Chapter 5. **The five-parted families**

The five-parted families:

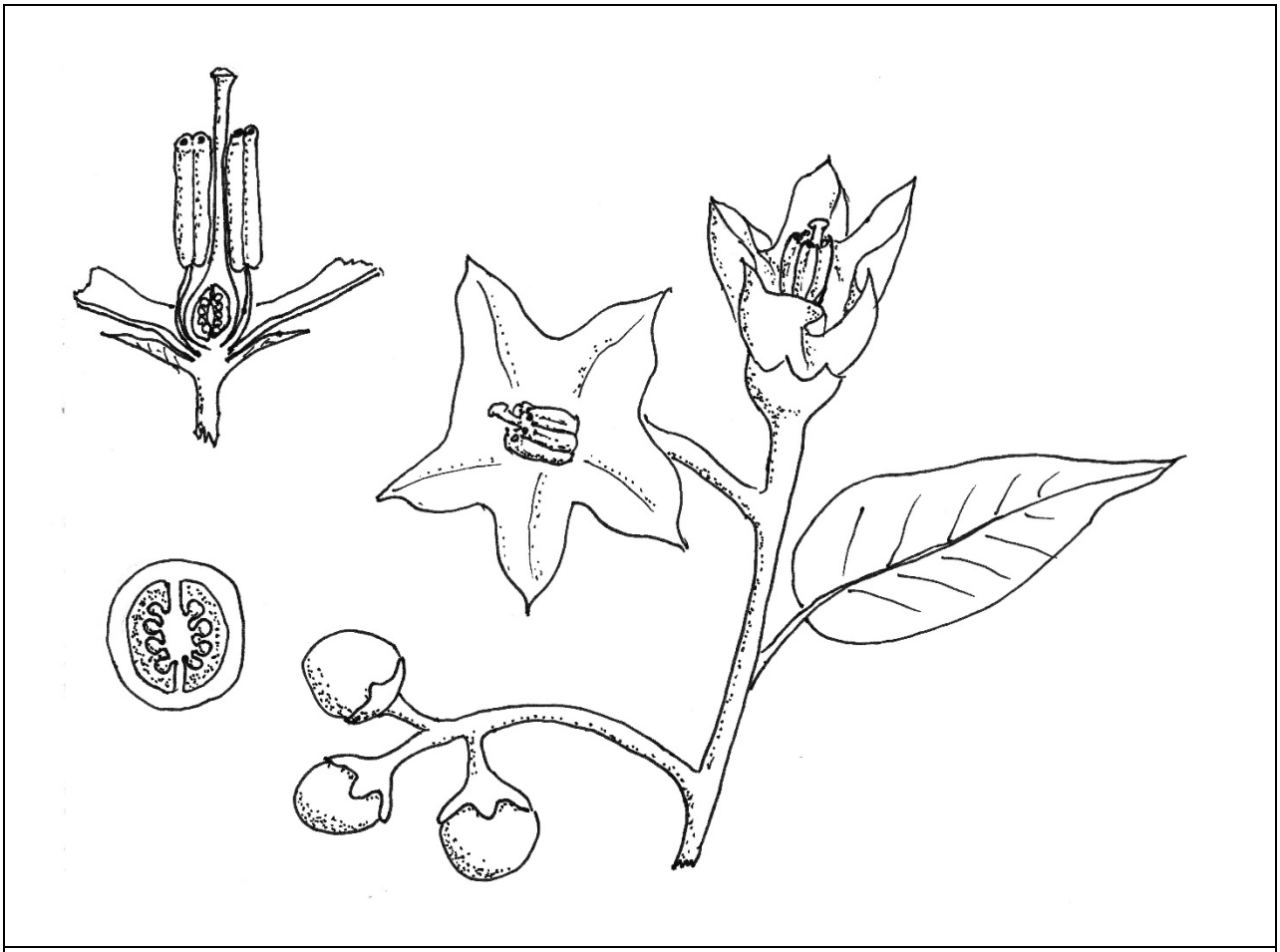
SOLANACEAE, HYDROPHYLLACEAE, BORAGINACEAE, LAMIACEAE, AND SCROPHULARIACEAE

SOLANACEAE (Nightshade Family)

General physiognomy. Plants with often foul-smelling, alternate leaves; saucer-, trumpet-shaped, or tubular flowers with pleated petals; fruit often a fleshy berry or a many-seeded capsule.

Vegetative morphology. Annuals, herbaceous perennials, or small shrubs with simple, alternate, often foul-smelling leaves.

Reproductive morphology. Flowers usually showy, saucer- or funnel-shaped or tubular, and in varied arrangements. Sepals 5, partly fused, petals 5, mostly fused and pleated in the bud, 5 stamens joined to the petals, anthers commonly connivent and with poricide dehiscence, a single pistil with a superior (usually) two-chambered ovary. Fruits are (usually) 2-carpelled berries and capsules, with many seeds.



The Solanaceae at a glance: Foul-smelling plants with alternate leaves, pleated (or plicate) petals in the opening flower bud, connivent anthers with poricidal dehiscence, ovary superior with two carpels and many ovules, axile placentation. Fruit a two carpelled berry or capsule (Illustration: *Solanum parishii*, "purple nightshade").

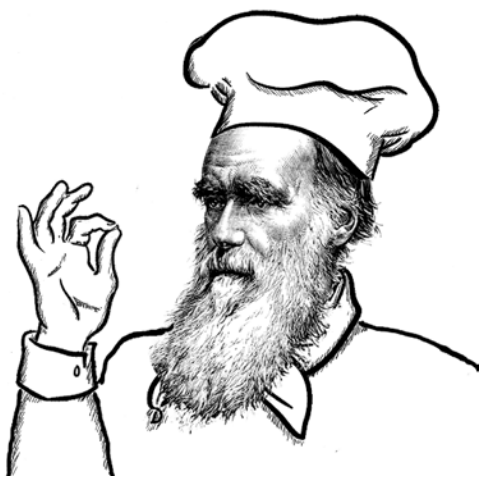
Taxonomic relationships. The flower design of many nightshades resembles morning glories (Convolvulaceae), including the pleated petals, but differences include the milky juice, vininess, and few seeds per capsule typical of the morning glory family. A few members of the snapdragon family (Scrophulariaceae), such as mulleins (*Verbascum* spp.), have nearly regular flowers that also suggest this family, but scrophs do not have pleated petals and never have fleshy berries.

Biodiversity and distributions. About 3,000 species of worldwide distribution, most diverse in the tropical Americas.

Economic uses and ethnobotany. The family is famous for its toxic compounds, including several alkaloids that in tiny doses are used medicinally. *Atropa belladonna*, the deadly nightshade, native to the Northern Hemisphere contains alkaloids that cause delirium and hallucinations. One of these compounds, atropine, is used by doctors as a muscle relaxant to dilate the pupils or control nausea. The European *Mandragora officinarum*, or mandrake, also contains highly toxic, delirium-inducing hallucinogenic alkaloids. Because the shape of their roots, which often resemble human figures, they have been associated with magic rituals throughout history. Similarly, the stramonium or Jimson-weed (*Datura stramonium*), also a powerful hallucinogen, is used in small doses to relieve asthma and as an analgesic, but can be fatal if slightly overdosed.

The family also has several major food plants including potatoes (*Solanum tuberosum*), tomatoes (*S. esculentum*), eggplants (*S. melongena*), tomatillos (*Physalis ixocarpa*), and chili peppers (*Capsicum annuum*, *C. frutescens*, *C. sinense*, and *C. baccatum*). Several ornamentals, particularly shrubs, include angel's trumpets (*Brugmansia* spp.), petunias, and nightshades, among many others.

Darwin in the kitchen: The domestication of the Solanaceae



Darwin realized that the same mechanisms that have shaped species through natural selection are in operation when farmers select forms of plants that are better for human consumption: non-toxic, more nutritious, easier to cultivate, or better adapted to specific climates. This process is called domestication, and it operates in the same manner as natural selection in the wild. In domestication, the farmer becomes the main force of selection, by saving every season the seeds of the plants with the more desirable traits and re-planting them again the next season. After a few generations of simple genetic selection, the plant starts to show exclusively the traits for which it was selected. One of the most fascinating cases of domestication can be seen in the Solanaceae, the nightshade family.

In the wild, most members of the family are mostly spineless and soft but contain potent secondary compounds or alkaloids that make them fetid or poisonous. Some are highly toxic, especially if their leaves are consumed, and others may have psychotropic properties in low doses (but can be deadly in higher concentrations!). However, the fruits of most (but not all!) of these plants are not toxic and can be safely eaten. In evolutionary terms, this is the result of a long process of natural selection. The alkaloids in the foliage deter herbivores from consuming their leaves, but the fruits are largely harmless allowing frugivores to eat them and disperse the seeds.

Despite their legendary toxicity, many species in this family, such as tomatoes, tomatillos, potatoes, eggplants, and chili peppers, are widely consumed. Have you ever wondered why we eat tomatoes, for example, but we do not consume tomato leaves in the form of greens? The reason is that foliage of all plants in the genus *Solanum* and allied genera (tomatoes, tomatillos, potatoes, and eggplant) contain in their leaves a very toxic and rather bitter glycol-alkaloid called solanine. Solanine and other toxic alkaloids are present in the tubers of wild potatoes, a fact

that forced early farmers in the Andes to freeze-dry, wash, and boil the potatoes for a long time to get rid of its toxicity. It is also often present in the unripe form of wild tomatoes, possibly as an adaptation that deters fruit-consumers to eat the berries before they are ready for seed dispersal. Through crop selection along thousands of years, humans have obtained varieties whose fruits and tubers are less toxic and can be eaten without risk. The leaves of these plants, however, are often still be quite toxic and should be avoided.

Plants in the genus *Nicotiana* contain a pyrrolidine alkaloid called nicotine, produced in large quantities in the tobacco plant (*Nicotiana tabacum*). In the wild, nicotine acts as a defense against herbivores, as it is a very effective neurotoxin especially against insects. In fact, boiled tobacco leaves (tobacco "tea") have been used for centuries as a very effective insecticide. At low concentrations, however, nicotine acts as a stimulant in mammals causing the well-known dependency in smokers.

Plants in the non-edible genera of the family contain a group of alkaloids known with the generic name of tropanes, named after the Greek goddess of fate, Atropos, who cut the thread of life and decided the end of human existence (this simple etymology should be enough to emphasize the sheer lethality of these compounds). Like nicotine, these alkaloids have evolved as an effective anti-herbivore defense, but they have been used repeatedly along human history both as poisons and, in lower doses, as medicinal or psychotropic plants. Tropanes include important medicinal compounds such as atropine, scopolamine, and hyoscyamine. They are found in various species, many of which have been associated historically to witchcraft, sorcery, or medieval alchemy, such as mandrake (*Mandragora autumnalis*), black henbane (*Hyoscyamus niger*), belladonna (*Atropa belladonna*), stramonium (*Datura stramonium*), and angel trumpet (*Brugmansia* sp.), among others.

A last alkaloid in the nightshade family is capsaicin, present in chili peppers of the genus *Capsicum*. The fascinating evolution of chilies deserves a separate description.

A burning question: The natural history of chili peppers

For over 6,000 years, humans have used chili peppers to add a spicy kick to their meals. Not only does chili spice add heat and flavor to our meals, it also deters microorganisms from spoiling food. Native peoples in the Americas have been breeding chilies for their flavor and spice for millennia. We humans now cultivate five different species of chilies, and all five contain the same spicy alkaloid, a compound called capsaicin. All other mammals, with the exception of humans, avoid wild chilies because they cannot tolerate the fiery spiciness of the fruits. This begs an interesting evolutionary question: why did chilies start making capsaicin in the first place? If dispersal of the seeds is the evolutionary reason for the fruits, why would any plant endow the fruits with an alkaloid that deters mammals from consuming them? Or, from an evolutionary perspective, what advantage does hot spicy-ness offer the plants that produce chilies?

Experiments have shown that small mammals (mostly rodents) avoid wild chilies, but many birds eat them with gusto. Birds do not chew the small fruits of the wild chilies but rather swallow them entire and grind them later in their gizzard, where they lack the taste receptors for capsaicin. Rodents, in contrast, chew the fruits they consume, like any other mammal, and have very sensitive taste receptors. When capsaicin binds to the receptor channel in their taste buds, it triggers calcium ions to enter nearby neurons resulting in that characteristic burning sensation (the same receptor is used by our body to detect burning temperature in food, and for this reason chilies give us a burning "hot" sensation, a reaction quite similar to the typical temperature-induced perspiration and rubefaction or red face).

A thrasher in Bolivia consuming wild chilies (photo credit: Joshua Tewksbury)

This is really a neat evolutionary adaptation for the *Capsicum* plants. When rodents eat chili seeds grinding them with their molars, most seeds are destroyed and unable to germinate. Consumption by birds like thrashers, on the other hand, allows the seeds to pass unharmed through the digestive tract of the birds. This ability to select one group of frugivores over other makes sense, because birds travel much longer distances than local burrowing mammals, and are important seed dispersers for many plants. Chilies direct their spice at rodents that grind up their seeds, while encouraging birds to disperse their seeds far away.

So birds, who scatter seeds far afield in their droppings, appear to be immune to the fiery flavor of chilies, but mammals, who are less efficient at spreading the plant's seeds, find the taste unbearable. Only humans have been able to tame the chilies' burning hot zest by using them not in pure form but rather as a spice, a food preservative, and a stimulant of flavor in otherwise dull food items.

California genera and species. The region has nine native or partly native genera and four nonnative genera. Locally-common species include the following:

Datura wrightii (toloache, Jimson weed) – A common perennial with velutinous (softly pubescent, or velvety) foliage, common in rocky slopes and sandy areas. The flower is large, white with pink- or blue-tinted margins, fruit a spiny capsule.

Nicotiana glauca (tree tobacco) – A slender shrub with glaucus, bluish-green leaves, often foul-smelling. Flowers with a long tubular corolla, very attractive to hummingbirds. Somewhat weedy, non-native.

Solanum elaeagnifolium (horse nettle) – A herbaceous weed with stiff spines; capable of perennating from underground rhizomes it is a serious pest of pastures and cultivated lands in California. Colorful lavender flowers, fruit a berry that dries in the plant and becomes capsule-like.

Solanum parishii (purple nightshade) – Much branched herbaceous perennial from dry chaparral. Purple funnel-shaped corolla, 2.0–2.5 cm wide; fruit a berry.

HYDROPHYLLACEAE (Waterleaf Family)

The Hydrophyllaceae are now considered part of Boraginaceae, the larger borage family.

General physiognomy. The family is composed of mostly herbaceous plants with flower buds in fiddlehead-like coils, flowers with a forked style, and a multi-seeded ovary that yields a capsule as fruit. In contrast with the bristly hairs of the borages, the epidermal hairs in the Waterleaf family are usually glandular (hence the name).

Vegetative morphology. Annuals, herbaceous perennials, and small shrubs with alternate simple to compound leaves and round stems. Plants usually bristly, with glandular hairs, but seldom stinging.

Reproductive morphology. Flowers small to medium-sized; showy; cup-shaped, bell-shaped, or tubular; white, blues, purple, or yellow, and in coiled scorpioid cymes. Sepals five, partly fused, five petals joined to form a tube, five stamens attached to the tube, and a single 2-carpelled pistil with a superior, 2-chambered ovary.

The Hydrophyllaceae at a glance: Glandular, or watery hairs, scorpioid cymes, ovary superior with a two-carpelled, multi-ovule pistil with a bifid stigma; fruit a capsule (Illustration: *Nemophila menziesii*, "baby blue eyes").

Taxonomic relationships. The waterleaves look a great deal like the borages (Boraginaceae) including the flower design, number of flower parts, and arrangement of flowers in scorpioid cymes, and are taxonomically closely related to them. The main differences are the 2-forked style (single in borages), 2-chambered ovary (4-lobed in borages), and capsule-type fruit (nutlets in borages). Recent molecular studies support the lumping of the waterleaf family with the borages.

Biodiversity and distributions. The family contains some 300 species; it is widely distributed but with the majority found in the Americas. The greatest diversity is in western North America and the highlands of Central and South America. A few species are grown in gardens, particularly some of the native phacelias and baby-blue-eyes (*Nemophila menziesii*). The glandular hairs of some species may cause contact dermatitis.

Economic uses and ethnobotany. Yerba santa (*Eriodictyon* spp.) has been used for centuries by the native Californians for medicinal purposes, especially as a poultice for wounds, insect bites, and sores.

California genera and species. The region has 13 native genera and many species. Some locally common plants are:

Eriodictyon trichocalyx (yerba santa) – Shrub, ca. 1.5 m tall, in rocky washes of chaparral slopes. The large, leathery leaves are glutinous and shiny with resin. Flowers white to pale lavender.

Eucrypta chrysanthemifolia (common eucrypta) – Early flowering annual occurring in canyons and humid chaparral slopes. Tiny white flowers in a coiled cyme.

Nemophila menziesii (baby blue eyes) – One of the earliest spring flowers, commonly growing with grasses. Vivid blue to pale blue flowers, mostly growing solitary from leaf axils.

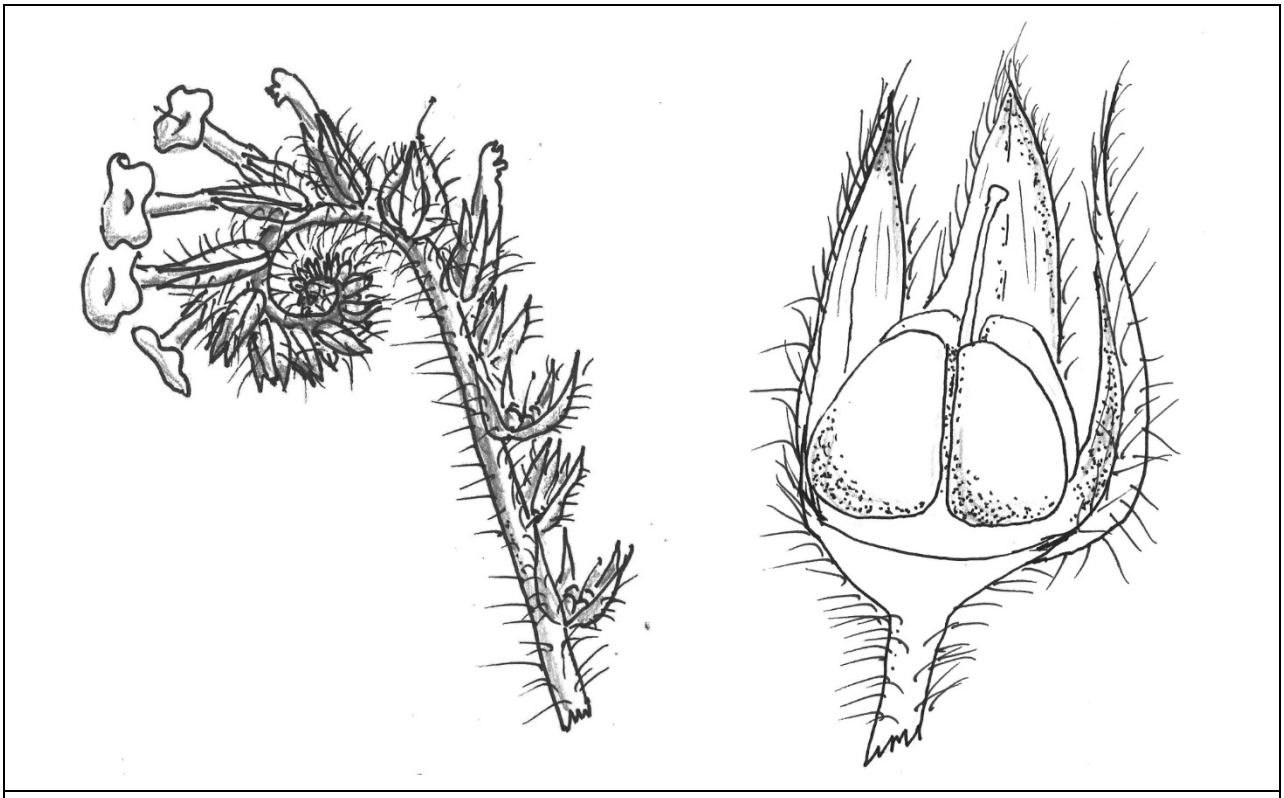
Phacelia minor (wild Canterbury bells) – Erect annual with purple, campanulate flowers.

BORAGINACEAE (Borage Family)

General physiognomy. Bristly-haired annuals or herbaceous perennials with simple, alternate leaves and "fiddlehead" coils (helicoid cymes) of flower buds, a single style and a 4-lobed ovary.

Vegetative morphology. The plants may have a combination of alternate and opposite leaves. The leaf blades usually have a narrow shape; many are linear or lance-shaped. Most plants in this family have bristly leaves, the coarse character of the hairs due to prickly crystals of silicon dioxide and calcium carbonate, which can induce adverse skin reactions.

Reproductive morphology. The flowers are small, open-bell-shaped, and arranged in tightly-coiled, scorpioid cymes that unroll as flower buds open. Each flower has five partly-fused sepals, five connate petals fused to form a tube, five stamens attached (adnate) to the corolla tube and a single pistil with a superior ovary of 4 segments. At flower maturity the mature pistil breaks into four segments, each one yielding a one-seeded nutlet (some may abort). Most pollination is by hymenopterans, such as bees.



The Boraginaceae at a glance: Bristly, often prickly hairs, scorpioid cymes, ovary superior with two-carpels bearing two ovules each that mature into four distinct segments; fruit formed by four nutlets that detach separately from the dry flower receptacle (Illustration: *Amsinckia menziesii*, "fiddleneck").

Taxonomic relationships. Borages are closely related to the waterleaf family (Hydrophyllaceae), which is now included in the borage family according to the most recent studies. The major distinction between the two taxa is that borages generally have a single style and a 4-lobed ovary, each lobe containing a single seed while the waterleafs have a 2-forked style and an unlobed ovary that dries into a capsule containing several to numerous seeds.

Biodiversity and distributions. The family contains some 2,000 species with a worldwide distribution; it is especially diverse in the Mediterranean region and the western United States. Among the many growth forms, the family has tropical trees (genus *Cordia*) with durable hardwood, and several garden ornamentals including heliotrope (*Heliotropium* spp.), forget-me-not (*Myosotis* spp.), blue-eyed Mary (*Omphalodes* sp.), tower-of-jewels and pride-of-Madeira (*Echium* spp.), and lungwort (*Pulmonaria* spp.).

Economic uses and ethnobotany. Several Eurasian species have been traditionally used for medicinal purposes, and are still widely used in the Mediterranean region, such as such as borage (*Borago officinalis*), for gastrointestinal and respiratory diseases, and comfrey (*Symphytum officinalis*), as a poultice for the healing of external burns and wounds. Alkanet or dyers' bugloss (*Alkanna tinctoria*) is a plant in the borage family whose roots are used as a red dye in the Mediterranean region. The root produces a fine red coloring material which has been used as a dye since antiquity to give color to wines and alcoholic tinctures, to vegetable oils, and to varnishes.

California genera and species. The region has 18 genera and many species; some (*Cryptantha* and *Plagiobotrys*) are difficult to key-out and require clear magnification of the fruiting nutlets and their attachment for proper identification. Some frequently-seen species include:

Amsinckia menziesii (common fiddleneck) – An erect, somewhat weedy spring annual with yellow flowers in beautiful coiled cymes.

Cryptantha intermedia (common crytantha) – White-flowered spring annual, the most common cryptantha in Riverside County.

Cryptantha sparsiflora (few-flowered cryptantha) – Similar to C. intermedia, but inflorescences sparse and open; common in chaparral and montane dry valleys.

Plagiobothrys spp. (popcorn flower) – Very similar to its sibling genus, *Cryptantha*, the popcorn flowers have somewhat larger and very white corollas that give the scorpioid cyme, at a distance, the appearance of white popcorn.

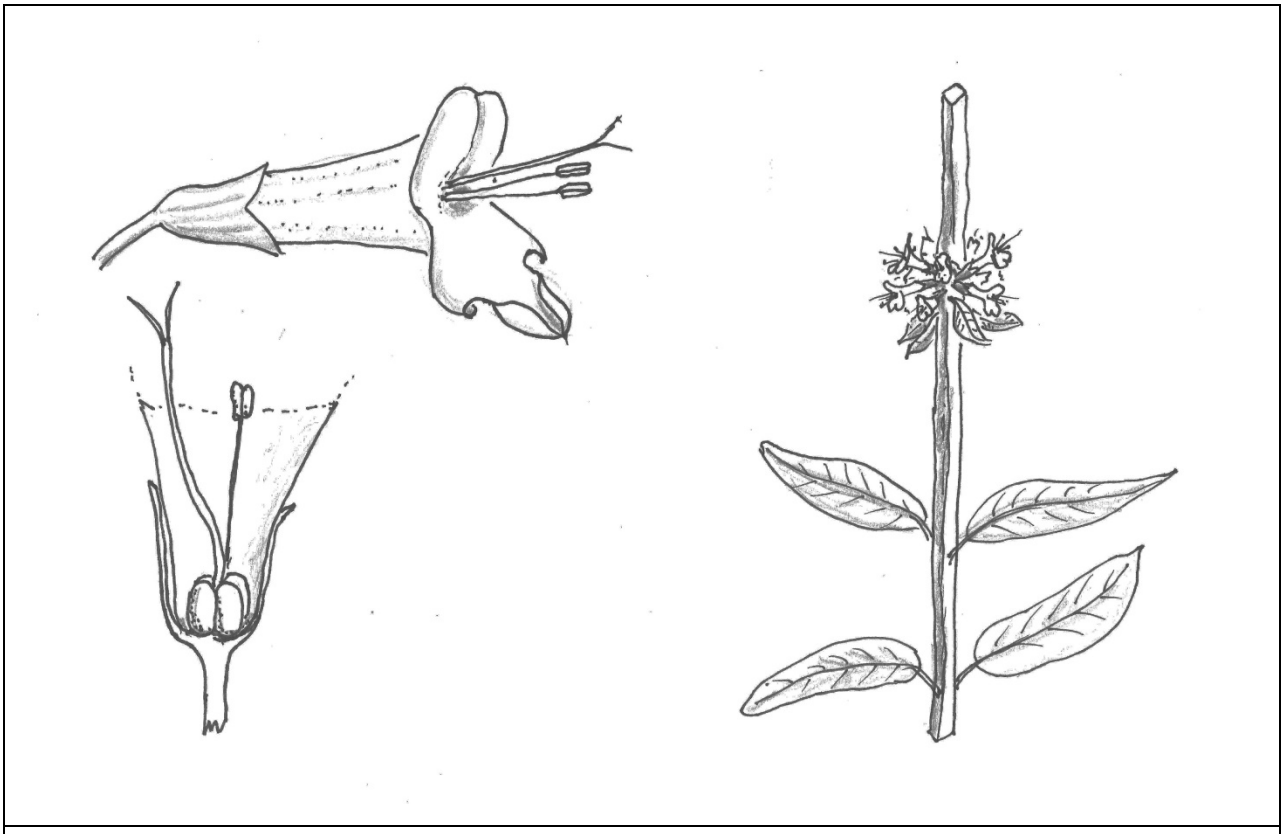
Plagiobothrys acanthocarpus (adobe popcornflower) – Common in valleys and plateaus of the San Bernardino mountains on moist clayey soil (hence the name "adobe"); nutlets are covered in distinctive long prickles.

LAMIACEAE (Mint Family)

General physiognomy. A combination of square stems, opposite leaves, and strong fragrance usually suffices to identify the family. In addition, the 2-lipped flowers have 4-lobed ovaries yielding 4 nutlets, as in the borage family.

Vegetative morphology. Mostly annuals and herbaceous perennials with square stems on the primary shoots and opposite, often simple, usually highly fragrant leaves due to the presence of volatile essential oils. Some species are shrubs, trees with valuable wood (such as the Asian teak), or, rarely, vines.

Reproductive morphology. Flowers showy, strongly zygomorphic and 2-lipped, sometimes small, commonly arranged in heads or whorled spikes. Sepals fused, often 5 but may vary in number; petals five, irregular, divided into two lips and joined midway to form a tube, stamens 2 or 4, adnate to the tube, and a single pistil with a 4-lobed, superior ovary. The fruits are 4 one-seeded nutlets per flower.



The Lamiaceae at a glance: Square stems, strongly fragant opposite leaves in a decussate phyllotaxis, flowers often arranged in spike-like clusters on stem nodes (but sometimes solitary in some species). Zygomorphic, two-lipped flowers, with a 2-capelled, 4-lobed pistil; fruits formed by four one-seeded nutlets (Illustration: *Salvia mellifera*, "black sage").

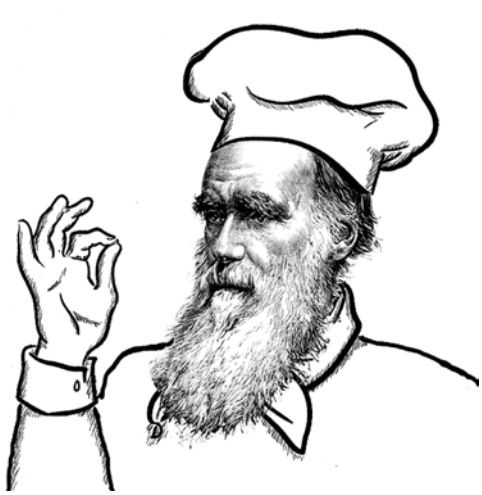
Taxonomic relationships. Several other families feature flowers with a 2-lipped design and similar number of stamens: Scrophulariaceae (figwort family), Acanthaceae (acanth family), Bignoniaceae (trumpet vine family), Orobanchaceae (broomrape family), and others. None of those families has a 4-lobed ovary, square stems, or highly fragrant leaves. The mints are also very closely related to the verbena family (Verbenaceae), which differs chiefly in having only slightly zygomorphic flowers (as opposed to strongly bilateral in the mints), less-fragrant leaves, sometimes woody stems, and ovaries that are not as deeply 4-lobed.

Biodiversity and distributions. The mint family is extremely cosmopolitan, with over 5,000 species widely distributed across the world. Many live in dry habitats. The family is richly represented in Mexico, South America, the Mediterranean region, and California.

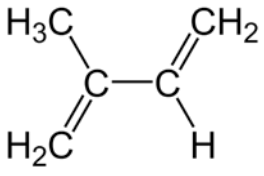
Lavender and essential oil.

Economic uses and ethnobotany. The fragrant, volatile oils in the foliage are used medicinally, in cosmetry, and to flavor food. The myriad culinary and aromatic herbs include rosemary (*Rosmarinus officinalis*), thyme (*Thymus vulgaris*), oregano (*Origanum vulgare*), marjoram (*Origanum majorana*), sage (*Salvia officinalis*), lavender (*Lavandula officinalis*), basil (*Ocimum basilicum*), holy basil or tulasi (*Ocimum sanctum*), and various mints (*Mentha* spp.). Some plants are used for their edible seeds, such as the chia (*Salvia hispanica*). Many beautiful ornamentals belong to this family including the salvias, popular for garden cultivation in California.

Darwin in the kitchen: Volatile messages from the mint family



The Lamiaceae are recognizable for their attractive scent. They share this pleasant trait with a number of other aromatic plants, such as citrus, pines, or eucalypts. For many centuries, perfume-makers-turned-chemists have been trying to capture the scent of these aromatic plants to make perfumes and cosmetics. They figured out that a light oily substance could be extracted from aromatic plants by boiling them in water and capturing the vapor, that is, through the process of distillation. Because they thought these substances captured the "essence" of the plant, they called them essential oils. Essential oils are really a mixture of volatile molecules called terpenes. Terpenes, in turn, are molecular combinations of one of the simplest molecules in living beings, isoprene (C_5H_8). Isoprene is the building block of terpenes. It can combine with other isoprene molecules to form longer and more complex chains of volatile organic compounds, giving origin to the diversity of terpenes found in nature. The combination of different terpenes in the essential oils of any plant gives them their characteristic scent. Terpenes are present in pine resin, in citrus oil glands, in eucalypt leaves, and, of course, in the foliage of the Lamiaceae.



The isoprene molecule

Given the fact that terpenes are so common in nature, they surely must play a role in the plant's metabolism, but, what role is it? Because essential oils are highly volatile, they send a number of messages in the ecosystem. Any animal (including *Homo sapiens*) can detect the scent of pine, orange blossom, or sage even before actually encountering the plant. In contrast with the stark toxicity of the nightshades, essential oils are not deadly poisonous but they make the plants that possess them quite indigestible. Animals may take a munch here and there from, say, sage or lavender without any significant consequence, but any herbivore daring to go on a diet of say, pure pine needles or pure sage will rapidly become sick in the stomach. The reason is because essential oils halt the activity of gut bacteria, called the microbiome of mammalian guts, which help all animals break-down food and digest it. The antibacterial properties of essential oils was very well known to our great-grandmothers, who boiled eucalyptus leaves or pine needles in the room of persons with respiratory infections, to generate an atmosphere rich in essential oils that would help the immune system fend-off the infection.

So, if the nightshades are the attack warriors of the anti-herbivore war of plants against animals, the Lamiaceae represent the diplomats of nature. Animals quickly learn that if they eat nightshades they might die or at least fall terribly ill, while eating aromatic herbs from the mint family is not dangerous, but has to be done in moderation. The

Lamiaceae are particularly abundant in winter-rain scrubs found in the mediterranean regions of the world, such as the California chaparral. They grow in association with other plants of other families, and natural selection has favored in the Lamiaceae a much gentler way to deter herbivores. The plants seem to be sending a message that says: "go eat some non-aromatic plants for volume and roughage, otherwise you will get a serious indigestion." The method might be as efficient as the lethal force of the nightshades. By not killing their enemies but rather directing them towards other plants they might be using herbivores to their advantage by guiding them against their competitors.

Humans learned these principles from the beginning of agriculture, and we follow them to this day. We read the chemical messages discreetly sent out by these diplomats of nature, and appreciate the different scents in different species. In the same way as chilies impact hot temperature receptors in our tongue, mints impact our cold temperature sensors with a lovely iciness. We consume aromatic herbs to season our food and to provide scent to our toiletries. We distill them to extract the pleasant aromas of lavender and thyme, we add oregano to pizza, basil to *caprese* salad, and mint to desserts and ice cream. But, following the golden rule of wild nature, we never eat them in overly large amounts, lest we may suffer from consuming too much of a good thing.

California genera and species. The State harbors 27 genera, seven of which are nonnative. The following rank among the most common wildflowers belonging to this family in Riverside County:

Marrubium vulgare (horehound) – Weedy perennial herb of European origin, has distinctive gray, verrucose leaves, whitish stems, and is one of the few species in the family that is not aromatic.

Mentha piperita (peppermint) – Widely distributed along ditches and wet soils; rich in essential oils, its fragant odor is unmistakable.

Salvia columbariae (chia) – Widespread small annual of dry sandy soils. Purple flowers arranged in dense verticillate clusters around the stem.

Salvia mellifera (black sage) – Erect, perennial shrub with dark green foliage and white-pinkish verticillate inflorescences.

Salvia apiana (white sage) – Perennial shrub with densely pubescent white foliage and tall inflorescences bearing large white flowers.

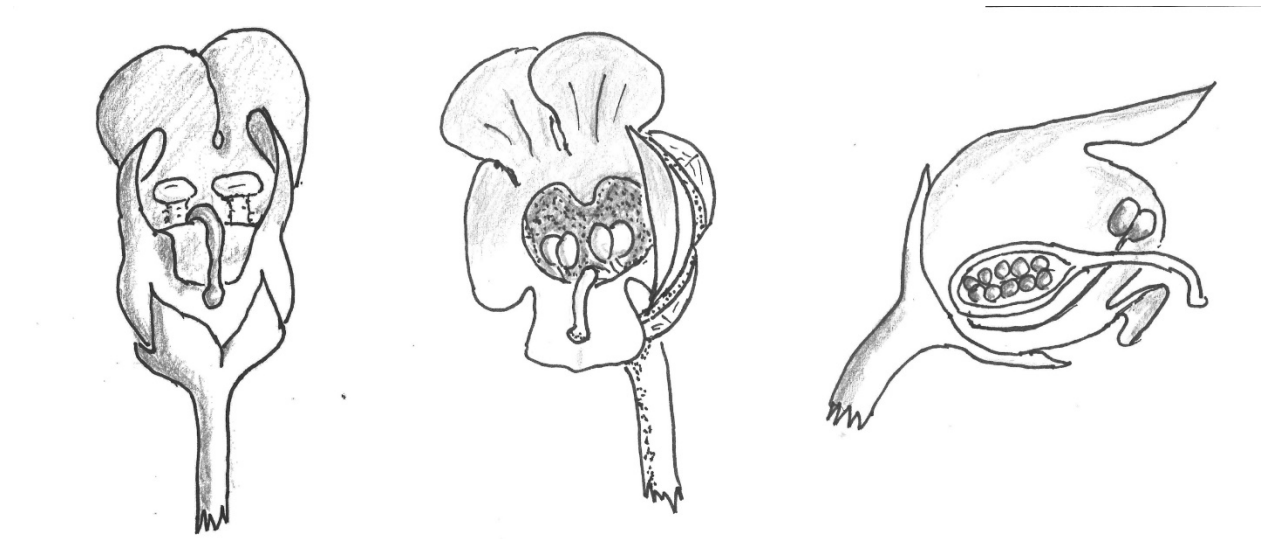
Trichostema lanatum (woolly bluecurls) – Native perennial shrub with flowers arranged in showy purple racemes; stamens an style long and exserted.

SCROPHULARIACEAE (Snapdragon Family)

General physiognomy. Mostly herbaceous plants with zygomorphic, 2-lipped flowers and 2-chambered capsules containing many small seeds.

Vegetative morphology. Herbaceous annuals, perennials, and small shrubs, often with opposite leaves. Leaves may be simple and entire, toothed, deeply lobed, or pinnately dissected.

Reproductive morphology. Two-lipped flowers, slightly to strongly zygomorphic, often showy in a variety of colors, mostly in spikes, racemes, or panicles. Five partly joined sepals, Five petals arranged in two-lipped petal lobes joined to form a tube, usually 4 (sometimes 2 or 5) stamens joined to the tube, and a single pistil with a superior, 2-carpelled and 2-chambered ovary. The fruits are capsules with many small seeds.



The Scrophulariaceae at a glance: Zygomorphic, two-lipped flowers, mostly clustered in spikes, racemes, or panicles. Usually four (sometimes 2 or 5) stamens joined to the tube, and a single pistil with a superior, 2-carpelled and 2-chambered ovary maturing into a multi-seeded capsule (Illustration: *Scrophularia californic*a, "California bee-plant").

Taxonomic relationships. The 2-lipped design of "scroph" flowers resembles flowers in several other families. The mints (Lamiaceae) have a similar design but usually have fragrant leaves and a deeply 4-lobed ovary. The acanths (Acanthaceae) have a similar design but the ovary only contains 4 large seeds expelled explosively from the capsule. The bignonias (Bignoniaceae) have a similar design but are woody plants with long, beanlike seed pods and winged seeds. The broomrapes (Orobanchaceae) are parasites with no green chlorophyll.

Recent molecular studies indicate that the Scrophulariaceae is not really a single, coherent family. A few species are being retained in the family, others are being separated into the Veronicaceae and the Plantaginaceae, while the monkeyflowers (*Mimulus* sp.) belong to their own family, the Phrymaceae. Genera with a galea-type (helmet-shaped) upper lip are now combined with the parasitic broomrape family (Orobanchaceae).

Biodiversity and distributions. The family harbors some 3,000 species worldwide. The highest diversity is in the Mediterranean region, California, and other semi-arid areas. Many genera are ornamentals in gardens, including snapdragon (*Antirrhinum majus*), monkeyflowers (*Mimulus* spp.), lady's pocket book (*Calceolaria* spp.), hebe (*Hebe* spp.), veronicas (*Veronica* spp.), penstemons (*Penstemon* spp.), toadflaxes (*Linaria* spp.), and mulleins (*Verbascum* spp.).

Economic uses and ethnobotany. Foxglove (*Digitalis purpurea*) is the source of digitalin, used to treat heart ailments and cardiac arrhythmias.

California genera and species. The region has 27 partly or mostly native genera and six nonnative genera. Some common species in Riverside County are listed below:

Collinsia heterophylla (chinese houses) – Common in moist chaparral and oak woodlands, verticillate purple flowers with a whitish upper lip.

Keckiella antirrhinoides (chaparral beard-tongue; yellow bush) – Widespread chaparral species, often 2 m high and profusely-branched and pale yellow flowers distributed along the stems.

Mimulus aurantiacus (bush monkey flower) – Woody perennials of scrubs and chaparral, often associated with rock outcrops; flowers highly variable in color from yellow to dark red-orange.

Mimulus guttatus (yellow monkeyflower) – Associated to moist banks and streams, with very distinctive yellow, speckled corollas.

Scrophularia californica (California bee plant) – Herbaceous perennial common on dry hillsides, flowers small and bee-like in shape.

Penstemon spectabilis (showy penstemon) – With large, showy purple flowers, and opposite leaves connate (fused) at the base, this species is common in chaparral and woodlands.

Penstemon centranthifolius (scarlet bugler) – Of scarlet tubular flowers, this species is hummingbird pollinated and grows in grasslands and open washes of the San Bernardino Mountains.