Chapter 7. The four-parted families

# The four-parted families:

# Brassicaceae, Onagraceae, and Papaveraceae

# BRASSICACEAE (Mustard Family)

**General physiognomy**. Herbaceous plants with 4 separate petals arranged like a cross, six stamens of 2 lengths, and a long, slender silique or a short, rounded silicle as their distinctive, 2-carpelled fruits. Because of the distinctive cross-like pattern of the petals, the family was also called the "Cruciferae" in the past for their cross-like petal arrangement. Most of the plants in this family have a characteristic tangy, or pungent, sharp flavor and smell, produced by a family of substances known as glucosinolates. The pungency of plants in this family is due to mustard oils produced from the glucosinolates when the plant material is chewed, cut or damaged. These natural chemicals contribute to plant defense against pests and diseases, but are also enjoyed in small amounts by humans and are believed to contribute to the health-promoting properties of these "cruciferous" vegetables. Most glucosinolates contain a sulfur atom in the molecule, which is sometimes released as sulfide when the plants are cooked, giving cauliflower and broccoli, for example, a distinctive "flatulence" smell as they boil in the kitchen.



The Brassicaceae at a glance: Sharp mustardy flavor, distinct cross-like petal arrangement, six tetradynamous stamens (four long, two short), superior 2-carpelled ovary with parietal placentation, fruit an elongated silique or a rounded silicle with a papery central partition (Illustration: *Brassica nigra*, "black mustard").

**Vegetative morphology**. Mostly herbaceous plants, with simple to pinnately-dissected leaves that, when crushed, often release a pleasant piquant odor and possess a mustardy flavor.

**Reproductive morphology.** The cross-like flowers are often arranged in racemes or panicles that keep growing and producing new flowers as the older ones ripen and yield fruit. The flower has 4 separate sepals; 4 separate, cross-like petals; six "tetradynamous" stamens (4 long and 2 short), and a superior, 2-carpelled ovary with parietal placentation. The fruits are long, slender siliques or short, round to squat silicles. The ovary and the fruit are separated lengthwise by a papery partition (a replum) that divides

the silique's chamber into two locules. The carpels dry and detach, leaving behind the seeds attached to the remaining placental veins along the suture lines.

**Taxonomic relationships**. Mustards are closely related to the caper family (Capparaceae), which is now often included as part of the mustard family. Capers differ in usually having palmately compound or divided, usually smelly, leaves, and a long-stalked gynophore on the flower that carries the ovary well beyond the petals. Several other families feature flowers with 4 petals but seldom in a crosslike arrangement, with 6 stamens of 2 lengths, or harboring the distinctive siliques of the Brassicaceae.

**Biodiversity and distributions**. Over 3,000 species with a worldwide distribution, most abundant in rocky places and mountains in the northern hemisphere. Diverse in the Mediterranean region and the Middle East.

**Economic uses and ethnobotany**. The family is of economic importance for its oil-yielding seeds and its vegetable crops. The main oil-producing crops are canola, *Brassica napus*, and rapeseed, *Brassica rapa*. The ability of some of these species to store nutrients and reserves in different parts of the plant has led to some extraordinary cases of selective breeding throughout history. For example, cabbage, broccoli, kale, Brussel sprouts, cauliflower, and kohlrabi, as different as they may look, are all varieties of only one species, *Brassica oleracea*. Similarly, turnip roots, turnip greens, bok-choy, rapini, and napa cabbage are all varieties of *Brassica rapa*, widely cultivated in Asia and central Europe. Other useful species in the family include watercress, arugula, radish, rutabaga, horseradish, wasabi, and various species producing piquant seeds used to make mustard condiments. For its ease of cultivation, *Arabidopsis thaliana*, a small, fast growing annual plant, has become a preferred organism for scientists in molecular and genomic studies, and is currently the most important model species in the study of the molecular biology of flowering plants.

Darwin in the kitchen: The domestication of the Brassicaceae



One of the most distinctive features of the Brassicaceae is the presence of a group of chemicals called **glucosinolates**, which give the plants in this family their characteristic pungent, or "piquant", taste. The glucosinolates themselves are tasteless, but when the cell is damaged an enzyme in the cytoplasm gets in contact with the glucosinolate molecule in the vacuoles and breaks it into glucose and sulfur cyanate called **mustard oil**. Mustard oil is toxic for most insects, and acts as a natural defense against herbivores. Glucosinolates are also present in taxa related to the Brassicaceae, such as the caper and the nasturtium families (the tangy taste of cooking capers and nasturtium flowers is due to their presence). We can accept, thus, that glucosinolates as defense chemicals evolved in this lineage before the bifurcation of these related families, around

80 million years ago. In that extremely long period of time insects have had the opportunity to evolve some counterdefense against the toxic effect of glucosinolates. A group of butterflies in the genus *Pieris* gradually adapted to the consumption of plants laden with mustard oil, developing the metabolic mechanisms to detoxify the mustard oil. The pesky *Pieris brassicae* and *Pieris rapa*, or "cabbage butterflies" as they are normally called, are now the nemesis of cabbage farmers all over the world. Their success is deeply rooted in millions of years of coevolution with the Brassicaceae: Like the monarch butterflies, who have evolved a metabolism that allows them to eat the lethally toxic milkweeds and store the poisonous alkaloids in their bodies as an anti-predator defense, some pierid butterflies can store the toxic mustard oil in their bodies as a defense against any bird that

It so happens that mustard oil, in moderate amounts, is not toxic to humans. We even seem to enjoy the pungent taste of cabbage, arugula, water cress, horse radish, or wasabi, and our digestive system is able to metabolize the glucosinolates without much consequence. So now, 80 million years after glucosinolates evolved as an anti-herbivore strategy, we fight and compete with the cabbage butterflies for the privilege of eating plants rich in mustard oils.

Glucosinolate structure (the side group R varies in the different species)

### Artificial selection and Brassica oleracea

#### "Cauliflower is nothing but cabbage with a college education." Mark Twain

Farmers have selected the most desirable plants for thousands of years. In so doing they domesticated some nutritionally important species, changing them over generations into the varieties that modern people recognize as our primary food plants.

Some species have undergone the domestication process multiple times, each domestication effort focusing on selecting different structures of the plant, producing a diversity of extraordinarily different vegetables or fruits from the same wild progenitor. The wild mustard (*Brassica oleracea*) is a weedy herbaceous plant of the Mediterranean region. It has a biennial growth form, storing reserves over the winter in its basal rosette to produce a raceme of yellow flowers at the end of its second summer before setting seed and dying. Farmers over the last several thousand years have domesticated several distinct lineages of *Brassica oleracea*, each amplifying different parts of the plant to produce several vegetable varieties such as kale and collard greens, Chinese broccoli, red and green cabbages, savoy cabbage, kohlrabi, Brussels sprouts, broccoli, and cauliflower. These varieties look so dramatically different that, for the untrained eye, they could be seen as entirely different species. In reality, however, they are

genetic variants of the same species and they are interfertile, that is, capable of mating with one another and producing fertile offspring.

Briefly, these are the parts that have been expanded in the different cultivated varieties or "cultivars": Kale, collard greens and Chinese broccoli have been selected for their large, expanded, nutrient-rich leaves. Cabbages and savoy cabbages are lineages selected for large terminal buds in the rosette. Brussels sprouts, in contrast, are the result of selection for large, expanded axillary buds in the flowering stem. Kohlrabi, on the other hand, is the result of selection for large, succulent stems in the vegetative rosette. Finally, broccoli and cauliflower are the result of selection for fleshy inflorescences.



If the flowers are consumed in some varieties, where do the farmers get the seeds to plant cauliflower and broccoli for example? Do these artificially-selected, soft, crowded inflorescences give any seed at all? The answer is yes, they do give seed. Even these varieties with mutated, deformed inflorescences will develop normal flowers and give fertile seed if left unharvested. The edible inflorescences are collected by farmers well before the flower buds mature and open into typical mustard flowers. So, if a cauliflower is left to develop instead of being picked when the inflorescence head (the "curd") is soft and dense, the inflorescence will continue developing and elongating until some of the floral buds produce fertile flowers.

**California genera and species**. The region has 63 genera with many species. Several are nonnative and weedy or garden escapes.

Stanleya pinnata (prince's plume) – Showy perennial herb or shrub producing several erect stems reaching up to 1.5 meters. The top of the stem is occupied by a long, dense raceme of yellow flowers.	
<i>Thysanocarpus curvipes</i> (fringepod) – Small, slender plants with white flowers in dense racemes. Fruit a rounded-oblong, non-dehiscent silicle.	
<i>Raphanus sativus</i> (wild radish) – The wild form of cultivated radish, this is a non-native weed of European origin. Flowers pinkish-white to lavender, and the swollen, ripe siliques break transversely.	
Sisymbrium altissimum (tumble mustard) – Easily recognizable by its two distinct leaf forms: deeply lobed in the basal rosette and threadlike in the stem. Flowers yellow.	
<i>Brassica nigra</i> (black mustard) – Old World weed that has invaded California. Yellow flowers in a terminal slender raceme, fruits long, narrow siliques with an apical beak formed by the style.	

# **ONAGRACEAE** (Evening Primrose Family)

**General physiognomy**. Herbaceous plants with simple leaves and showy flowers with 4 petals, 4 or 8 stamens, and an inferior ovary.



**Vegetative morphology**. Herbaceous annuals and perennials and simple, sometimes lobed, basal, alternate, or opposite leaves.

**Reproductive morphology.** Showy actinomorphic corollas, usually white, pink, or yellow, cup- or saucershaped, growing solitary or in terminal racemes. The flower has four separate sepals and four separate petals; 4 or 8 stamens partially joined to a tubular hypanthium, and an inferior, four-chambered ovary. The fruit is an elongated, four-chambered capsule with many seeds. The carpels open gradually to release the seeds to the ground with each rain event.

**Taxonomic relationships**. Only a few families consistently have flowers with parts in fours and separate petals. The most diverse is the mustard family (Brassicaceae, with the closely related caper family, Capparaceae), and the poppy family (Papaveraceae). However, all those families have superior ovaries and 6 tetradynamous stamens, in the Brassicaceae, or multiple stamens, in the Papaveraceae.

**Biodiversity and distributions**. The family is widely distributed, with the greatest diversity in western North America and the mountains of tropical America, and it harbors some 700 species. Many are garden ornamentals, the most popular of which is the genus *Fuchsia* from Mexico to South America, and widely cultivated in gardens worldwide. Other garden ornamentals include evening-primroses (*Oenothera* spp.), clarkias and godetias (*Clarkia* spp.), and the California fuchsia (*Epilobium canum*).

**Economic uses and ethnobotany**. The only known use for plants in this family is as ornamental garden plants.

**California genera and species**. The region has eight native genera. Some of the most common plants in the Inland Empire include the following:

<i>Oenothera californica</i> (evening primrose) – Herba- ceous, long-lived, clone-forming plant with large white-pinkish flowers.	
<i>Camissonia bistorta</i> (suncups) – Spreading annual with bright yellow flowers, common on dry sandy soils thoughout the Inland Empire region.	
<i>Clarkia purpurea</i> (clarkia) – Common spring annual throughout the Santa Ana River Basin, flowers bright lavender-red.	
<i>Epilobium ciliatum</i> (willow herb) – Somewhat weedy, herbaceous root-perennial. Widespread along road banks and disturbed sites, white tiny flowers that turn pink as they age.	

### PAPAVERACEAE (Poppy Family)

**General physiognomy**. The plants may be annual, biennial, or perennial. Usually herbaceous, a few species form shrubs. The simple leaves are alternate or sometimes whorled, usually lobed or much divided. Flowers with caducous sepals that pop off as petals open; sepals are half the number of petals. Multiple, often bright-colored stamens.



The Papaveraceae at a glance: Herbaceous plants or woody shrubs with 4-petalled actinomorphic corollas, six-to-numerous stamens, a many-carpelled superior ovary, and only 2 sepals, which are fused and form a green "hat" (calyptra) that covers the flower bud and is shed as the petals unfold. Fruit a many-seeded capsule (Illustration: *Eschscholzia californica*, "California poppy").

**Vegetative morphology**. Herbaceous annuals, perennials, or small shrubs. The plants are lactiferous, producing a caustic latex that may be milky or watery, coloured or plain. In some species the sap contains opiates. Leaves variable in shape, in several genera they are highly dissected and fernlike.

**Reproductive morphology.** Flowers mostly solitary, showy, with 4 petals (six in some species) forming a saucer-shaped corolla; 2 or 3 separate sepals that often fall away as the flowers open, 4 or 6 separate petals in an actinomorphic corolla, or 4 petals in two series forming a zygomorphic corolla. Stamens 6 to numerous, and a single pistil with a superior ovary. Plants with numerous stamens lack nectar and offer pollen as a reward to bees; those with 6 stamens and zygomorphic flowers produce nectar, and the larger pair of petals is saclike or spurred at the base. In all species the fruit is a capsule, sometimes releasing seeds explosively.

**Taxonomic relationships**. Other families with numerous stamens and wide open flowers often have several separate pistils or, for those with a single pistil, sepals that remain on the flower after it has opened. The fumitory family (Fumariaceae) is now included in the Papaveraceae because of the similar chemistry of its poisonous compounds and similar leaf design. Most of the poppies have regular

(actinomorphic) corollas, and multiple stamens. The fumitory branch of the poppy family is distinguished by its irregular, often spurred flowers, fixed number of stamens, and petals that are partly joined.

**Biodiversity and distributions**. The Papaveraceae are an economically important family with 44 genera and approximately 770 species of flowering plants worldwide. The family is cosmopolitan, occurring in temperate and subtropical climates, mostly in the northern hemisphere; a few live in the highlands of the tropics.

**Economic uses and ethnobotany**. The opium poppy (*Papaver somniferum*) has a long history of use for its opium-derived compounds and its seeds, which are widely used in baking. Opium, or "poppy tears", is the dried latex obtained from incisions in the green capsules of the opium poppy. Opium latex contains approximately 12% of the analgesic alkaloid morphine, which is processed chemically to produce heroin and other opioids. The latex also contains the closely related opiate codeine, used in the pharmaceutical to produce cough-suppressants and pain-killers. In modern times, other alkaloids that are used as raw material for the manufacturing of other semisynthetic opiates are obtained from the closely related *Papaver orientale* or *Papaver bracteatum*.

Due to the extent of ground disturbance in warfare during World War I, corn poppies (*Papaver rhoeas*, an agricultural weed) bloomed in between the trench lines on the Western front. Immortalized in the poem "In Flanders Fields" by John McCrae, corn poppies became a 20<sup>th</sup> Century symbol of remembrance for war casualties: "In Flanders fields the poppies blow / between the crosses, row on row..."

The family is also noted for many handsome garden flowers including poppies (*Papaver* spp.), California poppy (*Eschscholzia califomica*), and bleeding hearts (*Dicentra* spp.).

# Darwin in the drugstore: The evolution of latex in poppies



Plants have evolved physical defenses that are exuded from open wounds when the plant is attacked and protect the plant from herbivores or wood borers. These exudates are classified into three different types: resins, gums, and latex.

**Resins** are thick, sticky exudates formed by a complex mixture of terpenes, a group of organic compounds that are insoluble in water but soluble in organic solvents. Most commercial resins are obtained from the frankincense family (Burseraceae) and from the pine family. In contrast with resins, which are transported through the plant in specialized ducts, gums are produced *in situ* as a result of damage to the tissues. Gums consist of short chains of carbohydrates (polysaccharides) from the cellular walls of the damaged tissue that get hydrolyzed and dissolve in the plant's sap when the cells get damaged. They are rich in pectin, the same carbohydrate that thickens fruit spreads and marmalades, and

which forms a gel when dissolved in water. Finally, **latex**, in its raw form, is normally a milky-white liquid that consists of tiny droplets of organic matter suspended in an aqueous medium forming a colloid that looks very much like milk. The most well-known example is rubber latex from the tropical tree *Hevea braziliensis*. The colloidal particles suspended in latex can normally be coagulated to form a solid mass by boiling the latex or by simple evaporation. The principal components of the coagulum are isoprene polymers, which confer the typical rubbery elasticity to solidified latex. The main function of resins, gums, and latex is simply to physically provide a healing clot, a dry crust that closes the wound and prevents exposing live tissue to further attacks thus minimizing further damage. Additionally, because of their liquid nature latexes are often endowed with dissolved toxins and can be extremely poisonous, playing the double role of a physical healing agent and an anti-herbivore deterrent.

Like many other species in the family, the opium poppy *Papaver somniferum* is endowed with potent toxic alkaloids that run in its latex ducts mixed with the rubber-like isoprene polymers. If the latex ducts, or laticifers, are cut in the green seed pods they start

to bleed drops of latex from the incision, which dry around the wound. This dry latex, in its raw form, is called **opium**. Raw opium contains, apart from the rubbery latex, a complex array of toxic alkaloids —collectively called opiates— that include strongly psychotropic substances such as morphine, codeine, thebaine, and papaverine. Humans have learned from early times that, despite their toxicity, opiates in sufficiently low doses have sedative properties, inducing sleep and numbing painful sensations. Hence the Latin epithet *somniferum*, which means "sleep-bringing", given by Linnaeus to the opium poppy. From raw opium pure forms of the constituent alkaloids can be isolated by re-crystalization. This is the mechanism used to obtain strong sedatives, such as morphine or codeine, used in pure form for medicinal purposes. Morphine, in turn, may be modified chemically to produce synthetic opioids such as heroin.

Opium demonstrates in a classical manner the way humans have learned to manipulate toxic plants and regulate the dosage of alkaloids to transform their evolutionary role —anti-herbivore toxicity— into medicinal uses. Dilution and regulated dosage have been for millennia the tools of traditional medicine, a way to use toxic plants that, consumed in uncontrolled form, could kill us.

**California genera and species**. The region has 12 native genera and two nonnative genera. *Eschscholzia californica* (the California poppy) is native to the region and is the official state flower of California. Some botanists and historians believe that the massive golden blooms of California poppies in places such as Antelope Valley are what earned the symbolic name "Golden State" for California.

<i>Eschscholzia californica</i> (California poppy) – Annual with highly divided, fern-like leaves. Flowers golden- orange, fruit a long, slender capsule.	
<i>Dendromecon rigida</i> (bush poppy) – Woody shrub of chaparral, with simple, leathery leaves. The yellow flowers and elongate capsules resemble those of the California poppy.	
<i>Romneya coulteri</i> (matilija poppy) – Perennial bush with showy large flowers of white petals and orange- yellow stamens. Common in chaparral.	
<i>Dicentra chrysantha</i> (golden eardrops) – Herbaceous perennial with numerous flowering stalks and dense racemes of zygomorphic yellow flowers.	