MANZANITA

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Family Rosaceae, California Wild and Domesticated

Alicia Springer

Is any plant more emblematic of human engineering than the florist's long-stemmed rose? How about those ever-newer apple varieties bred for shiny skin and durable shipping? Roses, apples, pears, stone fruit, berries, almonds, and many other edibles and ornamentals belong to the same botanical family—but look beyond the garden, the orchard, and the Mother's Day special, and you'll find a family of astonishing breadth and diversity: Rosaceae, wild at heart.

That pretty little compact cinquefoil (*Potentilla* sp.) on a mountain trail? The toyon (*Heteromeles arbutifolia*) that might grow 30 feet tall in a hospitable site? Deciduous mountain mahogany (*Cercocarpus* sp.), chamise (*Adenostoma fasciculatum*), woodland rambler thimbleberry (*Rubus parviflorus*), and woodland strawberry (*Fragaria vesca*): they are among the many California native members of the rose clan. For all their diversity of habit and habitat, they are recognizably cousins of our brambly native wild rose, that beautifully simple, pink-petaled *Rosa californica*, with its diminutive red rose hips beloved by foraging wildlife. Family Rosaceae is found around the globe, mainly in temperate Northern Hemisphere zones, comprising some 87 genera and 3,000 species of incalculable economic and cultural value to people. While highly variable in physiognomy, from small trees and shrubs to woody perennials and herbaceous annuals, rose family members generally share a common morphological trait: rose-like flowers. Glenn Keator, in his *California Plant Families West of the Sierran Crest and Deserts* (2009 University Press), writes "Flowers resemble single roses with five separate sepals, petals, and numerous stamens attached to a shallow cuplike or bowl-shaped hypanthium. . . . Flowers are red, pink,

TOP: California wild rose (*Rosa californica*) in the Regional Parks Botanic Garden. • BOTTOM: Wild rose hips of *Rosa californica*. Photos by John Rusk.

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The fruit of the *Rosa* genus is an aggregate of achenes nestled in a fleshy hypanthium, which forms the familiar "hip," as seen in *Rosa californica*, Pinnacles National Park, San Benito County, California. Photo by Keir Morse (CC BY-NC-SA 3.0).

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Feathery achenes of mountain mahogany (*Cercocarpus betuloides*). Photo by Jeff Goddard.

yellow, or white; tiny to large; resembling single roses; arranged in varied ways."

Of course, taxonomy is never that neat and simple, and Keator goes on to qualify the rose-flower descriptor: "Mostly [five] separate sepals and petals (sometimes missing) and numerous (usually) stamens . . . Pistils may be single with a superior to inferior ovary, multiple on a flat receptacle, or borne inside a hypanthium." Exceptions that prove the rule aside, picture the blossoms of any wild or cultivated plum, strawberry, cinquefoil, and even the invasive members of the family such as thorny *Pyracantha* or Himalayan blackberry (*Rubus armeniacus*), and you come up with a lot of five-petaled rosy look-alikes. To distinguish the rose family from other five-petaled groups such as buttercups (Ranunculaceae) and saxifrages (Saxifragaceae), Keator suggests keeping in mind that "the herbaceous roses have stipules on their leaves and a row of sepal-like bracts outside the actual sepals." Leaves are another identification tangle, as rose family species have "(usually) alternate leaves that often bear stipules. Leaves may be simple, highly dissected, compound, entire, or toothed." (Beware those parentheticals.)

Rose family species produce many different types of fruits, wild and cultivated, including achenes (such as rose hips), drupes (such as wild cherries), pomes (such as toyon berries), follicles (such as the seeds of spiraea), accessory fruits (such as wild strawberries) and aggregate fruits (such as salmonberries). Most of these fruits taste good to a bird, human, or other creature who will happily eat the fruit and disperse the seed, but for sheer design flair, it's hard to beat the mountain mahogany: *Cercocarpus* adds a twirly, feathery plume to the end of its dry fruit achene and sends it off on the winds for dispersal.

In this issue of *Manzanita*, Dr. Dan Potter, Professor of Plant Sciences at UC Davis and director of the UC Davis herbarium, details the mind-boggling diversity among the 179 native or naturalized California species of Rosaceae, and guides us through a phylogenetic understanding of their 46 genera, 14 tribes, and three subfamilies—and helps us keep it all straight with a comprehensive reference table.

Rachel Prunier, an evolutionary biologist at UCLA, and Laurel Thomas, an environmental science student working and studying with Dr. Prunier, explain their research into toyon (*Heteromeles arbutifolia*), which they describe as "both a very typical and very strange CFP [California Floristic Province] shrub." We Californians think we know toyon—but read about this UCLA research project and discover how much we really don't know.

Family Rosaceae is an evocative part of California life, and not only because we all love to munch apricots and sniff roses. It's our natural and man-made history and environment all tumbled together, our beloved heirloom apple tree and our wild berry bramble, our chaparral shrubs and formal garden, our hillside cascade of wild rose. Orchard to outback, it's easy for a Californian to grow misty over family Rosaceae.

Toyon (*Heteromeles arbutifolia*) with blue orchard bee (*Osmia lignaria*). Photo by Alicia Springer.

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Diversity of the Rose Family (Rosaceae) in California

Dan Potter

Among the surprising facts that botanists enjoy sharing with their relatives, friends, and students is the revelation that the rose family includes not just roses but also many other economically important plants such as apples, plums, and strawberries, as well as many wild plants that don't have either showy flowers or edible fruits. On the other hand, many botanists are surprised to learn that the family's diversity extends beyond the most familiar north temperate members, including extensive representation in tropical regions and the Southern Hemisphere. And while California plant enthusiasts are aware of the amazing floristic diversity of the state, many don't realize that the native flora includes representatives of nearly all major evolutionary lineages in Rosaceae, most of which have ranges that extend to one or more other continents.

I began to study Rosaceae when I moved to California from the east coast to begin my position at UC Davis in 1996. Initially, my selection of the family was motivated primarily by my interest in investigating relationships between domesticated plants and their wild relatives. In the years since, I have been excited and delighted to learn that Rosaceae is also an excellent system for exploring the fascinating flora of California. While other plant families are represented by more species in the state, few, if any, exhibit the diversity of growth habits, leaf morphologies, fruit types, complex evolutionary histories, and intriguing biogeographic patterns seen in California Rosaceae.

Perhaps the most striking aspect of classification of the species in the Rosaceae family is the diversity of fruit types they exhibit. These include achenes, drupelets, drupes, pomes, follicles, and, rarely, capsules. In many members of the family, there is

LEFT: Bark detail of Santa Cruz Island ironwood (*Lyonothamnus floribundus* subsp. *asplenifolius*). Photo by Zoya Akulova-Barlow (CC BY-NC 3.0). RIGHT: Shasta snow wreath (*Neviusia cliftonii*). Photo by Julie Ann Kierstead (CC BY-NC 3.0).

more than one pistil per flower, each of which develops into a fruit; collectively, the fruits from two or more pistils in a single flower are called aggregates.

The diversity of fruit types in Rosaceae has contributed to their tremendous economic importance and to their interest from an evolutionary perspective. In addition, the family has attracted the attention of botanists because it exhibits multiple examples of important evolutionary phenomena that can cause challenges for delimiting plant species and understanding relationships among them. These include asexual reproduction, hybridization, and polyploidy, the latter referring to the presence of extra sets of chromosomes in the nucleus of a plant cell.

Chromosomes are the structures within the nuclei of cells where an organism's genes are found. In most cells of most plants and animals, chromosomes exist in pairs, with two copies of each chromosome type; the exceptions are cells involved in sexual reproduction (eggs, sperm, and, in plants, additional associated cells) which have just one copy of each chromosome. Diploid organisms have one pair (two copies) of each type of chromosome, and polyploids have more than one pair; e.g., tetraploids have two pairs, hexaploids have three pairs, etc.

Polyploidy is generally not tolerated by animals but is widespread in plants, and the phenomenon of whole genome duplication, which leads to polyploidy, is known to have occurred repeatedly over millions of years of evolution of the plant kingdom including multiple times and at multiple taxonomic levels within Rosaceae.

Molecular phylogenetic studies published over the past three decades have provided support for many of the species, genera, and tribes within Rosaceae that were originally established based on morphological features. These studies have also provided new insights into evolutionary relationships, sometimes requiring taxonomic changes. One key finding was that the division of the family into four subfamilies based primarily on fruit types, as in the most widely adopted classification system for much of the 20th century, resulted in some groupings that did not accurately reflect evolutionary relationships. A new classification system with three subfamilies was established in 2007 and will be followed here.

The rose family includes 87 genera and about 3,000 species, which are classified into three subfamilies and 16 tribes. In California, there are 179 native or naturalized species of Rosaceae, representing all three subfamilies, 14 tribes, and 46 genera (Table 1). These species occur in a broad range of habitats at elevations from sea level along the coast to alpine areas at 4,000 meters (over 13,000 feet) altitude. California's Rosaceae include taxa considered rare, threatened, and endangered; California endemics (Table 2); as well as non-native invasive weeds (Table 3).

Current evidence suggests that the family originated about 90 million years ago in western North America and that there have been multiple migration events among continents over time. Many native California species are more closely related to species in other parts of the world than to one another; thus, over millions of years of evolution, multiple lineages of Rosaceae arrived in California separately and independently at different times and via different routes, including migration over past connections between North America and Eurasia and, in at least one case, long-distance dispersal from South America. More recently, human-assisted introductions over the last several centuries have resulted in the naturalization of many non-native species, generally as escapees from cultivation.

Santa Cruz Island ironwood (*Lyonothamnus floribundus* subsp. *asplenifolius*). Photo by Zoya Akulova-Barlow (CC BY-NC 3.0).

In addition to their diversity of fruit types, species of Rosaceae exhibit a range of growth habits, leaf morphologies, presence/absence of glands, inflorescence types, floral colors and sizes, and number of pistils per flower. In general, members of the family are characterized by leaves usually alternate on the stem, stipules usually present, sepals and petals usually five, and stamens usually 15 or more. A well-developed hypanthium or floral cup, formed from the fused bases of the sepals, petals, and stamens, is always present, albeit less conspicuous in some species, especially those with small flowers.

Subfamily Dryadoideae

Dryadoideae is the smallest of the three subfamilies, consisting of just one tribe (Dryadeae), four genera, and about 30 species of shrubs and small trees that produce achene fruits. Members of this group are the only species in Rosaceae that engage in symbiotic nitrogen

TABLE 1. SUBFAMILIES, TRIBES, AND GENERA OF ROSACEAE REPRESENTED BY NATIVE AND/OR NATURALIZED SPECIES IN THE CALIFORNIA FLORA. A few genera not represented in California but mentioned in the text are also included.

Subfamily Tribe Subtribe Genus		Native Species in CA	Naturalized Species in CA
Dryadoideae			
Dryadeae			
Cercocarpus	mountain mahogany	4	0
Purshia	bitterbrush, cliffrose	2	0
Chamebatia	mountain misery	2	0
Rosoideae			
Ulmarieae			
Filipendula	meadowsweet	0	0
Roseae			
Rosa	rose	9	3
Rubeae			
Rubus	raspberry, blackberry	7	4
Agrimonieae			
Agrimoniinae			
Agrimonia	agrimony	2	0
Sanguisorbinae			
Acaena	biddy-biddy	1	2
Poteridium	burnet	1	0
Poterium	burnet	0	1
Sanguisorba	burnet	1	0
Colurieae			
Geum	avens, prairie smoke	3	0
Fallugia	Apache plume	1	0
Potentilleae			
Fragariinae			
Aphanes	lady's mantle	1	0
Comarum	marsh cinquefoil	1	0
Dasiphora	shrubby cinquefoil	1	0
Drymocallis	woodbeauty	6	0
Fragaria	strawberry	3	0
Sibbaldia	creeping sibbaldia	1	0
Potentillinae			
Duchesnea	mock strawberry	0	1
Horkelia	horkelia	20	0
Horkeliella	false horkelia	2	0
Ivesia	ivesia	22	0
Potentilla	cinquefoil	25	3

TOP TO BOTTOM: Birch-leaf mountain mahogany (*Cercocarpus betuloides* var. *betuloides*). Photo by Keir Morse (CC BY-NC-SA 3.0). • Thimbleberry (*Rubus parviflorus*). Photo by Keir Morse (CC BY-NC 3.0). • Dwarf ivesia (*Ivesia pygmaea*). Photo by Keir Morse (CC BY0-NC 3.0).

Subfamily Tribe Subtribe Genus		Native Species in CA	Naturalized Species in CA
Amygdaloideae			
Lyonothamneae			
Lyonothamnus	ironwood	1	0
Neillieae			
Physocarpus	ninebark	2	0
Spiraeeae			
Aruncus	goatsbeard	1	0
Holodiscus	ocean spray, cream-bush	1	0
Luetkea	partridge foot	1	0
Petrophytum	rock spiraea	1	0
Spiraea	spiraea	2	0
Exochordeae			
Oemleria	oso berry	1	0
Kerrieae			
Coleogyne	blackbrush	1	0
Neviusia	snow wreath	1	0
Amygdaleae			
Prunus	almond, apricot, cherry, peach, plum	8	3
Sorbarieae			
Adenostoma	chamise, greasewood	2	0
Chamaebatiaria	fern bush, desert sweet	1	0
Gillenieae			
Gillenia	Indian physic, Bowman's root	0	0
Maleae			
Lindleya		0	0
Kageneckia		0	0
Vauquelinia	Arizona rosewood	0	0
Malinae			
Amelanchier	serviceberry	2	0
Cotoneaster	cotoneaster	0	8
Crataegus	hawthorn	3	1
Eriobotrya	loquat	0	1
Heteromeles	Christmas berry, toyon	1	0
Malus	apple, crabapple	1	1
Peraphyllum	wild crabapple	1	0
Pyracantha	firethorn	0	3
Pyrus	pear	0	1
Sorbus	mountain ash	3	0

TOP TO BOTTOM: Pacific ninebark (*Physocarpus capitatus*). Photo by Keir Morse (CC BY-NC-SA 3.0). • Mountain spiraea (*Spiraea splendens*). Photo by Barry Breckling (CC BY-NC-SA 3.0). • Shasta snow wreath (*Neviusia cliftonii*). Photo by Julie Ann Kierstead (CC BY-NC 3.0). • Toyon (*Heteromeles arbutifolia*). Photo by Keir Morse (CC BY-NC-SA 3.0).

fixation, a phenomenon observed in some members of ten different families of flowering plants and best known in the legume family (Fabaceae). Species of Dryadoideae form root nodules that house nitrogen-fixing bacteria in the genus *Frankia* (in contrast to legumes, in which the bacterial symbionts belong to the genus *Rhizobium*).

Three genera and 12 species of this subfamily occur in California. Species of mountain mahogany (*Cercocarpus*) are small trees characterized by hard wood and persistent feathery styles on the fruits (one per flower); they are found in the foothills and mountains, with one endangered species known only from Santa Catalina Island. There are two species of mountain misery (*Chamaebatia*), one found in the Peninsular Ranges of southern California and adjacent Baja California (Mexico), the other endemic to California and common in the Sierra Nevada and Coast Ranges, where it forms dense stands. The density of growth, combined with the sticky, aromatic exudates from glands on the leaves present challenges to hikers and ranchers due to their tendency to rub off on clothing and sheep wool. Bitterbrushes (*Purshia*) are shrubs found in arid habitats; one species has fruits with persistent feathery styles, similar to those of mountain mahogany, but with several fruits per flower.

Subfamily Rosoideae

The subfamily Rosoideae, with six tribes, is represented by 20 genera and 121 species in the California flora, and includes perennial herbs and shrubs, as well as a few annual herbs and trees. The number of pistils per flower varies from one (rarely) to many.

Just one genus is included in each of three of the tribes of Rosoideae: Ulmarieae (*Filipendula*, meadowsweet), Roseae (*Rosa*, roses), and Rubeae (*Rubus*, raspberries and blackberries). The first of these is not represented in the California flora, while the latter two include both native and naturalized species. Roses are classified in the genus *Rosa*, the only member of tribe Roseae, which includes more than 100 species native primarily to north temperate regions but widely introduced as ornamentals throughout the world. Blackberries and raspberries belong to the huge (perhaps as many as 750 species), cosmopolitan genus *Rubus*, the only genus in the tribe Rubeae.

The fruits of *Rosa* are aggregates of achenes, borne within a fleshy concave hypanthium, the hip (edible in some species), while the fruits of *Rubus* are aggregates of drupelets borne on a convex receptacle, which remains dry in raspberries but becomes fleshy in blackberries. In addition to their tremendous economic importance, both *Rosa* and *Rubus* are notoriously challenging on several levels: physically because the stems of most species are armed with sharp, treacherous prickles; ecologically because some species are or have the potential to become invasive weeds while others are rare or endangered; and taxonomically due to extensive hybridization, polyploidy, and asexual reproduction.

Two genera of tribe Colurieae occur in California. Both Apache plume (*Fallugia paradoxa*, the only species in the genus) and prairie-smoke (*Geum triflorum* var. *ciliatum*) bear achenes with persistent feathery styles similar to those in mountain mahogany and cliff rose; phylogenetic analyses indicate that the similarity in style morphology is due to convergent evolution.

Species of tribe Agrimonieae are perennial herbs in which the hypanthium becomes hardened in fruit and sometimes bears prickles on the surface. Subtribe Agrimoniinae is represented in California by two native species of agrimony (*Agrimonia*). Subtribe Sanguisorbinae is the lineage in Rosaceae that is most strongly developed in the southern hemisphere, with several genera found primarily or exclusively in New Zealand, Australia, southern Africa, and South America, extending to southern polar regions. The largest of these genera, *Acaena* (biddy-biddy), is represented in California by three species found in coastal areas: two naturalized species introduced from Australia or New Zealand and one native species whose closest relative occurs

GLOSSARY OF TERMS USED IN "DIVERSITY OF THE ROSE FAMILY" *by Daniel Potter*

CALYX. Collective term for sepals; outermost or lowermost whorl of flower parts, generally green and enclosing remainder of flower in bud.

CARPEL. Basic female structure of a flower, consisting of ovary, stigma, and usually a style.

CHAMBER. Compartment or cavity within an ovary, capsule, or other hollow structure.

CHROMOSOME. A linear strand of DNA and associated proteins in the nucleus of cells that functions to transmit hereditary information.

CORYMB. A flat-topped flower cluster where individual flower stalks grow upwards from various places on the main stem to approximately the same height.

DIPLOID. Having two sets of chromosomes (maternal and paternal).

ENDEMIC. Native to and restricted to a defined geographic area.

EXUDATE. Material discharged (exuded) from a plant, often with characteristic odor, color, or texture (e.g., sticky, gummy, slippery).

GLAND. Small, often spheric body, on or embedded in the epidermis (outermost cell layers) or at the tip of a hair, that exudes a generally sticky substance.

HYPANTHIUM. Structure generally in the shape of a tube, cup, or bowl, derived from the fused lower portions of the perianth and stamens, from which these parts seem to arise, and to which the ovary wall is fused (in an inferior ovary), partially fused (in a half inferior ovary), or free (in a superior ovary).

INFLORESCENCE. Entire aggregation of flowers or flower clusters and associated structures; often difficult to determine as to type and boundaries but generally excluding full-sized foliage leaves.

NUCLEUS. A membrane-bounded component of cells that contains genetic material in multiple strands of DNA molecules.

OPPOSITE (LEAF). Arranged in pairs directly across from one another and along an axis.

OVARY. Structure bearing the ovule, which contains the egg and normally develops into a seed after fertilization; usually wide, at basal portion of pistil and normally develops into a fruit as ovules become seeds; may be simple (one carpel, one chamber) or compound (two or more carpels, one or more chambers).

PERIANTH. Calyx and corolla (collective term for petals), whether or not they are distinguishable.

PETIOLE. Leaf stalk connecting leaf blade to stem, sometimes more or less distinct.

PHYLOGENY. The evolutionary development and history of a species, genus, family, or other taxonomic grouping of plants.

PINNATE. Feather-like; pertaining to veins, lobes, leaflets, or other structures arranged along either side of an axis.

PISTIL. Female reproductive structure of a flower composed of an ovule-containing ovary at the base, one or more pollen-receiving stigmas at the tip, and generally one or more styles between the ovary and stigma.

POLYPLOIDY. Having three or more sets of chromosomes.

PSEUDOCARP. That portion of a fruit that is not derived from the ovary.

RACEME. An unbranched inflorescence in which flowers are borne on pedicels (stalks).

SEPAL. Individual member of the calyx, whether fused or not; generally green.

SIMPLE (LEAF). Composed of single part; undivided; unbranched.

STAMEN. Male reproductive structure of a flower.

STIGMA. Part of a pistil on which pollen germinates, generally terminal and elevated above the ovary on a style, usually sticky or hairy, sometimes lobed.

STIPULE. Appendage at base of a petiole, generally paired, variable in form but often leaf- or scale-like.

STYLE. In many but not all pistils, the stalk-like part that connects the ovary to the stigma.

Most definitions based on and adapted from The Jepson Manual*, Second Edition, University of California Press, 2012*

OPPOSITE PAGE, TOP TO BOTTOM: Apache plume (*Fallugia paradoxa*). Photo by Richard Spjut (CC BY-NC 3.0). • Black brush (*Coleogyne ramosissima*). Photo by Bart O'Brien. • Goatsbeard (*Aruncus dioicus*). Photo by Bart O'Brien.

TABLE 2. SPECIES OF ROSACEAE LISTED IN THE CALIFORNIA NATIVE PLANT SOCIETY (CNPS) INVENTORY OF RARE PLANTS. CRPR indicates California Rare Plant Rank (1A = presumed extirpated in California and either rare or extinct elsewhere; 1B = rare, threatened, or endangered in California and elsewhere; 2A = presumed extirpated in California but common elsewhere; 2B = rare, threatened, or endangered in California but common elsewhere; 3 = more information is needed; 4 = of limited distribution, a watch list. A number after a decimal point refers to the severity of the threat: .1 = seriously endangered in California; .2 = fairly endangered in California; .3 = not very endangered in California). CESA and FESA indicate, respectively, listing under the California and Federal Endangered Species Acts (- = not listed; C = candidate; E = endangered; T = threatened; R = rare).

Scientific Name	Common Name	CRPR	CESA	FESA	CA Endemic?
Cercocarpus betuloides var. *blancheae*	island mountain mahogany	4.3	-	-	+
Cercocarpus traskiae	Catalina Island mountain mahogany	1B.1	E	E	+
Chamaebatia australis	southern mountain misery	4.2	-	-	-
Crataegus castlegarensis	Castlegar hawthorn	3	-	-	-
Drymocallis cuneifolia var. *cuneifolia*	wedgeleaf woodbeauty	1B.1	-	-	+
Drymocallis cuneifolia var. *ewanii*	Ewan's woodbeauty	1B.3	-	-	+
Geum aleppicum	Aleppo avens	2B.2	-	-	-
Horkelia bolanderi	Bolander's horkelia	1B.2	-	-	+
Horkelia congesta var. *nemorosa*	Josephine horkelia	2B.1	-	-	-
Horkelia cuneata var. *puberula*	mesa horkelia	1B.1	-	-	+
Horkelia cuneata var. *sericea*	Kellogg's horkelia	1B.1	-	-	+
Horkelia daucifolia var. *indicta*	Jepson's horkelia	1B.1	-	-	+
Horkelia hendersonii	Henderson's horkelia	1B.1	-	-	-
Horkelia hispidula	White Mountains horkelia	1B.3	-	-	-
Horkelia howellii	Howell's horkelia	4.3	-	-	-
Horkelia marinensis	Point Reyes horkelia	1B.2	-	-	+
Horkelia parryi	Parry's horkelia	1B.2	-	-	+
Horkelia sericata	silky horkelia	4.3	-	-	-
Horkelia tenuiloba	thin-lobed horkelia	1B.2	-	-	+
Horkelia truncata	Ramona horkelia	1B.3	-	-	-
Horkelia tularensis	Kern Plateau horkelia	1B.3	-	-	+
Horkelia wilderae	Barton Flats horkelia	1B.1	-	-	+
Horkelia yadonii	Santa Lucia horkelia	4.2	-	-	+
Ivesia aperta var. *aperta*	Sierra Valley ivesia	1B.2	-	-	-
Ivesia aperta var. *canina*	Dog Valley ivesia	1B.1	-	-	-
Ivesia argyrocoma var. *argyrocoma*	silver-haired ivesia	1B.2	-	-	+
Ivesia arizonica var. *arizonica*	yellow purpusia	2B.3	-	-	-
Ivesia baileyi var. *baileyi*	Bailey's ivesia	2B.3	-	-	-
Ivesia baileyi var. *beneolens*	Owyhee ivesia	2B.3	-	-	-
Ivesia callida	Tahquitz ivesia	1B.3	R	-	+
Ivesia campestris	field ivesia	1B.2	-	-	+
Ivesia jaegeri	Jaeger's ivesia	1B.3	-	-	-
Ivesia kingii var. *kingii*	alkali ivesia	2B.2	-	-	-
Ivesia longibracteata	Castle Crags ivesia	1B.3	-	-	+
Ivesia paniculata	Ash Creek ivesia	1B.2	-	-	+
Ivesia patellifera	Kingston Mountains ivesia	1B.3	-	-	+
Ivesia pickeringii	Pickering's ivesia	1B.2	-	-	+

Scientific Name	Common Name	CRPR	CESA	FESA	CA Endemic?
Ivesia sericoleuca	Plumas ivesia	1B.2	-	-	+
Ivesia unguiculata	Yosemite ivesia	4.2	-	-	+
Ivesia webberi	Webber's ivesia	1B.1	-	T	-
Lyonothamnus floribundus subsp. *aspleniifolius*	Santa Cruz Island ironwood	1B.2	-	-	+
Lyonothamnus floribundus subsp. *floribundus*	Santa Catalina Island ironwood	1B.2	-	-	+
Neviusia cliftonii	Shasta snow wreath	1B.2	C	-	+
Petrophytum caespitosum subsp. *acuminatum*	marble rockmat	1B.3	-	-	+
Physocarpus alternans	Nevada ninebark	2B.3	-	-	-
Potentilla basaltica	Black Rock potentilla	1B.3	-	-	-
Potentilla concinna var. *proxima*	early cinquefoil	2B.3	-	-	-
Potentilla cristae	crested potentilla	1B.3	-	-	+
Potentilla hickmanii	Hickman's cinquefoil	1B.1	E	E	+
Potentilla morefieldii	Morefield's cinquefoil	1B.3	-	-	+
Potentilla multijuga	Ballona cinquefoil	1A	-	-	+
Potentilla newberryi	Newberry's cinquefoil	2B.3	-	-	-
Potentilla pulcherrima	beautiful cinquefoil	2B.2	-	-	-
Potentilla rimicola	cliff cinquefoil	2B.3	-	-	-
Potentilla uliginosa	Cunningham Marsh cinquefoil	1A	-	-	+
Prunus eremophila	Mojave Desert plum	1B.2	-	-	+
Prunus fasciculata var. *punctata*	sand almond	4.3	-	-	+
Rosa gymnocarpa var. *serpentina*	Gasquet rose	1B.3	-	-	-
Rosa minutifolia	small-leaved rose	2B.1	E	-	-
Rosa pinetorum	pine rose	1B.2	-	-	+
Rosa woodsii var. *glabrata*	Cushenbury rose	1B.1	-	-	+
Rubus glaucifolius var. *ganderi*	Cuyamaca raspberry	3.1	-	-	+
Rubus nivalis	snow dwarf bramble	2B.3	-	-	-
Sanguisorba officinalis	great burnet	2B.2	-	-	-

in Chile, thus providing the sole example of a species of Rosaceae native to California that arrived here due to long-distance dispersal from South America. The other representatives of this subtribe in California include three species, two native and one naturalized, that belong to three different genera but are morphologically similar and all go by the common name burnet. Flowers of Sanguisorbinae lack petals, which is unusual in Rosaceae.

Of all the tribes in Rosaceae, Potentilleae includes the greatest number of native species in California as well as the greatest number of rare and endangered species (Tables 1, 2), including two species of *Potentilla* that are presumed extinct.

Tribe Potentilleae also includes the strawberry genus, *Fragaria*, notable for its economic importance and for the fact that its roughly 20 species, which occur throughout the north temperate regions of the world, exhibit multiple different numbers of sets of chromosomes, ranging from diploids (with one pair of each chromosome type) to decaploids (with five pairs of each chromosome type).

In California, the genus *Fragaria* is represented by three native species: the diploid woodland strawberry (*F. vesca*), which occurs throughout much of North America and Europe, and two octoploid species, the beach strawberry (*F. chiloensis*), found along the Pacific coast from Alaska to California and in South America, and the mountain strawberry (*F. virginiana*), whose range extends to eastern North America. Hybrids between *F. vesca* and *F. chiloensis* may be found in coastal areas where they co-occur. The modern octoploid cultivated strawberry, *F.* x *ananassa*, originated from hybridization between

TABLE 3. NON-NATIVE SPECIES OF ROSACEAE LISTED IN THE CALIFORNIA INVASIVE PLANT COUNCIL (CAL-IPC) INVENTORY.

Scientific name	Common names	Rating
Acaena novae-zelandiae	biddy-biddy	Watch
Cotoneaster franchetii	orange cotoneaster	Moderate
Cotoneaster lacteus	milkflower cotoneaster	Moderate
Cotoneaster pannosus	silverleaf cotoneaster	Moderate
Crataegus monogyna	English hawthorn	Limited
Potentilla recta	sulphur cinquefoil	Watch
Prunus cerasifera	cherry plum	Limited
Pyracantha angustifolia	narrowleaf firethorn	Limited
Pyracantha coccinea	scarlet firethorn	Limited
Pyracantha crenulata	Nepalese firethorn	Limited
Pyrus calleryana	Callery pear	Watch
Rubus armeniacus	Himalayan blackberry	High

F. chiloensis and *F. vesca* in gardens in Europe in the 18th century.

The fruits of strawberries are aggregates of achenes borne on an enlarged, convex, fleshy receptacle that is usually red. Thus, nearly all of the edible part of a strawberry is not derived from the ovaries of the pistils and is therefore not true fruit tissue, leading to their designation as accessory or false fruits (pseudocarps). A similar morphology evolved independently in the mock strawberry (*Duchesnea indica*), also a member of Potentilleae but not closely related to true strawberries.

Subfamily Amygdaloideae

The third subfamily, Amygdaloideae, represented by 23 genera and 51 species in the California flora, exhibits all of the fruit types found in the family with the exception of drupelets, though achenes and capsules are uncommon. Most members of this subfamily are shrubs and trees, but a few are perennial herbs.

Tribe Lyonothamneae includes just one genus, *Lyonothamnus*, and one extant species, Catalina ironwood (*L. floribundus*) with two extant subspecies, both endemic to the Channel Islands and considered rare. Fossil evidence suggests that the genus included several other species that were found in the current states of Oregon, Nevada, and California between seven and 23 million years ago. Catalina ironwoods are trees with distinctive, peeling, reddish bark; evergreen leaves that are opposite (unusual for Rosaceae); and small, white flowers borne in large, flat-topped panicles. They are cultivated and sold in nurseries for use in landscaping.

Almonds and stone fruits (apricots, cherries, peaches, and plums) are classified in the genus *Prunus*, the only member of tribe Amygdaleae, which comprises 200-400 species of shrubs and trees and is characterized by the presence of drupe fruits; glands on the petioles and/or leaf blades; and leaves and bark that emit a strong almond extract-like odor when crushed.

As is the case with the family as a whole, *Prunus* is often considered a primarily north-temperate group, but in fact the genus harbors extensive diversity in tropical regions of Central and South America, with one species widely distributed in sub-Saharan Africa. Phylogenetic studies have resolved three major groups of lineages within *Prunus*, corresponding to three different inflorescence types: the solitary flower group, including almonds, peaches, and plums, represented in the California flora by Sierra plum (*P. subcordata*) and several other native and naturalized taxa, including several desert species; the corymb (flat-topped cluster) group, including cherries, represented in the California flora by the native bitter cherry (*P. emarginata*); and the raceme (elongated axes bearing numerous flowers) group, including bird-cherries and laurel-cherries, represented in California by holly-leafed cherry (*P. ilicifolia*) and western choke-cherry (*P. virginiana* var. *demissa*). The first two groups, which are the most economically important and familiar, are most diverse in temperate regions of the northern hemisphere, while the third group is well-developed in tropical regions. The genus as a whole is believed to have originated in east Asia. Within each of the three lineages, the species native to California are more closely related to species in Asia than to the California members of the other lineages, indicating that each lineage arrived here independently of the others.

All of the pome-bearing species of Rosaceae are classified in subtribe Malinae of tribe Maleae, which is well represented by native and cultivated

OPPOSITE PAGE, TOP TO BOTTOM: Oso berry (*Oemleria cerasiformis*). Photo by Steve Matson (CC BY-NC-3.0). • California sheepburr (*Acaena pinnatifida* var. *californica*). Photo by Vernon Smith (CC BY-NC-ND 3.0). • Blackbrush (*Coleogyne ramosissima*). Photo by Steve Matson (CC BY-NC 3.0).

species throughout the northern hemisphere. The tribe also includes several early-diverging genera with dry fruits (follicles or capsules), none of which are native to California, despite the misleading specific epithet of Arizona rosewood, *Vauquelinia californica*. These relationships suggest that the whole genome duplication event that gave rise to Maleae paved the way for the later evolution of the unique fruit type (pome) found in Malinae. Intriguingly, the closest relative of this widely distributed, species-rich tribe, whose members are all woody plants, is *Gillenia*, a genus with just two species of perennial herbs native to the eastern and central US.

The most familiar pomes, such as apples and pears, have papery or cartilaginous cores with five chambers, but in several genera, such as the cotoneasters (*Cotoneaster*), firethorns (*Pyracantha*), and hawthorns (*Crataegus*), the core consists of several bony-walled stones. One iconic California species, the toyon or Christmas-berry (*Heteromeles arbutifolia*) has pomes that are unusual in having a cartilaginous core that consists of two or three separate segments.

Tribe Spiraeeae is widely distributed in North America and Eurasia; five genera are native to California. Spiraeas (*Spiraea*), represented by two shrub species in montane conifer forests, and ocean spray (*Holodiscus discolor*), a highly variable species that occurs from the coast to the high Sierra, have simple leaves with toothed margins. Rock-spiraeas (*Petrophytum*) are mat-forming alpine shrubs (often on limestone) with simple, untoothed leaves, while partridge foot (*Luetkea pectinata*) is a trailing subshrub with ternately dissected leaves found in the Klamath and Cascade Ranges. Finally, goatsbeard (*Aruncus dioicus*) is a perennial herb with pinnately compound leaves found in northern California along streams and in forests below 2,000 meters.

Several of the tribes of Amygdaloideae exhibit disjunct distributions between North America and eastern Asia. Tribe Neillieae is represented in California by two species of ninebark (*Physocarpus*), which includes several other North American species and one in eastern Asia; *Neillia*, the only other member of the tribe, occurs only in eastern Asia. Tribe Exochordeae includes three genera of shrubs: *Exochorda* and *Prinsepia*, each with a few species in eastern Asia, and *Oemleria* (oso berry), small trees found from the coast to the Sierra Nevada in California and as far north as British Columbia. *Oemleria* is the only member of Rosaceae that produces aggregates of several fleshy drupes; based on the fruit type, the genus was placed in the same tribe as *Prunus* in some previous classifications, but that relationship has not been supported by recent molecular phylogenetic studies.

Tribe Sorbarieae includes four genera of shrubs with strikingly different morphologies and distributions: *Adenostoma* (chamise), with two species in California and Baja California that produce simple leaves (tightly clustered in *A. fasciculatum*) and are dominant in chaparral communities; *Chamaebatiaria* (fernbush, desert sweet), with one western North American species found in sagebrush scrub and pinyon/juniper woodland that produces glandular, twice-pinnately compound leaves remarkably similar to those of mountain misery (*Chamaebatia*); and two Asian genera: *Spiraeanthus*, with fern-like leaves, and *Sorbaria*, with once-pinnately compound leaves.

Perhaps the most intriguing biogeographic pattern is found in the tribe Kerrieae. Three of its four genera are monotypic (one species each), with two native to Asia and one, *Coleogyne* (blackbush), found in the eastern Sierra Nevada and deserts of California eastward to Colorado. The fourth genus, *Neviusia* (snow wreath) includes two North American species with limited distributions: *N. alabamensis*, known from a few occurrences in five states in the southeastern US, and *N. cliftonii*, known only from the Shasta Lake area.

Many species of Rosaceae are planted in the Regional Parks Botanic Garden and are worth a visit.

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Toyon with Our Hearts

Rachel Prunier and Laurel Thomas

As both a recent transplant from the East Coast (R. Prunier), and a California native (L. Thomas), we authors share a passion for ecology, evolution, and conservation of California plant species. These shared interests brought us together to study toyon, *Heteromeles arbutifolia*, (Lindl.) M. Roemer, a member of the Rosaceae family and an endemic to the California Floristic Province (CFP). After traveling all over California collecting over 200 individuals of toyon, it has become clear to us that toyon is both a very typical and very strange CFP shrub and that it deserves deeper study to determine how it can thrive in such a wide variety of environmental conditions.

We want to understand what allows this attractive evergreen shrub to grow seemingly everywhere, on lower (>4000 feet) mountain slopes and in coastal regions from Humboldt County to Baja California. Toyon is a dominant and co-dominant component of chaparral and woodland ecosystems and is found with species such as scrub oak, California sagebrush, and manzanita species.[1] Toyon is ecologically important, as one of the winter food sources for birds and a spring and summer nectar and pollen source for native bees.

In many ways, toyon is a typical CFP shrub. It is well adapted to the mediterranean climate that typifies much of the CFP. Regions with a mediterranean climate have cool, wet winters; hot, dry summers; and fires in the summer and autumn. Toyon can survive fires by resprouting from its root crown. It has tough, thick, toothed leaves which are resistant to herbivory and wilting when water is scarce. Like chia, toyon also has mucilaginous seeds (opposite page). The mucilaginous coating on the seeds has at least two functions, both related to the unpredictable, often intense rainfall in CFP winters. First, it helps the seeds retain water when it does rain, perhaps increasing germination success. Second, the sticky coating holds the seeds in place where they fall, preventing them from being washed away by the often-intense rainfall. This mucilaginous coating is intriguing, and next fall, students in the Prunier lab will be investigating these two functions as well as a third potential function—preventing fungal infections.

However, in some ways, toyon is unlike other CFP species. While collecting, we observed remarkable variation in leaf traits. Toyon leaves vary in shape, size, and amount of toothing. Some variation in leaf shape and size is to be expected (especially in plants growing in the shade versus the sun), but variation in toothing less so. In some locations the leaves were aggressively toothy, but in others we found plants with leaves so smooth that they looked like a bay tree (bottom left). We also noted a remarkable amount of variation in flowering time. Typically, an individual plant will flower at one time of year, and later its fruits will mature roughly simultaneously, but toyon appears to be less constrained. We found a plant with flowers, green immature fruit, and mature red fruit on it simultaneously. In addition to being strange morphologically and developmentally, toyon is also phylogenetically strange. Unlike many other CFP species, toyon does not have any close relatives in the region. While the CFP has many large genera (*Ceanothus* has more than 50 species and *Arctostaphylos* has more than 40 species endemic to California), toyon is the only species in its genus. This combination of typical and atypical characteristics makes toyon an intriguing species to study.

ABOVE: Toyon at the UC Santa Cruz Fort Ord Natural Reserve, Monterey. All photos by Laurel Thomas. • BOTTOM LEFT: Variation of toyon leaves. • BOTTOM RIGHT: A fruiting toyon.

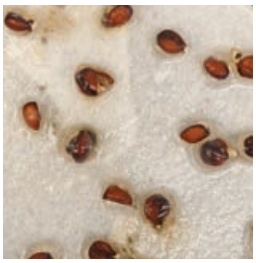
We have two alternate hypotheses for why toyon is able to live in so many different habitats: 1) Toyon individuals are adapted to their local environment and survive best where they are from, or 2) Toyon individuals are phenotypically plastic, and each individual could live in any number of environmental conditions.

These different modes of adaptation have consequences for the future of the species, especially in light of habitat fragmentation and climate change. As a result of human actions, California is experiencing increasing temperatures, decreasing snowpack, more intense and infrequent rainfall, and extreme fire regimes. All these changes will affect plant populations. While animals are physically moving to find more habitable homes,[2] plants cannot easily move. To survive the changing climate, plant populations have three options: they can alter their phenotype to match their environment (phenotypic plasticity), evolve to match the new environment, or move to a location with a more favorable climate.[3]

A species that is phenotypically plastic should be easier to conserve because individuals adapted to local conditions would be available to use in restoration projects or as possible sources for new populations beyond the species' current range. However, if populations are adapted to their local environment, not all populations will be good sources. We are using two approaches to determine the extent to which toyon is plastic versus locally adapted: conservation genomics and common-garden/reciprocal transplant experiments.

In a conservation genomic study individuals are sampled across the species' geographic range. Their genomic sequences can then be used to infer which genes are under selection and are undergoing local adaptation[4]; further, locations that are barriers to gene flow can be identified. With these data, critical populations and corridors for gene flow can be conserved, and potential sources for restoration can be identified. In our study, we are sequencing the genomes of 150 individuals collected across the species' range as part of the California Conservation Genomics Project (CCGP). The goal of CCGP is to bridge the gap between policy and research to address the growing extinction threat.[5]

Our genetic data will be paired with a detailed study of leaf and growth traits (e.g., branching patterns). By growing toyon sourced from across its range in the same location, we will determine the extent to which variation in these traits is due to genetic differences or phenotypic plasticity and the consequences of that variation on growth and survival. Using the offspring of 40 of the individuals sequenced for the genomics project, we are establishing two experimental gardens: one at Blue Oak Ranch UC Reserve near San Jose, California, and one at UCLA Stunt Ranch Santa Monica Mountains Reserve near Los Angeles, California. What we learn from these experimental gardens will then be applied to streamline conservation management strategies. If populations of toyon have adaptations to hotter and drier environments, high plasticity, or unique traits, those populations can be targeted for conservation and restoration projects. The work can also serve as a model for determining the relative importance of local adaptation and plasticity in species like toyon with wide geographic ranges. We are excited to continue our research on the plant that's been toy-on with our hearts.



Mucilaginous coating on toyon seeds.

RACHEL PRUNIER, PhD, is an evolutionary biologist at UCLA, awed by the new-to-her California flora. When she isn't teaching and mentoring students, she is exploring her new state. LAUREL THOMAS is studying Environmental Science at UCLA and working alongside Dr. Prunier to execute a toyon common-garden project within the UC Natural Reserve System.

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Sunday, February 12, 2023, at 2:00 PM:

Please join us at the East Bay Regional Parks Botanic Garden for a special docent-led, family-friendly, **PLANT ADAPTATION TO HABITAT TOUR**. On this tour, you will explore the different parts of California represented in the Garden. Each of these sections have different types of habitat—from the desert to the mountains to the sea bluffs to the rain forest—to which the plants have adapted. Meet in front of the Botanic Garden Visitor Center. *Rain cancels.*

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