and other dignitaries.

Gas plant (*Dictamnus albus*), Rutaceae

An old-fashioned garden flower, originally from southern Europe, North Africa, and Asia, that is not as commonly grown as it once was despite its dense stalks of fragrant flowers, which can be white (*D. albus*) or pink (*D. rubra*). One reason the plant is not frequently planted in gardens is that a painful contact dermatitis can occur when toxic compounds in the plant's sap, known as psoralens, react with sunlight to cause burning red lesions that result in long-lasting darker pigmentation in the skin.

Named for Mount Dicte on the island of Crete, *Dictamnus* is a member of the citrus family but bears little resemblance to any plants that commonly come to mind when we think of citrus (orange, lemon, etc.). It does, however, produce an oily substance in its above-ground parts that releases a lemony aroma, particularly on hot days. Rather astonishingly, this substance is so



Dictamnus albus
Gas plant

volatile that it can ignite, and this is the basis for two common names of the plant, “gas plant” and “burning bush” (not to be confused with the shrub *Euonymus alata*, which earned the name “burning bush” from its bright red autumn leaves).

For general queries contact webmaster@press.princeton.edu.

By striking a match close to the plant on a hot, dry day, which is common in the gas plant's native range, one can see a flash that consumes the oily substance on the plant so quickly that there is no harm to the plant. This is even more spectacular on a hot, dry night. The chemistry of the plant has been investigated, and of the twenty-seven compounds found, isoprene, a product of the breakdown of a form of benzene, is believed to be responsible for this phenomenon.

H **austorium**
A plant tissue that forms at the junction of a parasitic plant and its host, uniting the two plants and allowing the parasite to extract water and nutrients from the host. The word "haustorium" is derived from the Latin *haustor*, meaning "to drink," and *orium*, meaning a "device used for." Most haustoria have a holdfast that attaches the parasite to the host plant and holds it in place while an intrusive organ penetrates the host tissue by using both pressure and enzymatic action. When the parasite's xylem elements (the vascular tissue that conducts water and nutrients) encounter those of the host plant, a bridge is formed between the two conductive systems.

Some parasites produce just one such attachment to their host, which functions throughout the life of the parasite; such an attachment is called a primary haustorium. Most such attachments begin as the result of the germination of a seed that has been either excreted by a bird or wiped from its beak onto the branch of a host species. Other parasitic species may develop secondary haustoria from their root tissue; these penetrate

the host tissue at several to many more points along the branches. Still other species, such as dodder (*Cuscuta*), produce *only* secondary haustoria directly from the points where their twining stems contact the stem of the host.

Common examples of parasitic plants include the mistletoes (a common name given to parasitic members of three different families: Viscaceae, Loranthaceae, and Eremolepidaceae). We in temperate regions are most familiar with the small-flowered, white-fruited members of the Viscaceae (*Viscum album* in Europe and *Phoradendron* spp. in North America), which play a role in the Christmas tradition of kissing a person standing under a sprig or ball of mistletoe.

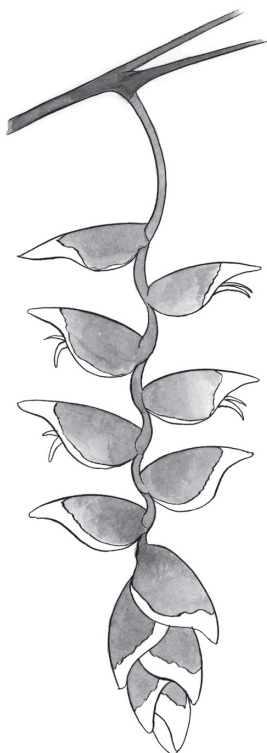
Heliconia (*Heliconia* spp.), Heliconiaceae

A genus in the monotypic family Heliconiaceae (meaning that the family has only one genus). *Heliconia* is related to bananas, gingers, and their relatives. The genus is native principally to tropical regions of Central and South America, except for a few species indigenous to islands in the western Pacific. The plants are generally large (but range from about twenty inches to fifteen feet in height), with big, banana-like leaves. Because of their dramatic, colorful inflorescences, many species are cultivated in tropical gardens and some have been given amusing descriptive names (e.g., lobster-claw and toucan-beak for *Heliconia rostrata*).

An inflorescence of heliconia immediately commands one's attention in the dark rain forest understory, its most common habitat. The most striking parts of the inflorescence are the strong, colorful bracts arranged

along the rachis (stalk) in either an upright or a pendent fashion. Within these bracts are the tough, three-parted flowers fused into a tube at their bases. Hummingbirds are the coevolved pollinators of New World species, with the beaks of different hummingbird species often modified to fit perfectly into the flowers of specific heliconia species.

The hummingbirds not only obtain nectar necessary to fuel their energy requirements, but also pollinate the flowers in the process. Aside from that typical exchange, hummingbirds perform another function as well—they provide livery service for tiny nectar- and pollen-feeding mites that otherwise spend their entire lives in the bracts of some heliconia species (this same system is found in other hummingbird-pollinated flowers as well [e.g., tropical members of the blueberry family]). The mites may choose to leave the currently inhabited flower when nectar secretion declines as the flower ages or when they need more space



Heliconia rostrata
Lobster claw
a.k.a. Toucan beak

and less competition for their offspring (gravid female mites disperse more frequently than male mites). Hummingbird flower mites are specific in their choice of host, using only one or a very few species of heliconia, but they may hop a ride on a variety of hummingbirds that visit that species; more specifically, they ride not *on* the birds but *within* the nares (nostrils) of the hummingbirds. If a hummingbird should visit the flowers of another species, the mite will stay put until the bird ultimately visits another plant of its preferred host. Thus, a hummingbird may carry several mite species at a time, with each disembarking when its host plant is encountered. The mites probably use aromatic cues from floral nectar to determine whether the correct “stop” has been reached.

If a heliconia species flowers throughout the year, the mites are more likely to consistently prefer that host, but if a preferred host flowers during only part of the year, the mite must shift host species when the first stops flowering.

Hemiepiphyte

A plant that grows for part of its life on other plants, *without* a connection to the ground, and for part of its life *with* a connection to the ground. It differs from a true epiphyte, which never has a connection to the ground (“epiphyte” is derived from the Greek *epi*, meaning “upon,” and *phyte* [from *phutón*], meaning “plant”; thus, a plant that grows on another plant). Examples of true epiphytes include many species of bromeliads and tropical orchids that begin life on the trunk or branch of a tree from a wind-dispersed seed or

a seed deposited by a bird. Epiphytes obtain water and nutrients from rainwater and debris that accumulates on or around them on the tree. They generally cause no harm to the host plant unless their number becomes great enough that a branch can no longer bear their combined weight.

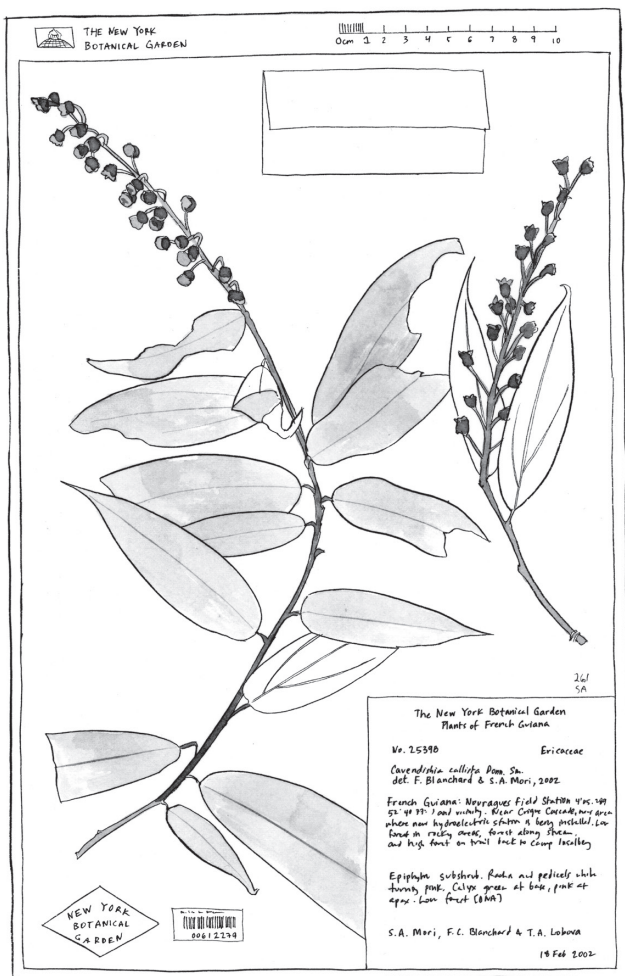
Hemiepiphytes, on the other hand, may begin life in the same way, from a seed that germinates in the treetops, but the plant eventually grows aerial roots that reach the ground and begin to absorb nutrients from the soil. Plants that behave in this way are referred to as primary hemiepiphytes (they begin life as an epiphyte). Such plants may become so large that they completely engulf the host tree, resulting in its death and gradual decay. The hemiepiphyte then appears to be an independent tree. An example is the strangler fig (*Ficus* spp.).

In another hemiepiphytic lifestyle, that of the secondary hemiepiphyte, a seed germinates on the ground and grows toward a dark shape (e.g., a tree trunk), where it will begin to grow as a vine clinging to the tree trunk. Once it reaches a level where it can obtain enough light, it will lose its connection to the ground and become epiphytic. Many tropical members of the Araceae (jack-in-the-pulpit family) grow in this manner. In some cases (as is also true in *Marcgravia*, treated elsewhere in this book), the leaves change dramatically in size and shape once the plant reaches higher light levels. Some argue that the term “secondary epiphyte” should be replaced with “nomadic vine,” since once a secondary hemiepiphyte loses its connection with the ground, it is difficult to determine in the field whether it began life on the ground.

Herbarium (plural: herbaria)

A collection of preserved plant specimens and the data associated with their collection (e.g., the collector's name, date and location of collection, description of aspects of the plant that might not be observable on the herbarium specimen, plant habit [e.g., tree, shrub, herb, etc.], habitat, and any animal interactions observed). Herbarium specimens are used for research and reference by botanists and ecologists. A specimen on which a new species name is based is referred to as a type collection and serves as the basis for determining whether another collection belongs to that species. Herbaria are generally organized taxonomically based on a classification system accepted by that institution. Plants identified as the same species are kept together in folders, and those are grouped into larger genus folders. Some herbaria are organized alphabetically by family.

Most herbarium collections consist of dried and pressed plants or plant parts that have been mounted on standard-sized, heavy, acid-free herbarium paper along with a label giving the collection data. Plant parts that are not pressable (e.g., woody fruits) are filed separately in boxes along with their collection data. Before being filed in shelved metal cabinets, the plants are usually frozen to ensure that any insects are killed. Delicate material such as extra flowers might be dried and stored in a small envelope that is affixed to the herbarium sheet or preserved in a vial of alcohol or FAA (a formaldehyde-based mixture). Mosses and lichens are generally dried and stored in paper envelopes. All of these materials are studied by botanists when they are



Herbarium specimen

writing descriptions of a species and by artists who are illustrating the species. Specialized herbarium collections may include fungi (termed a fungarium) or wood specimens (termed a xylarium). Today, many herbarium specimens have been digitized so that researchers can examine them from afar.

Herbaria date back to the sixteenth century, when sheets of pressed plants were bound into books. It was Linnaeus who realized that it would be wiser to maintain the specimens on separate sheets so that they could be reordered if their classification changed.

Hydathodes

Small openings in the epidermis of plants that exude water and usually occur at vein endings along the margins of leaves. These openings differ from the tiny pores called stomata (from the Greek for “mouths”) that cover the surface of the leaf (and other parts of the plant) and function in gas exchange—taking in carbon dioxide from the air and releasing oxygen as a by-product of photosynthesis; water vapor is also released.

In some plant species hydathodes are visible as thickenings or small openings near the leaf tips. The leaves of strawberry (*Fragaria* spp.), in the rose family, provide an easy-to-witness example of this phenomenon, though it may also be observed in plants of several other families. The release of water from these special openings is referred to as guttation and is most evident on young leaves during the early morning hours. This is not merely dew that forms as plants cool down at night and the ambient moisture in the air condenses into liquid droplets on their leaves.