MANZANITA

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The *Arctostaphylos andersonii-auriculata* Complex in the Greater Bay Area

by Bart O'Brien, Garden Director

John Rusk

John Rusk

Flowers and fruit of the Santa Cruz manzanita

The *Arctostaphylos andersonii-auriculata* complex is one of the most interesting and beautiful groups of manzanitas. The largest leaves, largest inflorescenses, and some of the tallest plants are found in this group. Like the rest of the genus, this group is a case of mix and match: smooth bark to fibrous bark, glandular to eglandular twigs and foliage, prostrate to treelike growth habit, green to grey and hairy to smooth foliage, and fruits of solid stones to fruits with separable stones. All are spectacular garden plants. The shared characteristics of this complex include strongly overlapping, spirally arranged leaves with extremely short petioles and auriculate leaf bases that clasp their stems. Each of these Bay Area obligate-seeder species is known to co-occur with the burl-forming *Arctostaphylos crustacea* in the vicinity. Each of these species grows on unusual substrates, most often sandstones or sandy substrates (and in one case sandstone and granite), while the rest grow on nutrient-poor shales. Many have especially colorful new growth. And virtually all of them are considered endangered or rare.

The heart of the *andersonii-auriculata* complex includes the nine endemic species from the San Francisco Bay Area to the Monterey Bay Area. Jepson considered all of them to be either *Arctostaphylos andersonii* or varieties of *A. andersonii*, but these admittedly similar manzanitas may be best considered examples of speciation in action.

Four of these nine species were named after their area of origin: *montaraensis* from Montara Mountain, *regismontana* from Kings Mountain, *pajaroensis* from the Pajaro Hills, and *gabilanensis* from the Gabilan Mountain Range. Three more species were named for attributes of their leaves: *auriculata* for its

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auriculate or ear-shaped leaf base, *pallida* for the pale color of the new leaves, *imbricata* for the arrangement of the leaves along the stems. *Arctostaphylos glutinosa* was named for its sticky fruits. And the last one, *andersonii*, honors a person, Dr. Charles Lewis Anderson (1827-1910). See below for more about Dr. Anderson.

It took 128 years for the greater Bay Area members of the *andersonii* complex to be named and described. It is informative to note the order in which these manzanitas were discovered and determined to be different enough from one another to warrant naming. The first of the group, *A. andersonii*, was named in 1876 from plants in the hills above Santa Cruz by Asa Gray (1810-1888), professor of botany at Harvard University. In 1905, the second, *A. auriculata* from the Mount Diablo area; in 1931, the third, *A. imbricata* from San Bruno Mountain; in 1933, the fourth, *A. pallida* from the East Bay foothills; and in 1933, the fifth, *A. regismontana* from Kings Mountain were all named by Alice Eastwood (1859-1953), curator of botany at the California Academy of Sciences in San Francisco. In 1940, *A. pajaroensis* from the Pajaro Hills, the sixth species in the group, was named in the monograph of the genus by Joseph Edison Adams (1903-1981), professor of botany at the University of North Carolina and a PhD student of Jepson's in the 1930s. Also, in 1940, Beryl Olive Schreiber (later Jespersen—often incorrectly spelled as Jesperson) (1911-1968), who worked for the US Forest Service and later *Sunset* magazine, described the seventh member of the group, *A. glutinosa*, from the "chalks" of Ben Lomond Mountain. James B. Roof (1910-1983), the first director of the Regional Parks Botanic Garden, named *A. montaraensis* from Montara Mountain as the eighth and last of the immediate Bay Area taxa of the group in 1967. The ninth and last of the regional members of this complex, *A. gabilanensis* from the Gabilan Range, was named in 2004 by manzanita researchers V. Thomas Parker and Michael C. Vasey, both of San Francisco State University.

Seven of the nine members of this group have distinctive and unique attributes: Santa Cruz manzanita (*A. andersonii*) is the only one with bifacial leaves. Gabilan manzanita (*A. gabilanensis*) is the only one with fruits composed of a single solid stone. San Bruno Mountain manzanita (*A. imbricata*) is the only one with a prostrate growth habit in the region, though there are some low-growing Montara Mountain manzanitas on exposed granitic ridges. Pajaro manzanita (*A. pajaroensis*) is the only species in the group with shaggy, fibrous bark. Mt. Diablo manzanita (*A. auriculata*) is the only species with whitish leaves that are densely covered with short hairs, at least when the leaves are young. Pallid manzanita (*A. pallida*) is the only species with glaucous-green leaves. Montara Mountain manzanita (*A. montaraensis*) has bright green, non-glaucous leaves. The other two species have suites of characters that make them unique: Kings Mountain manzanita (*A. regismontana*) is often tree-like and has long narrow hairy glandular leaves. Schreiber's manzanita (*A. glutinosa*) is shorter than most and has grey foliage, densely hairy stems, and sticky fruits.

Pattie Litton

Hairy stems of Santa Cruz manzanita

Santa Cruz Manzanita

Santa Cruz manzanita (*A. andersonii*) is the only greater Bay Area species in this group that has stomata only on the underside of its bifacial leaves, whereas all the rest, as well as the vast majority of manzanita species, are isofacial (having identical leaf faces, with stomata on both leaf surfaces). This species has the largest leaves in the genus, reaching up to six inches or more in length. Easy to grow in most of the Bay Area, this species is adaptable to many garden conditions as long as they do not involve excessive amounts of water. Of the

larger shrubby manzanita species, this one is the most tolerant of partial shade, and in the wild is often found in openings in redwood and mixed evergreen forests. With so many likeable traits, and so much variability, one would expect that there would be many selections of this species, but to date there are fewer than a handful and all have been identified by the staff of the UC Santa Cruz Arboretum.

I have always been curious about the person that Asa Gray honored by naming *Arctostaphylos andersonii*, and I don't recall ever having seen anything about "Anderson" before. This very early-named manzanita species was named in 1873 after the collector of a type specimen "from hills of Santa Cruz," listed only as C.L. Anderson: Dr. Charles Lewis Anderson of Santa Cruz. For someone born in 1827, Anderson moved around quite a bit. He was born in Virginia but moved to Indiana when he was ten years old. After college he lived in Minnesota for ten years, then Nevada in 1862 for four years, and, finally, in 1866, he moved to Santa Cruz, where he lived for the rest of his life. Dr. Anderson wrote parts of *The History of Santa Cruz County* by Edward Sanford Harrison in 1892. On page 304 of that volume, there's a brief biographical section about Dr. Anderson that includes this paragraph:

> Since Dr. Anderson began the practice of medicine, that has been his chief occupation. Most of his leisure time is devoted to scientific study, his favorite branches being: geology, botany, and zoology. His impulse in this direction is the result of early contact with professors and students of Harvard and Yale Colleges, whom he frequently accompanied on botanizing expeditions. In his scientific studies Dr. Anderson has been associated with several eminent men, notably, Asa Gray, Horace Mann, Jr., Henry D. Thoreau, D.C. Eaton, and M.G. Farlow. Dr. Anderson is a writer of ability, and a frequent contributor to the magazines. His articles are chiefly upon scientific topics, and his contributions to this volume are fair samples of his work.

In 1876, the holotype specimen for *Arctostaphylos andersonii* is cited by Asa Gray as being from "Hills behind Santa Cruz, California, Dr. C. L. Anderson, 1873" on page 83 of *Proceedings of the American Academy of Arts and Sciences* (*New Series, Vol. 3. Whole Series, Vol. 11. From May 1875 to May 1876*). Currently, there is a Gray Herbarium specimen that does not appear to have a sheet number but does have a barcode number: 00014665. The information on this specimen reads in part: "Redwoods, above Santa Cruz, California 1873. C.L. Anderson." An isotype for this species, listed as US #62464, is a specimen at the US National Herbarium at the Smithsonian Institution. Interestingly, there are a number of specimens in Paris that may also be isotypes for this species.

John Rusk

Flowers of Mount Diablo manzanita

Mount Diablo Manzanita

The Mount Diablo manzanita (*A. auriculata*) was the second species in this group to be described, in 1905, by none other than Alice Eastwood. This very distinctive species has grey-white leaves, hairier than most in this complex. Plants are confined to sandstone substrates in the vicinity of Mt. Diablo and can also be found at Black Diamond Mines Regional Preserve. In gardens, they are adaptable to garden conditions as long as they have well-drained soils. There are two little known, but extremely desirable, cultivars: 'Knobcone Point' and 'Diablo Blush'. Both have atypically small, nearly round leaves with extremely short internodes. 'Knobcone Point' has serrated leaves and never blooms as it is effectively a permanently juvenile form. 'Diablo Blush' has small gray leaves and a profusion of small clusters of pink flowers. It will slowly reach about six feet tall and ten feet wide.

'Knobcone Point' has serrated leaves and never blooms as it is effectively a permanently juvenile form. . .

When thinking of juvenile plants, most Californians correctly think of Eucalyptus, as one can readily see differences in juvenile versus mature specimens—the former often have grey, perfoliate leaves and do not bloom. The juvenile foliage of manzanitas is typically serrated, but manzanitas grow out of this phase quickly, usually within months, sometimes taking as long as a year. There are four manzanita cultivars that appear to be permanently juvenile: 'Green Witch', 'Baby Bun', 'Small Change', and 'Knobcone Point'. (The first one is my selection, the second and third are Roger Raiche's, and the last was selected by Steve Edwards.) It is certainly possible that over time any of these might eventually produce adult foliage and flowers, but to date that has not been observed, and the oldest of these clones has been in cultivation since 1982.

Bart O'Brien

Arctostaphylos auriculata 'Knobcone Point' was collected from Mount Diablo in 1985 and currently grows in the Canyon section of the garden. Note the serrated leaves of its perpetually juvenile foliage.

Pallid Manzanita

Pallid manzanita (*A. pallida*) is our most local species, with plants found just outside the Botanic Garden and almost entirely on East Bay Regional Park District lands from Sobrante Ridge Regional Preserve south to Huckleberry Botanic Regional Preserve, with a few outliers in Redwood Regional Park. Some of the largest specimens of pallid manzanita are found at Sobrante Ridge and are among the most beautiful ancient manzanitas I've ever seen. This species is a federally listed threatened species and a State of California listed endangered species. This is the only manzanita that should be planted in the El Sobrante Ridge area and along Manzanita Drive and Skyline Boulevard in the Oakland Hills in the vicinity of Huckleberry Preserve.

Peter Thomas

Pallid manzanita in the Botanic Garden

John Rusk

John Rusk

San Bruno Mountain Manzanita

San Bruno Mountain manzanita (*A. imbricata*) has a prostrate growth habit of low intertwined branches, though in cultivation it piles up upon itself leaving a skeleton of leafless branches beneath a thin layer of active growth. It is not often seen in cultivation, but it is not particularly difficult to grow. It even tolerates clay soils—just don't overwater. Plants easily reach six to ten feet across. This is a State of California listed endangered species. It is most easily seen on Kamchatka Point northeast of the road to the summit of San Bruno Mountain.

Pattie Litton

San Bruno Mountain manzanita branch tips

Pattie Litton

Tangled branches of San Bruno Mountain manzanita

Montara Mountain Manzanita

Montara Mountain manzanita (*A. montaraensis*) is an interesting case for a number of reasons. It has one of the most unusual natural distributions of all manzanitas, as it is known only from Montara Mountain itself and a very small population on San Bruno Mountain. In the early 1960s, there was but a single known plant on San Bruno Mountain, and it was discussed as an upright form of the nearby, always prostrate, San Bruno Mountain manzanita. That single individual was thought to be 33 years old when it was consumed by the fire of 1964; however, by the time *A Flora of the San Bruno Mountains* was written in 1990, there were "about two dozen plants" present. It is not known if this represents a recent expansion of the population from Montara Mountain to San Bruno Mountain, or if the species had been present in the past and reduced to that single individual known in the early 1960s. The pleasing-sounding name *montara* is a happy accident: "Montara is a made-up word when somebody misread a map. An 1838 map labeled the valley of the south fork of San Pedro Creek Cañada Montosa (wooded valley). The next mapmaker (in the 1850s) misspelled the name and applied it to the mountain, hence Montara Mountain." (*Montara Mountain* by Barbara VanderWerf. 1994. Page 9.) This species is easily grown in the Bay Area but is not often seen in gardens or in many collections, most likely because there are other desirable and more easily obtained species and selections in this "large shrub" category.

Two views of Montara Mountain manzanita in the Botanic Garden John Rusk

Pattie Litton

stickpen

Montara Mountain manzanita in the UC Botanical Garden

John Rusk

Avoid dusty places! Kings Mountain manzanita

Pattie Litton

Hairy glandular leaves of Kings Mountain manzanita

Kings Mountain Manzanita

Kings Mountain manzanita (*A. regismontana*) is extremely rare and threatened by conversion of its chaparral habitat into forest. I remember seeing beautiful specimens in the mid-1980s in an abandoned quarry off Skyline Boulevard in San Mateo County, but that entire population is gone, and the area is now Douglas fir forest with just a few gray weather-beaten branch fragments of Kings Mountain manzanita remaining. The most easily accessible plants are found along Kings Mountain Road at a very notable hairpin curve. Even in this location, there are large Douglas fir trees, casting ever more shade. From the 1940s through the 1970s, before *Arctostaphylos regismontana* was widely accepted as its own species, these plants were highly regarded horticulturally as the "Kings Mountain form" of *Arctostaphylos andersonii*. They have densely hairy glandular leaves, and, because of this characteristic, they are not the best choice for dusty, windy areas. Where they are well suited, they are spectacular and grow to resemble small trees, beautifully displaying their amazing rich-red, smooth bark.

John Rusk

Neal Kramer

Fiery copper-colored new growth on Pajaro manzanita near Prunedale, Monterey County

John Rusk

Flowers and fruit of Pajaro manzanita in the Botanic Garden

Pajaro Manzanita

Pajaro manzanita (*A. pajaroensis*) is best seen at Manzanita County Park in Prunedale. Some of the most beautiful and dependable manzanita cultivars are from the Pajaro manzanita. The most consistently and widely available has been our Botanic Garden's selection 'Paradise' that has been widely grown for over 40 years. It is not the easiest selection to grow in hot inland conditions, but it is one of the most spectacular manzanitas with its deep-pink flowers, fiery copper-colored new growth, and slate-blue-grey mature foliage. 'Paradise' also has rough shaggy bark and an open spreading growth habit to ten feet tall with a slightly wider spread.

Coincidentally, the hybrid 'Sunset' has been grown for just as long but was not as consistently available until the late 1990s. 'Sunset' was named for the 75th anniversary of *Sunset* magazine and is a hybrid with *A. hookeri*, which gives this clone its small white flower clusters. The dense shiny green leaves make this selection an excellent choice for an informal hedge or screen.

There are also two cultivars selected by notable native plant horticulturist-botanist Roger Raiche: 'Warren Roberts' and 'Myrtle Wolf'. Originally, 'Warren Roberts' was known as "Roger's bronze" for its rich bronzy new growth and "eucalyptoides" for its broadly triangular blue-grey eucalyptus-like leaves. Stems on this cultivar are strongly upright. Myrtle Wolf was a major supporter of Bay Area horticulture and was particularly fond of pink flowers, so it is not surprising that this selection was originally known as "best pink." In addition to its profusion of deep pink flowers, this cultivar has much smaller leaves and a more compact growth habit. Though I suspect it will grow taller, the largest specimen I have seen of 'Myrtle Wolf' is only about four feet tall and wide.

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Sticky fruits of Schreiber's manzanita, Lockheed 'chalks' on Ben Lomond Mountain, Santa Cruz County

Schreiber's Manzanita

Schreiber's manzanita (*A. glutinosa*) is restricted to chaparral and knobcone pine (*Pinus attenuata*) woodlands in the "chalks" area of Ben Lomond Mountain in the Santa Cruz Mountains. Nearly all of this rare plant's habitat is on property owned by Lockheed Martin Space Systems. The whitish soils that give the chalks their name are derived from the highly siliceous Monterey shale. This species is the only member of the group to have flower ovaries densely covered with long white hairs that may be glandular or nonglandular. This unusual locality also harbors the entire population of the even rarer Ohlone manzanita (*Arctostaphylos ohloneana*), described in 2009 by Michael Vasey and Thomas Parker.

Bart O'Brien

Gabilan manzanita in the Botanic Garden

Gabilan Manzanita

The last of the northern endemics in the *andersonii* complex is the most recently described and the least known: Gabilan manzanita (*A. gabilanensis*). In its general look, it favors Mt. Diablo manzanita, with its gray foliage, upright growth habit, and smooth red bark. It occurs in two different locations in the Gabilan Range, the rugged mountains that straddle the border between Monterey and San Benito counties. Almost all these plants are on private land that is inaccessible to the public. The larger population is southeast of Fremont Peak, and the much smaller, southern population is near La Gloria Road. Currently, this species is very rare in cultivation, but can sometimes be found for sale in specialized native plant nurseries and botanic gardens.

There are another nine members of the auriculate-leaved group found in San Luis Obispo and Santa Barbara counties and on Santa Cruz Island. These are perhaps even more complicated than those of the greater Bay Area and may be the focus of a subsequent article in the *Manzanita*.

A Tale of Manzanita Gall Aphids from Butte County

by Donald G. Miller III, Department of Biological Sciences, California State University, Chico

Part I: A Drama in Miniature Between Insects and Their Host Plants

Try to imagine, if you can, a gall aphid, a poppy seed-sized animal with a fondness for tight spaces and an insatiable thirst for plant sap. "Tamalia" (formally a gall-inducing aphid, *Tamalia coweni*) hatched from an egg laid last summer at the base of a common manzanita (*Arctostaphylos manzanita*), a member of the heath family (Ericaceae), with tough, waxy leaves and sinewy branches. Tamalia's natal shrub is on a hillside in the chaparral along the old Humboldt Road in Butte County, California. A century and a half earlier, pioneer and gold-seeker turned agriculturist John Bidwell helped finance this road in an effort to link the Sacramento Valley with the silver mines of Nevada and beyond. Today, only portions of the Humboldt Road remain, but in places the ruts from the old freight wagon wheels are still visible.

Tamalia climbs the bush purposefully and doggedly, negotiating rough bark and the occasional ant. The shrub seems of Andean proportions, but eventually she finds a newly unfolding leaf and slakes her thirst by tapping directly into the phloem with her slender beak. This seems a good place to make a home, so she begins by feeding methodically, penetrating the leaf with her beak time and again, leaving a neat little row of holes like so many rivets on a ship's hull. She continues feeding, artfully directing the leaf to envelop her body. The view of the sky is shrinking fast. Tamalia has initiated a gall (Figure 1), a benign plant tumor providing necessary food and shelter to her at the expense of her natal shrub.

Figure 1. Galls induced by the aphid *Tamalia coweni* on common manzanita (*Arctostaphylos manzanita*) at Big Chico Creek Ecological Reserve, Butte County, California

Another *Tamalia coweni* aphid shows up and invites herself into the gall (in this generation, *Tamalia* individuals are always female). We'll call her "Communia" as the gall is now communally-occupied. Communia is starved and exhausted, and immediately begins feeding alongside Tamalia (Figure 2). Like her ancestors, Tamalia has a tolerance for strangers and pays Communia no heed. This will be a joint venture. The gall continues to swell, the leaf now reddening and thickening.

The next day, "Inquilina" (formally *Tamalia inquilinus*, Figure 3) shows up at the entrance to the gall. Inquilina, a close phylogenetic relative, comes from a rogue branch of the aphid family that long ago gave up initiating galls to become professional freeloaders. Inquilina couldn't produce a gall even if she tried, but she has managed to present herself at Tamalia's doorstep, and she walks right in. In her youth, Inquilina is delicately built and seemingly innocuous, but that will soon change. The gall seals up, providing a moist, nourishing environment protected from the desiccating sun.

All three aphids feed furiously within the gall. Their sugary waste has to go somewhere: it crystallizes on the gall walls. (Humans call this stuff "honeydew" for some reason.) Soon they are getting too big for their skins and, like all insects, they must shed them. Each aphid will repeat this three more times before reaching adulthood. Tamalia and Communia now resemble miniature pincushions, with swollen bellies, tiny legs and no hint of wings. Inquilina has been transmogrified: like the werewolf, she has grown coarse and shaggy, a thick-skinned brute (Figure 4). At least she doesn't attack, but she is otherwise hardly benign.

Time to start a family. Fortunately for Tamalia, there is no need for romance. Like the water flea and a few other peculiarities of the animal kingdom, she is capable of parthenogenesis (virgin birth). In fact, she

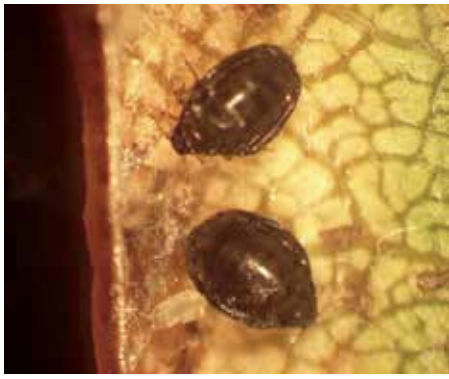


Figure 2. Two *Tamalia* gall-inducers in a communally occupied gall

Figure 3. Two early-instar heterospecific *Tamalia* aphids sharing a gall. The animal on the upper left, *Tamalia inquilinus*, is an inquiline parasite of the actual gall-inducer, *Tamalia coweni*, on the lower right. Note the pale, gracile aspect of *T. inquilinus* at this early stage.

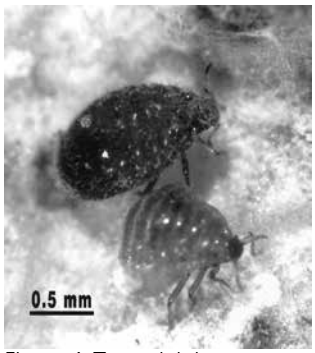


Figure 4. Two adult heterospecific *Tamalia* aphids sharing a gall. *Tamalia inquilinus*, on the upper left, is an obligate brood parasite of the gall-inducer, *Tamalia coweni*, on the lower right. Note the robustness and vestiture of *T. inquilinus* at this late stage.

clones herself. No worries about absentee fathers: they don't even exist (in this generation). But it gets better: not only is Tamalia carrying her daughters within; they are carrying *their* daughters, like so many Russian dolls telescoped together. The three aphids begin giving live birth to clonal daughters in the gall.

One day a buzzing commotion outside the gall signals the arrival of a silver fly (Family Chamaemyiidae). She cannot gain entrance to the gall, but deposits an egg on the gall's seam. Before long "Maggie" will hatch from this egg to enter the gall and cause mayhem. The gall has become a Horton-Hears-a-Who microcosm of high drama.

Inquilina was never a helper, but now she is the roommate from Hell. Not only is the gall chamber piling up with shed skins and aphid waste (much of it Inquilina's), but Inquilina somehow has the edge on reproduction: she is pumping out offspring faster than her gall-inducing hosts (Tamalia and Communia). Worse, Maggie has begun attacking the aphid offspring, by fiendishly penetrating their bodies with her hook-like mouthparts and draining their life juices. One day Maggie dispatches Communia too, but she will never touch Inquilina. Apparently silver fly maggots have no interest in woolly inquiline aphids.

Still, some of the brood survive to become as large as Tamalia. They cannot stay within the gall, but then, they're built for a completely different lifestyle. Unlike Tamalia and Inquilina, they possess large eyes, long legs and, most telling, wing buds. It is now six weeks after Tamalia hatched, and she and Inquilina are past middle age. The summer drought has begun, the gall dries and cracks open, providing an exit for the youngsters. One night they leave the gall and climb out of their skins for the last time. By morning, they have gossamer wings, and at the first breeze they lift to the sky and sail off as aerial plankton in search of more manzanita bushes. If they find a suitable plant, they will give birth to another generation of pincushion-like gall-makers. These, in turn, will produce yet another round of winged aphids, but with a twist: some of these will be sons; the rest, sexual daughters capable of mating and laying eggs for next year's cycle to repeat itself.

Figure 5. Eleni Mahlis-Miller, daughter of the author, sampling aphid galls from Roof's manzanita (*Arctostaphylos manzanita roofii*) at Cohasset Ridge, Butte County. August 2018.

Maggie, who has devoured half the aphids within the gall, now morphs from writhing monster to quiescent puparium. After the gall dries out, Maggie will emerge as an adult silver fly, who, like Inquilina, is entirely dependent on gall-makers like Tamalia.

Tamalia and Inquilina will live out their days within the gall. Amazing how two life histories, united in a common ancestor, have diverged in parallel: one, a parasite on plants; the other, a parasite of parasites on plants. In a remarkable manifestation of adaptation, each has succeeded in producing clonal subunits blanketing the landscape, all in a miniature drama along the old Humboldt Road.

Part II: A More Prosaic Account of Manzanita Gall Aphids and Their Host Plants

Butte County, situated in California's Northstate, stretches from the east bank of the Sacramento River to the mountains, where the granitic Sierra Nevada meets the volcanic Cascades. An elevational transect of Butte County runs from its western boundary, at about sea level, clear up to the Pacific Crest Trail in excess of 2000 meters; this is paralleled by a remarkable fourfold gradient in precipitation. The considerable variety in parent rock material, as well as climatic regime, supports upwards of seven *Arctostaphylos* taxa.

Although the majority of the 65+ species of *Arctostaphylos* in California are considered narrow endemics and "edaphic specialists" on particular soils, those in Butte County tend to be wide-ranging (with a couple of interesting exceptions). Beginning at about 100 meters elevation and continuing well up into the yellow pine belt at 1200 meters is common manzanita (*Arctostaphylos manzanita* subsp. *manzanita*).

Figure 6. Basal burl of Roof's manzanita (*Arctostaphylos manzanita* subsp. *roofii*) at Cohasset Ridge, Butte County. This subspecies was named for James B. Roof, founding director of the Regional Parks Botanic Garden and an avid student of *Arctostaphylos*.

In a narrow belt on Cohasset Ridge grows Roof's manzanita (*Arctostaphylos manzanita* subsp. *roofii*) (Figure 5), distinguished from the nominate subspecies especially by the presence of a burl or woody lignotuber (Figure 6), from which *A. m.* subsp. *roofii* can resprout following fire; *A. m.* subsp. *manzanita* is typically killed by fire. On the far opposite side of the Great Valley, in western Glenn County, is the only other known population of *A. m.* subsp. *roofii*. The available evidence suggests that Tamalia aphids induce galls on both subspecies without discriminating.

Figure 7. Early-season galls induced by *Tamalia coweni* on leaves of greenleaf manzanita (*Arctostaphylos patula*)

Ranging from the lowest to the highest elevations in Butte County is whiteleaf manzanita (*Arctostaphylos viscida*), so named for its resinous inflorescences and foliage. Although adventurous Tamalia aphids do occasionally become mired in the resin, some succeed in establishing galls on this host plant. At moderate elevations (750 meters) and higher, greenleaf manzanita (*Arctostaphylos patula*) is common in the understory of coniferous forests. Despite the fact that *A. patula* is typically clothed in tiny glandular hairs, *Tamalia coweni* uniquely induces galls on *A. patula* not only on the leaves (Figure 7), but on the inflorescences as well (Figure 8). Actually, these galls represent two different generations of the same aphid: the first generation of gall-inducers promotes galls on the leaves in late spring, whereas their granddaughters (wingless and adapted to induce galls like the first generation) establish galls especially on the nascent inflorescences in mid to late summer. Because these galls are morphologically and temporally distinct, scientists suspected two species of aphids were involved, but field experiments have confirmed the causative agent is in fact different phases of the same aphid life history.

Figure 8. Late-season galls induced by *Tamalia coweni* on nascent inflorescences of greenleaf manzanita (*Arctostaphylos patula*)

Arctostaphylos species have a reputation for hybridization and reticulate evolution, and Indian manzanita (*Arctostaphylos mewukka*) is an example of this: genetic and morphological evidence suggests it is the daughter species of *A. patula* and *A. viscida*. A correlate of this hybridization is the trait of giantism, especially evident in the huge leaves of *A. mewukka*, but the Tamalia galls are not commensurately larger than they are on other host plants. At the highest reaches of Butte County, approaching the subalpine zone at 2000 meters, grows the prostrate species pine mat manzanita (*Arctostaphylos nevadensis*). Stands of *A. nevadensis* are routinely buried by heavy snowpack in winter, but Tamalia eggs survive and release new gall-inducers following snowmelt. What is striking is that gall induction on *A. nevadensis* may not occur until July, four months after galls appear on *A. manzanita* and *A. viscida* in the foothills. The variation in seasonality and host plant habitat would appear to challenge *Tamalia* plant parasites, yet both *Tamalia* gall-inducers and their inquilines are efficient colonizers of these plants in wet years and dry, and capable of locating even singleton plants isolated in the forest.

In summary, the remarkable lineage of *Tamalia* gall aphids has evolved extreme specialization on its *Arctostaphylos* host plants and has diversified into a gall-inducing and an inquiline clade while doing so. Evolution by natural selection has produced exquisitely fine-tuned parasites of parasites of the fabulous genus *Arctostaphylos*.

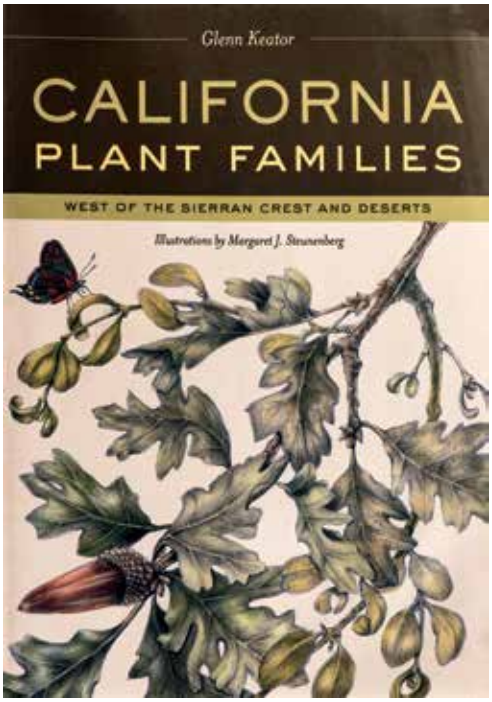
A native of Syracuse, New York, **Don Miller** *was introduced to monarch butterflies during their fall 1966 migration, when Don was in kindergarten. His interest in butterflies and other insects has never flagged. Don earned a bachelor's degree in Forest Biology from the State University of New York, College of Environmental Science and Forestry, where the names of many North American trees were drilled into him. He then earned a master's degree in Biological Anthropology at Oxford before completing a PhD in Entomology at UC Berkeley. In 2002, Don filled the entomology position at Chico State. For the last 25 years, Don has avidly researched the ecology and evolution of manzanita gall aphids while maintaining a keen interest in the Lepidoptera. Every June Don conducts a survey of local butterflies for the North American Butterfly Association. The survey, which is open to all, provides important information on the well-being of our butterflies and their increasingly threatened habitats. All photos by the author.*

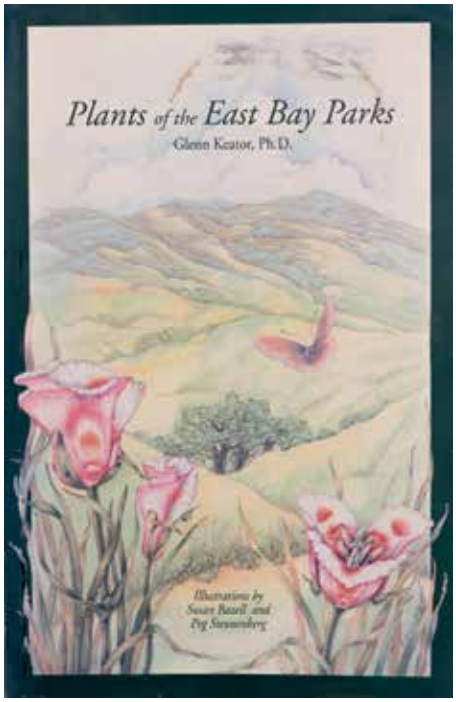
Missing Two Great Friends *by Rosie Andrews*

It is with sadness that we report the passing of two dedicated, longtime members of the *Friends* community at the beginning of this summer.

Margaret "Peg" Steunenberg was a natural sciences illustrator whose work focused on education. Peg was a member of the *Friends* Board of Directors for ten years, from 1998 to 2008. She designed the iconic *Friends* logo of a flowering manzanita branch, and over the years her beautiful illustrations graced the front of several *Friends* tee shirts and posters. Peg's work was featured in a wide variety of natural history publications and materials, including two books: *Plants of the East Bay Parks* and *California Plant Families*, both written by another founding member of the *Friends*, Dr. Glenn Keator.

Peg died on May 31, 2018. Another friend at the garden remembers her as "one of those particularly lovely people—bright and talented and, at the same time, gracious and caring."





Peg Steunenberg's artwork was featured in a wide variety of natural history publications, including two of Glenn Keator's books: *California Plant Families* and *Plants of the East Bay Parks*. Book cover photographs by Arlyn Christopherson.

Celia Zavatsky discovered the garden while taking a *Spring Wildflowers* class from Marian Reeve at Merritt College in the 1970s. Celia was a member of the garden's first docent class in 1995 and founding board member of the *Friends* in 1996. She volunteered at every plant sale for many years, prepping and labeling plants (especially the manzanitas) before the sale, and was a familiar presence at the Wayne Roderick lecture series.

Celia was a passionate admirer of California native plants, both in the garden and in the wild. Friends in the garden community were the lucky recipients of many animated invitations to see the slink pods blooming in the Redwood section or hop in the car for a field trip to one of her favorite places, among them Jepson Prairie (where she was also a docent), Point Reyes, Bear Valley/Walker Ridge, and anywhere a member of the genus *Fritillaria* might be found.

Celia died on June 25, 2018, following a lengthy illness. She gave the Botanic Garden an extensive collection of recordings, slides, and other materials. Her warmth and enthusiasm are missed.

Celia Zavatsky in the Botanic Garden

Rosie Andrews has been a docent at the garden since 2009 and is currently Chair of the Friends *Publications Committee.*

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REGIONAL PARKS BOTANIC GARDEN CLASSES – JANUARY TO JUNE, 2019

Plant Families of California I, Sundays, January 20, February 3 & 17, March 3 & 17, 10:00 a.m. – 2:00 p.m., Instructor: **Glenn Keator**
Zen and the Art of Mushroom Hunting, Sunday, January 27, 10:00 a.m. – 12:00 p.m., Instructor: **Debbie Viess**
Plant Families of California II, Sundays, March 31, April 28, May 5, May 19, June 2, 10:00 a.m. – 2:00 p.m., Instructor: **Glenn Keator**
Botanizing California: One-day field trips, Saturdays, March 9, March 30, April 13, May 4, 10:00 a.m., Instructor: **Glenn Keator**
Mojave Desert Trip, Monday, April 22 – Thursday, April, 25, Instructor: **Glenn Keator**
Landscape Alchemy – Spring Color With California Dye Plants, Saturday, May 11, 10:00 a.m. – 4:00 p.m.,Instructor: **Sasha Duerr**
"Make and Take" your own Watercolors with Natural Pigments, Saturday, June 8, 11:00 a.m. – 3:30 p.m., Instructor: **Judi Pettite**
Gardening for Butterflies, Saturday, June 15, 10:00 a.m. – 1:00 p.m., Instructor: **Charlotte Torgovitsky**
Landscape Drawing and Observation, Sunday, June 16, 10:00 a.m. – 2:00 p.m., Instructor: **Bobby Glass**

For more information and to register, visit **nativeplants.org** under Events and Classes.

Thank You to these Nurseries for Providing a Discount to *Friends* Members

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