

= Cactus =

A cactus (plural : cacti , cactuses , or cactus) is a member of the plant family Cactaceae , a family comprising ca 127 genera with some 1750 known species of the order Caryophyllales . The word " cactus " derives , through Latin , from the Ancient Greek ?????? , kaktos , a name originally used by Theophrastus for a spiny plant whose identity is not certain . Cacti occur in a wide range of shapes and sizes . Most cacti live in habitats subject to at least some drought . Many live in extremely dry environments , even being found in the Atacama Desert , one of the driest places on earth . Cacti show many adaptations to conserve water . Almost all cacti are succulents , meaning they have thickened , fleshy parts adapted to store water . Unlike many other succulents , the stem is the only part of most cacti where this vital process takes place . Most species of cacti have lost true leaves , retaining only spines , which are highly modified leaves . As well as defending against herbivores , spines help prevent water loss by reducing air flow close to the cactus and providing some shade . In the absence of leaves , enlarged stems carry out photosynthesis . Cacti are native to the Americas , ranging from Patagonia in the south to parts of western Canada in the north ? except for *Rhipsalis baccifera* , which also grows in Africa and Sri Lanka .

Cactus spines are produced from specialized structures called areoles , a kind of highly reduced branch . Areoles are an identifying feature of cacti . As well as spines , areoles give rise to flowers , which are usually tubular and multipetaled . Many cacti have short growing seasons and long dormancies , and are able to react quickly to any rainfall , helped by an extensive but relatively shallow root system that quickly absorb any water reaching the ground surface . Cactus stems are often ribbed or fluted , which allows them to expand and contract easily for quick water absorption after rain , followed by long drought periods . Like other succulent plants , most cacti employ a special mechanism called " crassulacean acid metabolism " (CAM) as part of photosynthesis . Transpiration , during which carbon dioxide enters the plant and water escapes , does not take place during the day at the same time as photosynthesis , but instead occurs at night . The plant stores the carbon dioxide it takes in as malic acid , retaining it until daylight returns , and only then using it in photosynthesis . Because transpiration takes place during the cooler , more humid night hours , water loss is significantly reduced .

Many smaller cacti have globe @-@ shaped stems , combining the highest possible volume for water storage , with the lowest possible surface area for water loss from transpiration . The tallest [1] free @-@ standing cactus is *Pachycereus pringlei* , with a maximum recorded height of 19 @.@ 2 m (63 ft) , and the smallest is *Blossfeldia liliputiana* , only about 1 cm (0 @.@ 4 in) in diameter at maturity . A fully grown saguaro (*Carnegiea gigantea*) is said to be able to absorb as much as 200 U.S. gallons (760 l ; 170 imp gal) of water during a rainstorm . A few species differ significantly in appearance from most of the family . At least superficially , plants of the genus *Pereskia* resemble other trees and shrubs growing around them . They have persistent leaves , and when older , bark @-@ covered stems . Their areoles identify them as cacti , and in spite of their appearance , they , too , have many adaptations for water conservation . *Pereskia* is considered close to the ancestral species from which all cacti evolved . In tropical regions , other cacti grow as forest climbers and epiphytes (plants that grow on trees) . Their stems are typically flattened , almost leaf @-@ like in appearance , with fewer or even no spines , such as the well @-@ known Christmas cactus or Thanksgiving cactus (in the genus *Schlumbergera*) .

Cacti have a variety of uses : many species are used as ornamental plants , others are grown for fodder or forage , and others for food (particularly their fruit) . Cochineal is the product of an insect that lives on some cacti .

= = Morphology = =

The 1 @,@ 500 to 1 @,@ 800 species of cacti mostly fall into one of two groups of " core cacti " : opuntias (subfamily Opuntioideae) and " cactoids " (subfamily Cactoideae) . Most members of these two groups are easily recognizable as cacti . They have fleshy succulent stems that are major organs of photosynthesis . They have absent , small , or transient leaves . They have flowers with

ovaries that lie below the sepals and petals , often deeply sunken into a fleshy receptacle (the part of the stem from which the flower parts grow) . All cacti have areoles ? highly specialized short shoots with extremely short internodes that produce spines , normal shoots , and flowers .

The remaining cacti fall into only two genera , *Pereskia* and *Maihuenia* , and are rather different , which means any description of cacti as a whole must frequently make exceptions for them . *Pereskia* species superficially resemble other tropical forest trees . When mature , they have woody stems that may be covered with bark and long @-@ lasting leaves that provide the main means of photosynthesis . Their flowers may have superior ovaries (i.e. , above the points of attachment of the sepals and petals) , and areoles that produce further leaves . The two species of *Maihuenia* have small , globe @-@ shaped bodies with prominent leaves at the top .

= = = Growth habit = = =

Cacti show a wide variety of growth habits , which are difficult to divide into clear , simple categories . They can be tree @-@ like (arborescent) , meaning they typically have a single more @-@ or @-@ less woody trunk topped by several to many branches . In the genus *Pereskia* , the branches are covered with leaves , so the species of this genus may not be recognized as cacti . In most other cacti , the branches are more typically cactus @-@ like , bare of leaves and bark , and covered with spines , as in *Pachycereus pringlei* or the larger opuntias . Some cacti may become tree @-@ sized but without branches , such as larger specimens of *Echinocactus platyacanthus* . Cacti may also be described as shrubby , with several stems coming from the ground or from branches very low down , such as in *Stenocereus thurberi* .

Smaller cacti may be described as columnar . They consist of erect , cylinder @-@ shaped stems , which may or may not branch , without a very clear division into trunk and branches . The boundary between columnar forms and tree @-@ like or shrubby forms is difficult to define . Smaller and younger specimens of *Cephalocereus senilis* , for example , are columnar , whereas older and larger specimens may become tree @-@ like . In some cases , the " columns " may be horizontal rather than vertical . Thus , *Stenocereus eruca* has stems growing along the ground , rooting at intervals .

Cacti whose stems are even smaller may be described as globular (or globose) . They consist of shorter , more ball @-@ shaped stems than columnar cacti . Globular cacti may be solitary , such as *Ferocactus latispinus* , or their stems may form clusters that can create large mounds . All or some stems in a cluster may share a common root .

Other cacti have a quite different appearance . In tropical regions , some grow as forest climbers and epiphytes . Their stems are typically flattened , almost leaf @-@ like in appearance , with fewer or even no spines . Climbing cacti can be very large ; a specimen of *Hylocereus* was reported as 100 meters (330 ft) long from root to the most distant stem . Epiphytic cacti , such as species of *Rhipsalis* or *Schlumbergera* , often hang downwards , forming dense clumps where they grow in trees high above the ground .

= = = Stems = = =

The leafless , spiny stem is the characteristic feature of the majority of cacti (and all of those belonging to the largest subfamily , the Cactoideae) . The stem is typically succulent , meaning it is adapted to store water . The surface of the stem may be smooth (as in some species of *Opuntia*) or covered with protuberances of various kinds , which are usually called tubercles . These vary from small " bumps " to prominent , nipple @-@ like shapes in the genus *Mammillaria* and outgrowths almost like leaves in *Ariocarpus* species . The stem may also be ribbed or fluted in shape . The prominence of these ribs depends on how much water the stem is storing : when full (up to 90 % of the mass of a cactus may be water) , the ribs may be almost invisible on the swollen stem , whereas when the cactus is short of water and the stems shrink , the ribs may be very visible .

The stems of most cacti are some shade of green , often bluish or brownish green . Such stems

contain chlorophyll and are able to carry out photosynthesis ; they also have stomata (small structures that can open and close to allow passage of gases) . Cactus stems are often visibly waxy .

=== Areoles ===

Areoles are structures unique to cacti . Although variable , they typically appear as woolly or hairy areas on the stems from which spines emerge . Flowers are also produced from areoles . In the genus *Pereskia* , believed similar to the ancestor of all cacti , the areoles occur in the axils of leaves (i.e. in the angle between the leaf stalk and the stem) . In leafless cacti , areoles are often borne on raised areas on the stem where leaf bases would have been .

Areoles are highly specialized and very condensed shoots or branches . In a normal shoot , nodes bearing leaves or flowers would be separated by lengths of stem (internodes) . In an areole , the nodes are so close together , they form a single structure . The areole may be circular , elongated into an oval shape , or even separated into two parts ; the two parts may be visibly connected in some way (e.g. by a groove in the stem) or appear entirely separate (a dimorphic areole) . The part nearer the top of the stem then produces flowers , the other part spines . Areoles often have multicellular hairs (trichomes) that give the areole a hairy or woolly appearance , sometimes of a distinct color such as yellow or brown .

In most cacti , the areoles produce new spines or flowers only for a few years , and then become inactive . This results in a relatively fixed number of spines , with flowers being produced only from the ends of stems , which are still growing and forming new areoles . In *Pereskia* , a genus close to the ancestor of cacti , areoles remain active for much longer ; this is also the case in *Opuntia* and *Neoraimondia* .

=== Leaves ===

The great majority of cacti have no visible leaves ; photosynthesis takes place in the stems (which may be flattened and leaflike in some species) . Exceptions occur in three groups of cacti . All the species of *Pereskia* are superficially like normal trees or shrubs and have numerous leaves . Many cacti in the *Opuntia* group (subfamily *Opuntioideae* , *Opuntioideae*) also have visible leaves , which may be long @-@ lasting (as in *Pereskopsis* species) or be produced only during the growing season and then be lost (as in many species of *Opuntia*) . The small genus *Maihuenia* also relies on leaves for photosynthesis . The structure of the leaves varies somewhat between these groups . *Pereskia* species have " normal " leaves , with a midrib and a flattened blade (lamina) on either side . *Opuntioideae* and *Maihuenia* have leaves that appear to consist only of a midrib .

Even those cacti without visible photosynthetic leaves do usually have very small leaves , less than 0 @. @ 5 mm (0 @. @ 02 in) long in about half of the species studied and almost always less than 1 @. @ 5 mm (0 @. @ 06 in) long . The function of such leaves cannot be photosynthesis ; a role in the production of plant hormones , such as auxin , and in defining axillary buds has been suggested .

=== Spines ===

Botanically , " spines " are distinguished from " thorns " : spines are modified leaves , and thorns are modified branches . Cacti produce spines , always from areoles as noted above . Spines are present even in those cacti with leaves , such as *Pereskia* , *Pereskopsis* and *Maihuenia* , so they clearly evolved before complete leaflessness . Some cacti only have spines when young , possibly only when seedlings . This is particularly true of tree @-@ living cacti , such as *Rhipsalis* or *Schlumbergera* , but some ground @-@ living cacti , such as *Ariocarpus* , also lack spines when mature .

The spines of cacti are often useful in identification , since they vary greatly between species in number , color , size , shape and hardness , as well as in whether all the spines produced by an

areole are similar or whether they are of distinct kinds . Most spines are straight or at most slightly curved , and are described as hair @-@ like , bristle @-@ like , needle @-@ like or awl @-@ like , depending on their length and thickness . Some cacti have flattened spines (e.g. *Schlerocactus papyracanthus*) . Other cacti have hooked spines . Sometimes , one or more central spines are hooked , while outer spines are straight (e.g. , *Mammillaria rekoii*) .

In addition to normal @-@ length spines , members of the subfamily *Opuntioideae* have relatively short spines , called glochids that are barbed along their length and easily shed . These enter the skin and are difficult to remove , causing long @-@ lasting irritation .

== Roots ==

Most ground @-@ living cacti have only fine roots , which spread out around the base of the plant for varying distances , close to the surface . Some cacti have taproots ; in genera such as *Copiapoa* , these are considerably larger and of a greater volume than the body . Taproots may aid in stabilizing the larger columnar cacti . Climbing , creeping and epiphytic cacti may have only adventitious roots , produced along the stems where these come into contact with a rooting medium .

== Flowers ==

Like their spines , cactus flowers are variable . Typically , the ovary is surrounded by material derived from stem or receptacle tissue , forming a structure called a pericarpel . Tissue derived from the petals and sepals continues the pericarpel , forming a composite tube ? the whole may be called a floral tube , although strictly speaking only the part furthest from the base is floral in origin . The outside of the tubular structure often has areoles that produce wool and spines . Typically , the tube also has small scale @-@ like bracts , which gradually change into sepal @-@ like and then petal @-@ like structures , so the sepals and petals cannot be clearly differentiated (and hence are often called " tepals ") . Some cacti produce floral tubes without wool or spines (e.g. *Gymnocalycium*) or completely devoid of any external structures (e.g. *Mammillaria*) . Unlike the flowers of other cacti , *Pereskia* flowers may be borne in clusters .

Cactus flowers usually have many stamens , but only a single style , which may branch at the end into more than one stigma . The stamens usually arise from all over the inner surface of the upper part of the floral tube , although in some cacti , the stamens are produced in one or more distinct " series " in more specific areas of the inside of the floral tube .

The flower as a whole is usually radially symmetrical (actinomorphic) , but may be bilaterally symmetrical (zygomorphic) in some species . Flower colors range from white through yellow and red to magenta .

== Adaptations for water conservation ==

All cacti have some adaptations to promote efficient water use . Most cacti ? opuntias and cactoids ? specialize in surviving in hot and dry environments (i.e. they are xerophytes) , but the first ancestors of modern cacti were already adapted to periods of intermittent drought . A small number of cactus species in the tribes *Hylocereeae* and *Rhipsalideae* have become adapted to life as climbers or epiphytes , often in tropical forests , where water conservation is less important .

== Leaves and spines ==

The absence of visible leaves is one of the most striking features of most cacti . *Pereskia* (which is close to the ancestral species from which all cacti evolved) does have long @-@ lasting leaves , which are , however , thickened and succulent in many species . Other species of cactus with long @-@ lasting leaves , such as the opuntiid *Pereskopsis* , also have succulent leaves . A key issue in retaining water is the ratio of surface area to volume . Water loss is proportional to surface area ,

whereas the amount of water present is proportional to volume . Structures with a high surface area @-@ to @-@ volume ratio , such as thin leaves , necessarily lose water at a higher rate than structures with a low area @-@ to @-@ volume ratio , such as thickened stems .

Spines , which are modified leaves , are present on even those cacti with true leaves , showing the evolution of spines preceded the loss of leaves . Although spines have a high surface area @-@ to @-@ volume ratio , at maturity they contain little or no water , being composed of fibers made up of dead cells . Spines provide protection from herbivores and camouflage in some species , and assist in water conservation in several ways . They trap air near the surface of the cactus , creating a moister layer that reduces evaporation and transpiration . They can provide some shade , which lowers the temperature of the surface of the cactus , also reducing water loss . When sufficiently moist air is present , such as during fog or early morning mist , spines can condense moisture , which then drips onto the ground and is absorbed by the roots .

== Stems ==

The majority of cacti are stem succulents , i.e. , plants in which the stem is the main organ used to store water . Water may form up to 90 % of the total mass of a cactus . Stem shapes vary considerably among cacti . The cylindrical shape of columnar cacti and the spherical shape of globular cacti produce a low surface area @-@ to @-@ volume ratio , thus reducing water loss , as well as minimizing the heating effects of sunlight . The ribbed or fluted stems of many cacti allow the stem to shrink during periods of drought and then swell as it fills with water during periods of availability . A mature saguaro (*Carnegiea gigantea*) is said to be able to absorb as much as 200 U.S. gallons (760 l ; 170 imp gal) of water during a rainstorm . The outer layer of the stem usually has a tough cuticle , reinforced with waxy layers , which reduce water loss . These layers are responsible for the grayish or bluish tinge to the stem color of many cacti .

The stems of most cacti have adaptations to allow them to conduct photosynthesis in the absence of leaves . This is discussed further below under Metabolism .

== Roots ==

Many cacti have roots that spread out widely , but only penetrate a short distance into the soil . In one case , a young saguaro only 12 cm (4 @. @ 7 in) tall had a root system with a diameter of 2 m (7 ft) , but no more than 10 cm (4 in) deep . Cacti can also form new roots quickly when rain falls after a drought . The concentration of salts in the root cells of cacti is relatively high . All these adaptations enable cacti to absorb water rapidly during periods of brief or light rainfall . Thus , *Ferocactus cylindraceus* reportedly can take up a significant amount of water within 12 hours of as little as 7 mm (0 @. @ 3 in) of rainfall , becoming fully hydrated in a few days .

Although in most cacti , the stem acts as the main organ for storing water , some cacti have in addition large taproots . These may be several times the length of the above @-@ ground body in the case of species such as *Copiapoa atacamensis* , which grows in one of the driest places in the world , the Atacama Desert in northern Chile .

== Metabolism ==

Photosynthesis requires plants to take in carbon dioxide gas (CO_2) . As they do so , they lose water through transpiration . Like other types of succulents , cacti reduce this water loss by the way in which they carry out photosynthesis . " Normal " leafy plants use the C_3 mechanism : during daylight hours , CO_2 is continually drawn out of the air present in spaces inside leaves and converted first into a compound containing three carbon atoms (3 @-@ phosphoglycerate) and then into products such as carbohydrates . The access of air to internal spaces within a plant is controlled by stomata , which are able to open and close . The need for a continuous supply of CO_2 during photosynthesis means the stomata must be open , so water vapor is continuously being lost . Plants using the C_3 mechanism lose as much as 97 % of the water taken up through their roots in

this way . A further problem is that as temperatures rise , the enzyme that captures CO₂ starts to capture more and more oxygen instead , reducing the efficiency of photosynthesis by up to 25 % .

Crassulacean acid metabolism (CAM) is a mechanism adopted by cacti and other succulents to avoid the problems of the C₃ mechanism . In full CAM , the stomata open only at night , when temperatures and water loss are lowest . CO₂ enters the plant and is captured in the form of organic acids stored inside cells (in vacuoles) . The stomata remain closed throughout the day , and photosynthesis uses only this stored CO₂ . CAM uses water much more efficiently at the price of limiting the amount of carbon fixed from the atmosphere and thus available for growth . CAM @-@ cycling is a less efficient system whereby stomata open in the day , just as in plants using the C₃ mechanism . At night , or when the plant is short of water , the stomata close and the CAM mechanism is used to store CO₂ produced by respiration for use later in photosynthesis . CAM @-@ cycling is present in *Pereskia* species .

By studying the ratio of ¹⁴C to ¹³C incorporated into a plant ? its isotopic signature ? it is possible to deduce how much CO₂ is taken up at night and how much in the daytime . Using this approach , most of the *Pereskia* species investigated exhibit some degree of CAM @-@ cycling , suggesting this ability was present in the ancestor of all cacti . *Pereskia* leaves are claimed to only have the C₃ mechanism with CAM restricted to stems . More recent studies show that " it is highly unlikely that significant carbon assimilation occurs in the stem " ; *Pereskia* species are described as having " C₃ with inducible CAM . " Leafless cacti carry out all their photosynthesis in the stem , using full CAM . As of February 2012 , it is not clear whether stem @-@ based CAM evolved once only in the core cacti , or separately in the *Opuntias* and cactoids ; CAM is known to have evolved convergently many times .

To carry out photosynthesis , cactus stems have undergone many adaptations . Early in their evolutionary history , the ancestors of modern cacti (other than one group of *Pereskia* species) developed stomata on their stems and began to delay developing bark . However , this alone was not sufficient ; cacti with only these adaptations appear to do very little photosynthesis in their stems . Stems needed to develop structures similar to those normally found only in leaves . Immediately below the outer epidermis , a hypodermal layer developed made up of cells with thickened walls , offering mechanical support . Air spaces were needed between the cells to allow carbon dioxide to diffuse inwards . The center of the stem , the cortex , developed " chlorenchyma " ? a plant tissue made up of relatively unspecialized cells containing chloroplasts , arranged into a " spongy layer " and a " palisade layer " where most of the photosynthesis occurs .

= = Taxonomy and classification = =

Naming and classifying cacti has been both difficult and controversial since the first cacti were discovered for science . The difficulties began with Carl Linnaeus . In 1737 , he placed the cacti he knew into two genera , *Cactus* and *Pereskia* . However , when he published *Species Plantarum* in 1753 ? the starting point for modern botanical nomenclature ? he relegated them all to one genus , *Cactus* . The word " cactus " is derived through Latin from the Ancient Greek ?????? (*kaktos*) , a name used by Theophrastus for a spiny plant , which may have been the cardoon (*Cynara cardunculus*) .

Later botanists , such as Philip Miller in 1754 , divided cacti into several genera , which , in 1789 , Antoine Laurent de Jussieu placed in his newly created family *Cactaceae* . By the early 20th century , botanists came to feel Linnaeus 's name *Cactus* had become so confused as to its meaning (was it the genus or the family ?) that it should not be used as a genus name . The 1905 Vienna botanical congress rejected the name *Cactus* and instead declared *Mammillaria* was the type genus of the family *Cactaceae* . It did , however , conserve the name *Cactaceae* , leading to the unusual situation in which the family *Cactaceae* no longer contains the genus after which it was named .

The difficulties continued , partly because giving plants scientific names relies on " type specimens " . Ultimately , if botanists want to know whether a particular plant is an example of , say , *Mammillaria mammillaris* , they should be able to compare it with the type specimen to which this name is permanently attached . Type specimens are normally prepared by compression and drying , after

which they are stored in herbaria to act as definitive references . However , cacti are very difficult to preserve in this way ; they have evolved to resist drying and their bodies do not easily compress . A further difficulty is that many cacti were given names by growers and horticulturalists rather than botanists ; as a result , the provisions of the International Code of Nomenclature for algae , fungi , and plants (which governs the names of cacti , as well as other plants) were often ignored . Curt Backeberg , in particular , is said to have named or renamed 1 @, @ 200 species without one of his names ever being attached to a specimen , which , according to David Hunt , ensured he " left a trail of nomenclatural chaos that will probably vex cactus taxonomists for centuries . "

= = = Classification = = =

In 1984 , it was decided that the Cactaceae Section of the International Organization for Succulent Plant Study should set up a working party , now called the International Cactaceae Systematics Group (ICSG) , to produce consensus classifications down to the level of genera . Their system has been used as the basis of subsequent classifications . Detailed treatments published in the 21st century have divided the family into around 125 ? 130 genera and 1 @, @ 400 ? 1 @, @ 500 species , which are then arranged into a number of tribes and subfamilies . The ICSG classification of the cactus family recognizes four subfamilies , the largest of which is divided into nine tribes . The subfamilies are :

Subfamily Pereskioideae K. Schumann

The only genus is *Pereskia* . It has features considered closest to the ancestors of the Cactaceae . Plants are trees or shrubs with leaves ; their stems are smoothly round in cross section , rather than being ribbed or having tubercles . Two systems may be used in photosynthesis , both the " normal " C3 mechanism and crassulean acid metabolism (CAM) ? an " advanced " feature of cacti and other succulents that conserves water .

Subfamily Opuntioideae K. Schumann

Some 15 genera are included in this subfamily . They may have leaves when they are young , but these are lost later . Their stems are usually divided into distinct " joints " or " pads " (cladodes) . Plants vary in size from the small cushions of *Maihueniopsis* to treelike species of *Opuntia* , rising to 10 m (33 ft) or more .

Subfamily Maihuenioideae P. Fearn

The only genus is *Maihuenia* , with two species , both of which form low @-@ growing mats . It has some features that are primitive within the cacti . Plants have leaves , and crassulean acid metabolism is wholly absent .

Subfamily Cactoideae

Divided into nine tribes , this is the largest subfamily , including all the " typical " cacti . Members are highly variable in habit , varying from tree @-@ like to epiphytic . Leaves are normally absent , although sometimes very reduced leaves are produced by young plants . Stems are usually not divided into segments , and are ribbed or tuberculate . Two of the tribes , *Hylocereeae* and *Rhipsalideae* , contain climbing or epiphytic forms with a rather different appearance ; their stems are flattened and may be divided into segments .

Molecular phylogenetic studies have supported the monophyly of three of these subfamilies (not *Pereskioideae*) , but have not supported all of the tribes or even genera below this level ; indeed , a 2011 study found only 39 % of the genera in the subfamily *Cactoideae* sampled in the research were monophyletic . Classification of the cacti currently remains uncertain and is likely to change .

= = Phylogeny and evolution = =

= = = Phylogeny = = =

A 2005 study suggested the genus *Pereskia* was basal within the Cactaceae , but confirmed earlier suggestions it was not monophyletic , i.e. , did not include all the descendants of a common

ancestor . The Bayesian consensus cladogram from this study is shown below .

A more recent 2011 study using fewer genes but more species also found that *Pereskia* was divided into these two clades , but was unable to resolve the members of the " core cacti " clade . It was accepted that the relationships shown above are " the most robust to date . "

The two clades of *Pereskia* differ in their geographical distribution ; with one exception , clade A is found around the Gulf of Mexico and the Caribbean Sea , whereas clade B occurs south of the Amazon Basin . Species of *Pereskia* within clade A always lack two key features of the stem present in most of the remaining " caulocacti " : like most non @-@ cacti , their stems begin to form bark early in the plants ' life and also lack stomata ? structures that control admission of air into a plant and hence control photosynthesis . By contrast , caulocacti , including species of *Pereskia* clade B , typically delay forming bark and have stomata on their stems , thus giving the stem the potential to become a major organ for photosynthesis . (The two highly specialized species of *Maihuenia* are something of an exception .)

The first cacti are thought to have been only slightly succulent shrubs or small trees whose leaves carried out photosynthesis . They lived in tropical areas that experienced periodic drought . If *Pereskia* clade A is a good model of these early cacti , then , although they would have appeared superficially similar to other trees growing nearby , they had already evolved strategies to conserve water (some of which are present in members of other families in the order Caryophyllales) . These strategies included being able to respond rapidly to periods of rain , and keeping transpiration low by using water very efficiently during photosynthesis . The latter was achieved by tightly controlling the opening of stomata . Like *Pereskia* species today , early ancestors may have been able to switch from the normal C3 mechanism , where carbon dioxide is used continuously in photosynthesis , to CAM cycling , in which when the stomata are closed , carbon dioxide produced by respiration is stored for later use in photosynthesis .

Pereskia clade B marks the beginnings of an evolutionary switch to using stems as photosynthetic organs . Stems have stomata and the formation of bark takes place later than in normal trees . The " core cacti " show a steady increase in both stem succulence and photosynthesis accompanied by multiple losses of leaves , more @-@ or @-@ less complete in the Cactoideae . One evolutionary question at present unanswered is whether the switch to full CAM photosynthesis in stems occurred only once in the core cacti , in which case it has been lost in *Maihuenia* , or separately in *Opuntioideae* and Cactoideae , in which case it never evolved in *Maihuenia* .

Understanding evolution within the core cacti clade is difficult as of February 2012 , since phylogenetic relationships are still uncertain and not well related to current classifications . Thus , a 2011 study found " an extraordinarily high proportion of genera " were not monophyletic , so were not all descendants of a single common ancestor . For example , of the 36 genera in the subfamily Cactoideae sampled in the research , 22 (61 %) were found not monophyletic . Nine tribes are recognized within Cactoideae in the International Cactaceae Systematics Group (ICSG) classification ; one , Calymmantheae , comprises a single genus , *Calymmanthium* . Only two of the remaining eight , Cacteae and Rhipsalideae , were shown to be monophyletic in a 2011 study by Hernández @-@ Hernández et al . For a more detailed discussion of the phylogeny of the cacti , see Classification of the Cactaceae .

= = = Evolutionary history = = =

No known fossils of cacti exist to throw light on their evolutionary history . However , the geographical distribution of cacti offers some evidence . Except for a relatively recent spread of *Rhipsalis baccifera* to parts of the Old World , cacti are plants of South America and mainly southern regions of North America . This suggests the family must have evolved after the ancient continent of Gondwana split into South America and Africa , which occurred during the Early Cretaceous , around 145 to 101 million years ago . Precisely when after this split cacti evolved is less clear . Older sources suggest an early origin around 90 ? 66 million years ago , during the Late Cretaceous . More recent molecular studies suggest a much younger origin , perhaps in very Late Eocene to early Oligocene periods , around 35 ? 30 million years ago . Based on the phylogeny of the cacti ,

the earliest diverging group (*Pereskia* clade A) may have originated in Central America and northern South America , whereas the caulocacti , those with more @-@ or @-@ less succulent stems , evolved later in the southern part of South America , and then moved northwards . Core cacti , those with strongly succulent stems , are estimated to have evolved around 25 million years ago . A possible stimulus to their evolution may have been uplifting in the central Andes , some 25 ? 20 million years ago , which was associated with increasing and varying aridity . However , the current species diversity of cacti is thought to have arisen only in the last 10 ? 5 million years (from the late Miocene into the Pliocene) . Other succulent plants , such as the Aizoaceae in South Africa , the Didiereaceae in Madagascar and the genus *Agave* in the Americas , appear to have diversified at the same time , which coincided with a global expansion of arid environments .

= = Distribution = =

Cacti inhabit diverse regions , from coastal plains to high mountain areas . With one exception , they are native to the Americas , where their range extends from Patagonia to British Columbia and Alberta in western Canada . A number of centers of diversity exist . For cacti adapted to drought , the three main centers are Mexico and the southwestern United States ; the southwestern Andes , where they are found in Peru , Bolivia , Chile and Argentina ; and eastern Brazil , away from the Amazon Basin . Tree @-@ living epiphytic and climbing cacti necessarily have different centers of diversity , as they require moister environments . They are mainly found in the coastal mountains and Atlantic forests of southeastern Brazil ; in Bolivia , which is the center of diversity for the subfamily Rhipsalideae ; and in forested regions of Central America , where the climbing Hylocereeae are most diverse .

Rhipsalis baccifera is the exception ; it is native to both the Americas and the Old World , where it is found in tropical Africa , Madagascar , and Sri Lanka . One theory is it was spread by being carried as seeds in the digestive tracts of migratory birds ; the seeds of *Rhipsalis* are adapted for bird distribution . Old World populations are polyploid , and regarded as distinct subspecies , supporting the idea that the spread was not recent . The alternative theory is the species initially crossed the Atlantic on European ships trading between South America and Africa , after which birds may have spread it more widely .

Many other species have become naturalized outside the Americas after having been introduced by people , especially in Australia , Hawaii , and the Mediterranean region . In Australia , species of *Opuntia* , particularly *Opuntia stricta* , were introduced in the 19th century for use as natural agricultural fences and in an attempt to establish a cochineal industry . They rapidly became a major weed problem , but are now controlled by biological agents , particularly the moth *Cactoblastis cactorum* . The weed potential of *Opuntia* species in Australia continues however , leading to all opuntoid cacti except *O. ficus* @-@ *indica* being declared Weeds of National Significance by the Australian Weeds Committee in April 2012 .

= = Reproductive ecology = =

Cactus flowers are pollinated by insects , birds and bats . None are known to be wind @-@ pollinated and self @-@ pollination occurs in only a very few species ; for example the flowers of some species of *Frailea* do not open (cleistogamy) . The need to attract pollinators has led to the evolution of pollination syndromes , which are defined as groups of " floral traits , including rewards , associated with the attraction and utilization of a specific group of animals as pollinators . "

Bees are the most common pollinators of cacti ; bee @-@ pollination is considered to have been the first to evolve . Day @-@ flying butterflies and nocturnal moths are associated with different pollination syndromes . Butterfly @-@ pollinated flowers are usually brightly colored , opening during the day , whereas moth @-@ pollinated flowers are often white or pale in color , opening only in the evening and at night . As an example , *Pachycereus schottii* is pollinated by a particular species of moth , *Upiga virescens* , which also lays its eggs among the developing seeds its caterpillars later consume . The flowers of this cactus are funnel @-@ shaped , white to deep pink ,

up to 4 cm (1 @. @ 6 in) long , and open at night .

Hummingbirds are significant pollinators of cacti . Species showing the typical hummingbird @-@ pollination syndrome have flowers with colors towards the red end of the spectrum , anthers and stamens that protrude from the flower , and a shape that is not radially symmetrical , with a lower lip that bends downwards ; they produce large amounts of nectar with a relatively low sugar content . Schlumbergera species , such as *S. truncata* , have flowers that correspond closely to this syndrome . Other hummingbird @-@ pollinated genera include *Cleistocactus* and *Disocactus* .

Bat @-@ pollination is relatively uncommon in flowering plants , but about a quarter of the genera of cacti are known to be pollinated by bats ? an unusually high proportion , exceeded among eudicots by only two other families , both with very few genera . Columnar cacti growing in semidesert areas are among those most likely to be bat @-@ pollinated ; this may be because bats are able to travel considerable distances , so are effective pollinators of plants growing widely separated from one another . The pollination syndrome associated with bats includes a tendency for flowers to open in the evening and at night , when bats are active . Other features include a relatively dull color , often white or green ; a radially symmetrical shape , often tubular ; a smell described as " musty " ; and the production of a large amount of sugar @-@ rich nectar . *Carnegiea gigantea* is an example of a bat @-@ pollinated cactus , as are many species of *Pachycereus* and *Pilosocereus* .

The fruits produced by cacti after the flowers have been fertilized vary considerably ; many are fleshy , although some are dry . All contain a large number of seeds . Fleshy , colorful and sweet @-@ tasting fruits are associated with seed dispersal by birds . The seeds pass through their digestive systems and are deposited in their droppings . Fruit that falls to the ground may be eaten by other animals ; giant tortoises are reported to distribute *Opuntia* seeds in the Galápagos Islands . Ants appear to disperse the seeds of a few genera , such as *Blossfeldia* . Drier spiny fruits may cling to the fur of mammals or be moved around by the wind .

= = Uses = =

= = = Early history = = =

As of March 2012 , there is still controversy as to the precise dates when humans first entered those areas of the New World where cacti are commonly found , and hence when they might first have used them . An archaeological site in Chile has been dated to around 15 @,@ 000 years ago , suggesting cacti would have been encountered before then . Early evidence of the use of cacti includes cave paintings in the Serra da Capivara in Brazil , and seeds found in ancient middens (waste dumps) in Mexico and Peru , with dates estimated at 12 @,@ 000 ? 9 @,@ 000 years ago . Hunter @-@ gatherers likely collected cactus fruits in the wild and brought them back to their camps .

It is not known when cacti were first cultivated . *Opuntias* (prickly pears) were used for a variety of purposes by the Aztecs , whose empire , lasting from the 14th to the 16th century , had a complex system of horticulture . Their capital from the 15th century was Tenochtitlan (now Mexico City) ; one explanation for the origin of the name is that it includes the Nahuatl word *n?chtli* , referring to the fruit of an *opuntia* . The coat of arms of Mexico shows an eagle perched on a cactus while holding a snake , an image at the center of the myth of the founding of Tenochtitlan . The Aztecs symbolically linked the ripe red fruits of an *opuntia* to human hearts ; just as the fruit quenches thirst , so offering human hearts to the sun god ensured the sun would keep moving .

Europeans first encountered cacti when they arrived in the New World late in the 15th century . Their first landfalls were in the West Indies , where relatively few cactus genera are found ; one of the most common is the genus *Melocactus* . Thus , melocacti were possibly among the first cacti seen by Europeans . *Melocactus* species were present in English collections of cacti before the end of the 16th century (by 1570 according to one source ,) where they were called *Echinomelocactus* , later shortened to *Melocactus* by Joseph Pitton de Tourneville in the early 18th century . Cacti , both

purely ornamental species and those with edible fruit , continued to arrive in Europe , so Carl Linnaeus was able to name 22 species by 1753 . One of these , his *Cactus opuntia* (now part of *Opuntia ficus @-@ indica*) , was described as " fructu majore ... nunc in Hispania et Lusitania " (with larger fruit ... now in Spain and Portugal) , indicative of its early use in Europe .

= = = Food = = =

The plant now known as *Opuntia ficus @-@ indica* , or the Indian fig cactus , has long been an important source of food . The original species is thought to have come from central Mexico , although this is now obscure because the indigenous people of southern North America developed and distributed a range of horticultural varieties (cultivars) , including forms of the species and hybrids with other opuntias . Both the fruit and pads are eaten , the former often under the Spanish name tuna , the latter under the name nopal . Cultivated forms are often significantly less spiny or even spineless . The nopal industry in Mexico was said to be worth US \$ 150 million in 2007 . The Indian fig cactus was probably already present in the Caribbean when the Spanish arrived , and was soon after brought to Europe . It spread rapidly in the Mediterranean area , both naturally and by being introduced ? so much so , early botanists assumed it was native to the area . Outside the Americas , the Indian fig cactus is an important commercial crop in Sicily , Algeria and other North African countries . Fruits of other opuntias are also eaten , generally under the same name , tuna . Flower buds , particularly of *Cylindropuntia* species , are also consumed .

Almost any fleshy cactus fruit is edible . The word pitaya or pitahaya (usually considered to have been taken into Spanish from Haitian creole) can be applied to a range of " scaly fruit " , particularly those of columnar cacti . The fruit of the saguaro (*Carnegiea gigantea*) has long been important to the indigenous peoples of northwestern Mexico and the southwestern United States , including the Sonoran Desert . It can be preserved by boiling to produce syrup and by drying . The syrup can also be fermented to produce an alcoholic drink . Fruits of *Stenocereus* species have also been important food sources in similar parts of North America ; *Stenocereus queretaroensis* is cultivated for its fruit . In more tropical southern areas , the climber *Hylocereus undatus* provides pitahaya orejona , now widely grown in Asia under the name dragon fruit . Other cacti providing edible fruit include species of *Echinocereus* , *Ferocactus* , *Mammillaria* , *Myrtillocactus* , *Pachycereus* , *Peniocereus* and *Selenicereus* . The bodies of cacti other than opuntias are less often eaten , although Anderson reported that *Neowerdermannia vorwerkii* is prepared and eaten like potatoes in upland Bolivia .

= = = Psychoactive agents = = =

A number of species of cacti have been shown to contain psychoactive agents , chemical compounds that can cause changes in mood , perception and cognition through their effects on the brain . Two species have a long history of use by the indigenous peoples of the Americas : peyote , *Lophophora williamsii* , in North America , and the San Pedro cactus , *Echinopsis pachanoi* , in South America . Both contain mescaline .

L. williamsii is native to northern Mexico and southern Texas . Individual stems are about 2 ? 6 cm (0 @. @ 8 ? 2 @. @ 4 in) high with a diameter of 4 ? 11 cm (1 @. @ 6 ? 4 @. @ 3 in) , and may be found in clumps up to 1 m (3 ft) wide . A large part of the stem is usually below ground . Mescaline is concentrated in the photosynthetic portion of the stem above ground . The center of the stem , which contains the growing point (the apical meristem) , is sunken . Experienced collectors of peyote remove a thin slice from the top of the plant , leaving the growing point intact , thus allowing the plant to regenerate . Evidence indicates peyote was in use more than 5 @, @ 500 years ago ; dried peyote buttons presumed to be from a site on the Rio Grande , Texas , were radiocarbon dated to around 3780 ? 3660 BC . Peyote is perceived as a means of accessing the spirit world . Attempts by the Roman Catholic church to suppress its use after the Spanish conquest were largely unsuccessful , and by the middle of the 20th century , peyote was more widely used than ever by indigenous peoples as far north as Canada . It is now used formally by the Native American Church

Echinopsis pachanoi is native to Ecuador and Peru . It is very different in appearance from L. williamsii . It has tall stems , up to 6 m (20 ft) high , with a diameter of 6 ? 15 cm (2 @. @ 4 ? 5 @. @ 9 in) , which branch from the base , giving the whole plant a shrubby or tree @-@ like appearance . Archaeological evidence of the use of this cactus appears to date back to 2 @, @ 000 ? 2 @, @ 300 years ago , with carvings and ceramic objects showing columnar cacti . Although church authorities under the Spanish attempted to suppress its use , this failed , as shown by the Christian element in the common name " San Pedro cactus " ? Saint Peter cactus . Anderson attributes the name to the belief that just as St Peter holds the keys to heaven , the effects of the cactus allow users " to reach heaven while still on earth . " It continues to be used for its psychoactive effects , both for spiritual and for healing purposes , often combined with other psychoactive agents , such as Datura ferox and tobacco . Several other species of Echinopsis , including E. peruviana , also contain mescaline .

= = = Ornamental plants = = =

Cacti were cultivated as ornamental plants from the time they were first brought from the New World . By the early 1800s , enthusiasts in Europe had large collections (often including other succulents alongside cacti) . Rare plants were sold for very high prices . Suppliers of cacti and other succulents employed collectors to obtain plants from the wild , in addition to growing their own . In the late 1800s , collectors turned to orchids , and cacti became less popular , although never disappearing from cultivation .

Cacti are often grown in greenhouses , particularly in regions unsuited to the cultivation of cacti outdoors , such the northern parts of Europe and North America . Here , they may be kept in pots or grown in the ground . Cacti are also grown as houseplants , many being tolerant of the often dry atmosphere . Cacti in pots may be placed outside in the summer to ornament gardens or patios , and then kept under cover during the winter . Less drought @-@ resistant epiphytes , such as epiphyllum hybrids , Schlumbergera (the Thanksgiving or Christmas cactus) and Hatiora (the Easter cactus) , are widely cultivated as houseplants .

Cacti may also be planted outdoors in regions with suitable climates . Concern for water conservation in arid regions has led to the promotion of gardens requiring less watering (xeriscaping) . For example , in California , the East Bay Municipal Utility District sponsored the publication of a book on plants and landscapes for summer @-@ dry climates . Cacti are one group of drought @-@ resistant plants recommended for dry landscape gardening .

= = = Other uses = = =

Cacti have many other uses . They are used for human food and as fodder for animals , usually after burning off their spines . In addition to their use as psychoactive agents , some cacti are employed in herbal medicine . The practice of using various species of Opuntia in this way has spread from the Americas , where they naturally occur , to other regions where they grow , such as India .

Cochineal is a red dye produced by a scale insect that lives on species of Opuntia . Long used by the peoples of Central and North America , demand fell rapidly when European manufacturers began to produce synthetic dyes in the middle of the 19th century . Commercial production has now increased following a rise in demand for natural dyes .

Cacti are used as construction materials . Living cactus fences are employed as barricades . The woody parts of cacti , such as Cereus repandus and Echinopsis atacamensis , are used in buildings and in furniture . The frames of wattle and daub houses built by the Seri people of Mexico may use parts of Carnegiea gigantea . The very fine spines and hairs (trichomes) of some cacti were used as a source of fiber for filling pillows and in weaving .

= = Conservation = =

All cacti are included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which " lists species that are not necessarily now threatened with extinction but that may become so unless trade is closely controlled . " Control is exercised by making international trade in most specimens of cacti illegal unless permits have been issued , at least for exports . Some exceptions are allowed , e.g. , for " naturalized or artificially propagated plants " . Some cacti , such as all Ariocarpus and Discocactus species , are included in the more restrictive Appendix I , used for the " most endangered " species . These may only be moved between countries for scientific purposes , and only then when accompanied by both export and import permits .

The three main threats to cacti in the wild are development , grazing and over @-@ collection . Development takes many forms . The construction of a dam near Zimapan , Mexico , caused the destruction of a large part of the natural habitat of Echinocactus grusonii . Urban development and highways have destroyed cactus habitats in parts of Mexico , New Mexico and Arizona , including the Sonoran Desert . The conversion of land to agriculture has affected populations of Ariocarpus kotschoubeyanus in Mexico , where dry plains were plowed for maize cultivation , and of Copiapoa and Eulychnia in Chile , where valley slopes were planted with vines . Grazing , in many areas by introduced animals , such as goats , has caused serious damage to populations of cacti (as well as other plants) ; two examples cited by Anderson are the Galápagos Islands generally and the effect on Browningia candelaris in Peru . Over @-@ collection of cacti for sale has greatly affected some species . For example , the type locality of Pelecyphora strobiliformis near Miquihuana , Mexico , was virtually denuded of plants , which were dug up for sale in Europe . Illegal collecting of cacti from the wild continues to pose a threat .

Conservation of cacti can be in situ or ex situ . In situ conservation involves preserving habits through enforcement of legal protection and the creation of specially protected areas such as national parks and reserves . Examples of such protected areas in the United States include Big Bend National Park , Texas ; Joshua Tree National Park , California ; and Saguaro National Park , Arizona . Latin American examples include Parque Nacional del Pinacate , Sonora , Mexico and Pan de Azúcar National Park , Chile . Ex situ conservation aims to preserve plants and seeds outside their natural habitats , often with the intention of later reintroduction . Botanical gardens play an important role in ex situ conservation ; for example , seeds of cacti and other succulents are kept in long @-@ term storage at the Desert Botanical Garden , Arizona .

= = Cultivation = =

The popularity of cacti means many books are devoted to their cultivation . Cacti naturally occur in a wide range of habitats and are then grown in many countries with different climates , so precisely replicating the conditions in which a species normally grows is usually not practical . A broad distinction can be made between semidesert cacti and epiphytic cacti , which need different conditions and are best grown separately . This section is primarily concerned with the cultivation of semidesert cacti in containers and under protection , such as in a greenhouse or in the home , rather than cultivation outside in the ground in those climates that permit it . For the cultivation of epiphytic cacti , see Cultivation of Schlumbergera (Christmas or Thanksgiving cacti) , and Cultivation of epiphyllum hybrids .

= = Growing medium = =

The purpose of the growing medium is to provide support and to store water , oxygen and dissolved minerals to feed the plant . In the case of cacti , there is general agreement that an open medium with a high air content is important . When cacti are grown in containers , recommendations as to how this should be achieved vary greatly ; Miles Anderson says that if asked to describe a perfect growing medium , " ten growers would give 20 different answers " . Roger Brown suggests a mixture of two parts commercial soilless growing medium , one part hydroponic clay and one part coarse

pumice or perlite , with the addition of soil from earthworm castings . The general recommendation of 25 ? 75 % organic @-@ based material , the rest being inorganic such as pumice , perlite or grit , is supported by other sources . However , the use of organic material is rejected altogether by others ; Hecht says that cacti (other than epiphytes) " want soil that is low in or free of humus " , and recommends coarse sand as the basis of a growing medium .

= = = Watering = = =

Semi @-@ desert cacti need careful watering . General advice is hard to give , since the frequency of watering required depends on where the cacti are being grown , the nature of the growing medium , and the original habitat of the cacti . Brown says that more cacti are lost through the " untimely application of water than for any other reason " and that even during the dormant winter season , cacti need some water . Other sources say that water can be withheld during winter (November to March in the Northern Hemisphere) . Another issue is the hardness of the water ; where it is necessary to use hard water , regular re @-@ potting is recommended to avoid the build up of salts . The general advice given is that during the growing season , cacti should be allowed to dry out between thorough waterings . A water meter can help in determining when the soil is dry .

= = = Light and temperature = = =

Although semi @-@ desert cacti may be exposed to high light levels in the wild , they may still need some shading when subjected to the higher light levels and temperatures of a greenhouse in summer . Allowing the temperature to rise above 32 ° C (90 ° F) is not recommended . The minimum winter temperature required depends very much on the species of cactus involved . For a mixed collection , a minimum temperature of between 5 ° C (41 ° F) and 10 ° C (50 ° F) is often suggested , except for cold @-@ sensitive genera such as *Melocactus* and *Discocactus* . Some cacti , particularly those from the high Andes , are fully frost @-@ hardy when kept dry (e.g. *Rebutia minuscula* survives temperatures down to ? 9 ° C (16 ° F) in cultivation) and may flower better when exposed to a period of cold .

= = = Propagation = = =

Cacti can be propagated by seed , cuttings or grafting . Seed sown early in the year produces seedlings that benefit from a longer growing period . Seed is sown in a moist growing medium and then kept in a covered environment , until 7 ? 10 days after germination , to avoid drying out . A very wet growing medium can cause both seeds and seedlings to rot . A temperature range of 18 ? 30 ° C (64 ? 86 ° F) is suggested for germination ; soil temperatures of around 22 ° C (72 ° F) promote the best root growth . Low light levels are sufficient during germination , but afterwards semi @-@ desert cacti need higher light levels to produce strong growth , although acclimatization is needed to conditions in a greenhouse , such as higher temperatures and strong sunlight .

Reproduction by cuttings makes use of parts of a plant that can grow roots . Some cacti produce " pads " or " joints " that can be detached or cleanly cut off . Other cacti produce offsets that can be removed . Otherwise , stem cuttings can be made , ideally from relatively new growth . It is recommended that any cut surfaces be allowed to dry for a period of several days to several weeks until a callus forms over the cut surface . Rooting can then take place in an appropriate growing medium at a temperature of around 22 ° C (72 ° F) .

Grafting is used for species difficult to grow well in cultivation or that cannot grow independently , such as some chlorophyll @-@ free forms with white , yellow or red bodies , or some forms that show abnormal growth (e.g. , cristate or monstrose forms) . For the host plant ? the " stock " ? growers choose one that grows strongly in cultivation and is compatible with the plant to be propagated ? the scion . The grower makes cuts on both stock and scion and joins the two , binding them together while they unite . Various kinds of graft are used ? flat grafts , where both scion and stock are of similar diameters , and cleft grafts , where a smaller scion is inserted into a cleft made in

the stock .

Commercially , huge numbers of cacti are produced annually . For example , in 2002 in Korea alone , 49 million plants were propagated , with a value of almost US \$ 9 million . Most of them , 31 million plants , were propagated by grafting .

= = = Pests and diseases = = =

A range of pests attack cacti in cultivation . Those that feed on sap include : mealybugs , living on both stems and roots ; scale insects , generally only found on stems ; whiteflies , which are said to be an " infrequent " pest of cacti ; red spider mites , which are very small but can occur in large numbers , constructing a fine web around themselves and badly marking the cactus via their sap sucking , even if they do not kill it ; and thrips , which particularly attack flowers . Some of these pests are resistant to many insecticides , although there are biological controls available . Roots of cacti can be eaten by the larvae of sciarid flies and fungus gnats . Slugs and snails also eat cacti .

Fungi , bacteria and viruses attack cacti , the first two particularly when plants are over @-@ watered . Fusarium rot can gain entry through a wound and cause rotting accompanied by red @-@ violet mold . " Helminosporium rot " is caused by *Bipolaris cactivora* (syn . *Helminosporium cactivorum*) ; *Phytophthora* species also cause similar rotting in cacti . Fungicides may be of limited value in combating these diseases . Several viruses have been found in cacti , including cactus virus X. These appear to cause only limited visible symptoms , such as chlorotic (pale green) spots and mosaic effects (streaks and patches of paler color) . However , in an *Agave* species , cactus virus X has been shown to reduce growth , particularly when the roots are dry . There are no treatments for virus diseases .