Chapter 11. **Cactaceae: The cactus family**
The cactus family:

Cactaceae

General physiognomy. Plants with enlarged, fleshy green photosynthetic stems studded with clusters of spines arranged in rows or in spirals along the stem and producing showy, multi-petaled flowers with numerous stamens and an inferior ovary.

Vegetative morphology. Cacti in California are all leafless (some tropical cacti in the genus *Pereskia* have large leaves), and grow as stem-succulent plants varying from small globose individuals 3–5 cm in diameter to giant columnar stems 50 cm in diameter and sometimes 10 or more meters tall. In the prickly pears (genus *Opuntia*) the stems are flat and have determinate growth, producing a chained series of oblong or circular pads called cladodes. Leaves are usually transformed into spines and clustered into sharp, prickly bundles called areoles, derived from axillary buds and located at the nodes of the stems. Areoles are arranged along the stem in rows or in spirals. In large cacti, such as the saguaro, the stems are ribbed longitudinally in distinct rows, while in small globose cacti the areoles are arranged spirally around the stem usually sitting on tightly-packed, prominent nipple-like tubercles. Each areole features several to many radiating spines that may have different colors.

Reproductive morphology. Flowers are usually large and showy, often arranged in a circle near the top crown of the stems. Flowers may be white, cream-colored, yellow, pink, rose-red, greenish, brownish, or other colors. Flowers display numerous spirally-arranged sepals that grade into numerous petals, together with numerous separate stamens and a single pistil with an inferior ovary and many fingerlike stigma lobes. The fruits are berries, often very fleshy and sweet, commonly bright red or yellow when ripe. Because the ovary is inferior, the fruits, like the stems, are covered with areoles (clusters of spines).

Taxonomic relationships. Few other families are likely to be confused with the cacti, which are easily identified by the combination of showy, multi-petaled flowers and highly modified, succulent stems with spines. Some confusion may exist with ocotillo (*Fouquieria splendens*) in the boojum-tree family (Fouquieriaceae), which has cactus-like stems lined with spines. However, the stems are not truly fleshy, the plants do not have spiny areoles but rather the spines develop from the petiole of single leaves, and the flowers are tubular, with five fused petals, and have a superior ovary. Ocotillo occurs in the Sonoran Desert of California and in many drylands in Mexico.

Biodiversity and distributions. Around 2,000 species confined —with one exception— to the New World (the exception is *Rhipsalis baccifera*, a native of the Tropical Americas that is also found naturally occurring in Madagascar and Sri Lanka). The range includes southern Canada, the United States, Mexico, Central America, and South America. The greatest diversity is found in Mexico and in the dry highlands of South America. Several species are epiphytes in tropical forests, but the majority favors hot tropical drylands and deserts.

Ecology. *CAM photosynthesis*. Cacti have a very particular mode of photosynthesis, known as crassulacean acid metabolism, or CAM photosynthesis. CAM is a carbon fixation pathway that evolved as an adaptation to arid conditions. The stomata (gas-exchange pores) remain shut during the day to reduce evapotranspiration, but open at night, when temperatures and evaporative demand are lower, to collect carbon dioxide (CO₂). The CO₂ is stored in the form of four-carbon malic acid (C₄H₆O₅) in vacuoles at night, and then in the daytime the malic acid is transported to chloroplasts where it is used for photosynthesis to build larger and more complex organic molecules. This metabolism occurs mainly on succulent species.
The “nurse plant” effect. Because cacti have their stomata (epidermal pores) closed during the day, they cannot use transpiration, i.e., the evaporative loss of water, to thermoregulate and mitigate the lethal temperatures of the desert at ground level. Many columnar cacti establish and survive by germinating under the protective shade of larger trees that play the role of “nurse” plants, creating a shaded microhabitat where the cactus may develop and grow upwards, away from the sizzling ground-level temperatures. The nurse plant phenomenon has a large bearing in the context of ecological conservation: If the trees that serve as nurse plants, such as mesquite or ironwood, are cut, the regeneration of the cactus populations becomes seriously threatened. The conservation of the entire ecosystem is needed in order to protect and conserve threatened cacti.

The Cactaceae at a glance: (a) Green, succulent stems with leaves transformed into spines and arranged in spine-clusters (areoles). (b) Flower with multiple tepals transitioning from outer leaf-like bracts on to large showy petals; multiple stamens surrounding a columnar style that opens radially into multiple stigmas. Ovary inferior, containing many seeds surrounded by sweet fleshy arils. (c) Areoles, formed by highly transformed axillary buds with leaves transformed into spines, develop on elevated tubercles (coastal prickly pear, *Opuntia littoralis*).
Economic uses and ethnobotany. Prickly-pears (*Opuntia*) have been cultivated since pre-Hispanic times by many native groups throughout the Americas. They yield sweet, juicy fruits, called *tunas*, that are consumed directly or made into jelly. Their newly-formed pads are harvested in springtime and cooked as vegetables (*nopales*). Many other cacti are cultivated for their fruits, called *pitayas* in Mesoamerica. Among them, the scarlet-skinned and white-fleshed pitaya (*Hylocereus undatus*) is cultivated throughout the New World tropics and is highly appreciated in Asian markets, where it is called “dragon fruit.” Peyote (*Lophophora williamsii*), a small, spineless cactus of the Chihuahuan Desert, defends itself from predators with an assortment of toxic alkaloids, one of which, mescaline, is also strongly psychoactive and produces powerful hallucinations when ingested. Under the guidance of trained shamans, peyote and a handful of other hallucinogenic cacti are ingested during indigenous religious rituals. Besides their economic and medicinal uses, cacti are passionately cultivated by some plant lovers for their strange morphologies and beautiful flowers.

California genera and species. California has 66 species in 11 genera. Expectedly, only a few species are endemic to the winter-rain coastal California ecosystems, such as coastal sage scrub, chaparral, oak woodland, or conifer forests. The most common coastal-fringe cacti include the velvet cactus (*Bergerocactus emoryi*), the coastal prickly pear (*Opuntia littoralis*), and the valley cholla (*Cylindropuntia californica*). The highest diversity of cacti in California is observed in the dry inland deserts, east of the peninsular ranges and the sierras. Locally-common species include the following:

*Opuntia basilaris* (beavertail cactus) – A cold-tolerant prickly pear from the Mojave Desert, easily identifiable by its lack of long spines, velvety areoles, and showy purple flowers. Common in the mountains around Riverside and San Bernardino.

*Opuntia littoralis* (coastal prickly pear) – Common along the coasts and western slopes of Southern California, this species is clearly identified by its long, whitish, retrorse (backward-bent) spines and yellow flowers.

*Cylindropuntia californica* (syn. *Opuntia parryi*; valley cholla) – A cholla cactus (cylindrical stems) with unconspicuous pale-yellow to green flowers, common on the Pacific slopes of the peninsular ranges.
Carnegiea gigantea (saguaro) – A legendary giant columnar cactus from the Sonoran Desert, in California it is only present on a few patches along the border with Arizona.

Ferocactus cylindraceus (barrel cactus) – A massive, barrel-shaped cactus with yellow flowers, common in the dry mountain slopes of the Mojave and Lower Colorado deserts.

Mammilaria dioica (strawberry cactus) – A small, globose cactus with a disjunct distribution: A population survives on coastal cliffs and ridges from San Diego to Orange County, and a second population thrives on the dry eastern slopes of the peninsular ranges in San Diego and Riverside counties.