



Ceanothus Diversity in California

by Dylan O. Burge



Deer brush (*Ceanothus integerrimus*) above Seiad Valley, Siskiyou County

Emerald Canary

C*eanothus* is among the best known of California's native plants, appreciated by travelers for the color it lends to spring landscapes, by horticulturists and gardeners for the variety and beauty of its cultivars, and by botanists for its diversity of form and ecology. *Ceanothus* contains 53 species of evergreen or deciduous shrubs and small trees, all restricted to North America. Though the

genus is widespread in the United States, Canada, and Mexico, the center of diversity is in California, which is home to all but five of the known species.

The profuse, delicate, and attractively colored flowers of *Ceanothus*—often in rare shades of blue—have made it a favorite of horticulturists, resulting in the development of a great diversity of garden selections, including the hazy blue *Ceanothus* x

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MANZANITA

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Deadline for submission of announcements and editorial material for the winter issue is October 1, 2014.

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delilianus ‘Gloire de Versailles’, and the enigmatic ‘Dark Star’. *Ceanothus* also provides some of the most drought-hardy cultivars for native gardening and has recently proliferated in urban plantings, allowing arborists and landscapers to create water-thrifty plantings that don’t skimp on color. In fact, the great variety of *Ceanothus* species and cultivars means that there is a *Ceanothus* selection suitable for most garden settings.

However, to truly understand the roles of *Ceanothus* in the garden, one must consider the wild origins of the genus and the evolutionary forces that led to its astonishing diversity. Fortunately, recent research has shed some light on the evolution of *Ceanothus*, suggesting how and when the genus diversified, how new species of *Ceanothus* evolve, and how hybridization and soil chemistry may play a role in the ecology of this remarkable North American genus.

Introducing *Ceanothus* diversity—While the center of *Ceanothus* diversity is in California, particularly the biotic region known as the California Floristic Province, the genus is distributed throughout most of North America, from Panama to southernmost Canada, and from the eastern seaboard of the United States to maritime California. Within this area, *Ceanothus* is a dominant component of many ecosystems, particularly in the California Floristic Province, and adds large amounts of nitrogen to forests and shrublands through its symbiotic relationship with nitrogen-fixing bacteria known as *Frankia*. Gardeners who have needed to protect their *Ceanothus* from voracious deer know first hand that nitrogen-rich *Ceanothus* is a desirable food item for browsing wildlife.

Ceanothus has also provided traditional medicinals to Native Americans, who used some species—particularly New Jersey tea (*Ceanothus americanus*)—to treat infections of the upper respiratory tract and as a source of dye. *Ceanothus* became familiar to European colonists of eastern North America during the Revolutionary and Civil Wars, when leaves of New Jersey tea were used in the same way.

Visually striking and profuse floral displays have made *Ceanothus* the darling of professional horticulturists and gardeners. Starting with a group of North American species imported to Europe by savvy garden enthusiasts during the eighteenth and nineteenth centuries, careful hybridization and selection of *Ceanothus* strains has resulted in the development of many dozens of interesting and beautiful cultivars.

Subgenera of *Ceanothus*—*Ceanothus* diversity is traditionally divided between two subgenera, which are sometimes referred to as sections: *Cerastes* (24 species) and *Ceanothus* (29 species). Subgenus *Ceanothus* is sometimes referred to as *Euceanothus*, but this name is not taxonomically accepted. The two subgenera differ strongly in their morphology, physiology, and life history. In comparative genetic studies based on DNA sequences, the two subgenera are very strongly divergent. In fact, there is good evidence that the two groups have been evolutionarily separate for at least 13 million years, allowing them to develop a great number of morphological differences. Subgenus *Cerastes*, in particular, is quite different from most members of the family that contains *Ceanothus*, Rhamnaceae. For example, the succulent leaves of *Cerastes*, with the stomata sunken in deep pits, are unique among Rhamnaceae, as are its swollen stipules.

The two subgenera of *Ceanothus* are so different, in fact, that they may justify recognition as separate genera, an idea that is the subject of ongoing research. Sometime in the near future, California plant enthusiasts may be referring to the 24 *Cerastes* species as members of the genus *Cerastes* instead of the genus *Ceanothus*. Rather than sowing confusion, this change in nomenclature would help to emphasize the vast differences between members of the two subgenera. In the long run, such a change would lead to greater appreciation of these plants in nature as well as in the garden.

For the time being, the two subgenera of *Ceanothus* remain part of a single genus, albeit a heterogeneous one. However, *Ceanothus* has some tricks up its sleeve: In a few cases, species from different subgenera look quite similar and often occupy similar habitats. This observation is consistent with what biologists call *convergent evolution*, when species with very different evolutionary histories end up looking the same due to random chance or similar environmental pressures.

Dylan O. Burge



Wedgeleaf ceanothus (*Ceanothus cuneatus*), a member of the *Cerastes* subgenus

Dylan O. Burge



Coast whitethorn (*Ceanothus incanus*), a member of the *Ceanothus* subgenus

Wedgeleaf ceanothus (*Ceanothus cuneatus*) on Mount Diablo in 2010

An example may clarify this idea. In the North Bay, Sonoma ceanothus (*C. sonomensis*) and wavyleaf ceanothus (*C. foliosus* var. *foliosus*) present a remarkable case of convergence. Both plants are small shrubs up to about four feet tall with smooth, gray bark, and both have small leaves that are clustered on the stems. In terms of their gross appearance—their *gestalt*—the plants are difficult to tell apart from farther than a few feet away. But close examination reveals them as members of separate subgenera that have been evolutionarily isolated for many millions of years. Other examples are found all over California, especially in coastal habitats, for example sandscrub ceanothus (*C. dentatus*) and Monterey ceanothus (*C. rigidus*) of the central coast, or Lompoc ceanothus (*C. cuneatus* var. *fascicularis*) and Santa Barbara ceanothus (*C. impressus*) from a bit farther south.

Though once treated simply as an evolutionary accident, the odd combination of divergence and convergence between the *Ceanothus* subgenera has implications for the evolution of *Ceanothus* as a whole. Some researchers have suggested that by using water in different ways—*Cerastes* tends to have shallow roots and use water efficiently, while *Ceanothus* has deep roots and is more wasteful with water—the two groups are able to avoid competition, allowing them to occupy the same habitats despite their superficial similarity. Sharing of this kind may partly explain the high diversity observed in the genus, as it would

allow more species to persist in the same environment than would be possible if all the species had identical ecological requirements.

The how and when of *Ceanothus* diversification

Although the subgenera of *Ceanothus* probably became evolutionarily separate around 13 million years ago, they did not begin to diversify until much later. Researchers have speculated that diversification of the two subgenera was a response to climate change, specifically the advent of a Mediterranean-type climate in parts of western North America. However, this change in climate probably occurred around two million years ago, while the most recent data indicate that the accumulation of species in both of the *Ceanothus* subgenera began much earlier—about six million years ago. The new dates for *Ceanothus* diversification do agree well with the age of California's major mountain ranges. Thus, it may have been the uplift of mountain ranges, rather than climate change, that stimulated the evolution of the enormous ecological and morphological diversity that is observed today in *Ceanothus*.

Jack of all trades: ecological diversity in *Ceanothus*

Ceanothus is one of the most ubiquitous shrub genera in California, found from sea level to above tree line, and in nearly every plant community type. On coastal terraces of western California, such well-known and spectacular plants as blueblossom (*C. thyrsiflorus* var. *thyrsiflorus*), coast whitethorn (*C. incanus*), and glory mat (*C. gloriosus*) are very common. In the warm interior foothills of the Coast Ranges and Sierra Nevada, the iconic buckbrush (*C. cuneatus*) becomes common, along with a number of other widespread and ecologically significant species, including deer brush (*C.*

Miguel Vieira

Blueblossom (*Ceanothus thyrsiflorus*) at Point Reyes

James Gaither

Musk brush (*Ceanothus jepsonii*)

integerrimus), hoary leaf ceanothus (*C. crassifolius*), and jim bush (*C. oliganthus* var. *sorediatus*).

At higher elevations in the mountains, a completely different suite of species takes over, although the exact set of species varies by mountain range and latitude. In the Sierra Nevada, the very hardy and cold tolerant whitethorn (*C. cordulatus*) is common at moderate to high elevations, along with a number of prostrate species of subgenus *Cerastes*, such as Mahala mat (*C. prostratus*), the most common of the set. In the highest and driest mountains, tobacco bush (*C. velutinus*) appears. Tobacco bush is a widespread and unusual species that is common in mountains of the western United States. It is also one of just two *Ceanothus* species that reach into Canada (the other is redstem ceanothus, *C. sanguineus*). Above treeline in the Sierra Nevada, it is occasionally possible to find isolated shrubs of *C. velutinus*, along with the occasional mat of *C. prostratus*. At these locations, *Ceanothus* reaches some of the highest altitudes known for the genus.

In addition to the very widespread species, *Ceanothus* contains a large number of uncommon to extremely rare taxa. In fact, the bulk of *Ceanothus* diversity is to be found in these geographically localized, narrow endemics. Some examples of this type of species include Pine Hill ceanothus (*C. roderickii*), known only from gabbro-derived soils in the central Sierra Nevada; musk brush (*C. jepsonii*), known only from serpentine soils in California's Coast Ranges; hollyleaf ceanothus (*C. purpureus*), found only on volcanic terraces in the North Bay; and Hearst's ceanothus (*C. hearstiorum*) and maritime ceanothus (*C. maritimus*), an enigmatic pair of species that is found on just a few coastal bluffs in northwestern San Luis Obispo County.

A unifying theme of narrow endemism in *Ceanothus* is soil chemistry. As many as twelve *Ceanothus* species

are considered soil specialists. These species are known from just a single soil type, and it is thought that these soils may have facilitated their origin. In fact, recent research suggests that strong soil chemistry differences, such as that between serpentine and sedimentary types of soils, may limit gene flow between populations by killing hybrid seedlings before they reach adulthood, a type of natural selection that is thought to be very common in nature but is very rarely documented. This mechanism would tend to create soil-specialized populations, which could eventually turn into new species. This pattern may also apply to climate, with strong climatic gradients, such as that between cold valleys and warm hillsides, providing the selective pressure that is needed to cause speciation.

Extreme habitat specialization in *Ceanothus* has also led to the development of some very interesting areas of high *Ceanothus* diversity. In areas of California where diverse soils and climate converge—for example in the North Bay or the Peninsular Ranges of southern California—a great number of species can be found in a very small area.

In the North Bay, a drive from Point Reyes to the summit of Mount Tamalpais allows botanists to observe as many as eight different taxa in just one day. Near Point Reyes, glory mat (*C. gloriosus* var. *gloriosus*) can be found growing amongst the grasses of the wind-swept point. Just east of Point Reyes, Mount Vision ceanothus (*C. gloriosus* var. *porrectus*) is abundant, along with huge old specimens of blueblossom (*C. thyrsoiflorus* var. *thyrsoiflorus*). After crossing the San Andreas Fault and beginning the ascent of Bolinas Ridge, jim bush (*C. oliganthus* var. *sorediatus*) becomes frequent, mixed with blueblossom. Near the crest of the ridge, very small populations of the rare Mason's ceanothus (*C. masonii*) grow, although you might need a guide to find them. Beyond and below the crest of the ridge, mixed up patches of serpentine and sedimentary soils are home to a complex array of buckbrush (*C. cuneatus*) and musk bush (*C. jepsonii*) populations, some of which contain complex hybrids. Finally, in its upper reaches, the road to the summit of Mount Tamalpais passes through populations of wavyleaf ceanothus (*C. foliosus* var. *foliosus*).

Jeff Moser

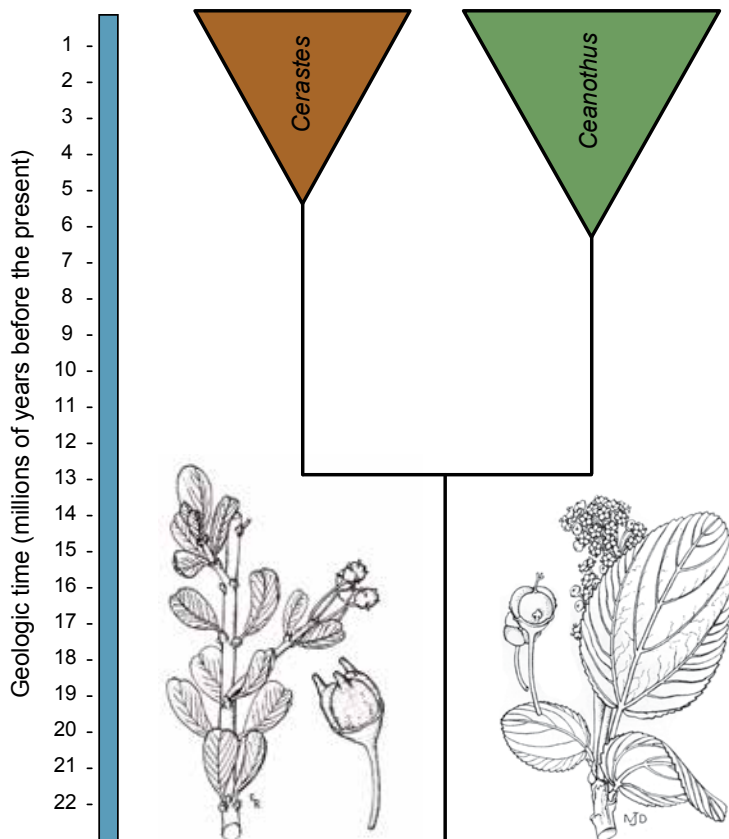
Tobacco bush (*Ceanothus velutinus*)



Ceanothus foliosus var. *vineatus*

Schematic of *Ceanothus* Evolution

- Stomata in crypts Stomata on leaf surface
- Thick leaves Thin leaves
- Stipules swollen Stipules thin
- Evergreen Evergreen or deciduous



The “tree” and the geological time scale at the left indicate the major events in *Ceanothus* evolution, including the split of the genus into two subgenera around 13 million years ago, and the subsequent diversification of both subgenera, beginning around 6 million years ago. Characters shown at the top of the figure are those that always differentiate the subgenera; they can be used in the field when it is not immediately obvious what subgenus a plant belongs to. The drawings at the bottom show typical examples of each subgenus, with buckbrush (*C. cuneatus*) at left and redstem ceanothus (*C. sanguineus*) at right.

The great diversity of *Ceanothus* found in this small area of California is probably due to the complex array of climates and soils found there, which supports an extremely diverse flora within a very small area. The slopes of Mount Tamalpais are home to more than 900 plant species, including plants associated with habitats as diverse as coniferous forest, chaparral, and grassland.

Farther north, in the Wine Country, *Ceanothus* diversity reaches its zenith: It is a little-known fact that Napa and Sonoma counties host the greatest concentration of *Ceanothus* diversity in the world, including many local endemics that are found in no other place. A total of 22 *Ceanothus* taxa are found in this small area, many of them in close proximity on the dissected and geologically complex terrain of the Mayacamas Mountains, where chemically stringent serpentines are juxtaposed with a confusing array of volcanic and sedimentary rocks. In fact, this tiny region is one of the most botanically diverse parts of California, and also one of the most endangered. Much of the original habitat has been converted to vineyards, and remaining stands of native vegetation are under strong pressure from the very lucrative wine industry. The extremely rare Vine Hill ceanothus (*C. foliosus* var. *vineatus*), for example, is known from just a handful of plants growing on or around the grounds of Vine Hill School in Sonoma County.

Hybridization in *Ceanothus* evolution—Botanists frequently cite *Ceanothus* as an example of a plant group in which rampant hybridization and exchange of genetic material among species is the rule rather than the exception. Whenever two members of the same subgenus come into contact, it is almost guaranteed that some hybrids will be produced. Indeed, careful crossing studies carried out by pioneering—and exceedingly patient—botanists have shown that all of the species within a given subgenus can be crossed with one another, and that the hybrid seeds result in healthy, fertile adults. Interestingly, the two subgenera are not highly interfertile; seeds produced from such crosses between members of different subgenera are usually not viable, and the few resulting plants are always sterile mules. This difference in fertility underscores the very different biology of the *Ceanothus* subgenera: The two groups have been evolutionarily separate for so long that their suites of genes (their genomes) no longer complement one another.

Facile crossability (ease of interbreeding) between members of the same subgenus is, of course, a major reason for the success of *Ceanothus* as a garden plant: Horticulturists are able to mix *Ceanothus* lineages as if they were oil paint, creating completely new plants from the large palette of genes provided by the 53 species of wild *Ceanothus*. Strong interfertility may also have played a role in the evolution of *Ceanothus*, and may provide an explanation for some of the patterns of diversity observed in the genus.

Beginnings by Bart O'Brien, Garden Director



In Wayne Roderick parlance, I have been “plant happy” from as far back as I can remember. I was born in Hollister, California, as were my parents and grandparents. I am a fifth-generation Californian, the third of four siblings. Some of my earliest memories are of plants and gardening. For a number of years when I was very young, I would cut out pictures of plants from magazines, tape them into scrapbooks, identify them from various plant books, and my mother would then write their names by them (as this was before I could write). When my mother recently moved, she gave me

a small box of some of my childhood mementos and I was surprised to find that the box contained two of these long-forgotten scrapbooks—and that many of the plants are correctly identified by their generic common names.

Perhaps my earliest California native plant memory is when I was six or seven years old and I got into trouble for riding my bicycle down to the railroad tracks to see the arroyo lupines (*Lupinus succulentus*). I had spotted the lupines out the car window when we had driven to the grocery store. (I’ve always had a talent for spotting interesting plants from speeding cars.) The railroad tracks where the lupines were growing were quite a distance from our house, and my parents had told me not to go there by myself because I was too little; they would take me to see the plants the following weekend. For some reason, I couldn’t wait that long, so I went to see them—and paid consequences that I don’t particularly remember. Needless to say, we didn’t go see them that following weekend. But for a number of years afterwards, we would all get in the car and go on a spring wildflower drive through Cienega (in the Gavilan Range south of Hollister), with one or two stops along the way. The rest of my family was not particularly interested in plants, but they indulged me in this regard.

Fast forward through my college years, when I received a BS degree from UC Davis in Environmental Planning and Management and a Masters in Landscape Architecture from Harvard University Graduate School of Design. After returning to the Bay Area, I worked in two landscape architecture/design offices before I was hired by Gerda Isenberg to be the manager of Yerba Buena Nursery in the Santa Cruz Mountains. This was my first full-time paid position working with native plants, and as for so many of Gerda’s employees, it was a career-defining experience for me.

For the past 24 years, I worked at Rancho Santa Ana Botanic Garden (RSABG) in Claremont. During that time, I wrote numerous papers and articles, and coauthored three books: *California Native Plants for the Garden*, *Reimagining the California Lawn* (my coauthors on both of these publications were Carol Bornstein and David Fross), and the bilingual *Care &*

Maintenance of Southern California Native Plant Gardens—Cuidado y mantenimiento de jardines de plantas nativas del sur de California (with Betsey Landis and Ellen Mackey).

Throughout the past 33 years (considerably longer as a volunteer), I have been professionally involved with documenting, collecting, growing, and selecting California native plants for conservation, display, and horticultural purposes.

My most recent projects at RSABG included co-curating the “When They Were Wild” exhibit of California native plant art and objects at the Boone Gallery of The Huntington last spring; leading the rare, endangered, and endemic plants of northwestern Baja California, Mexico, project; and coauthoring a checklist of the flora of northwestern Baja California, Mexico. These two Baja California projects are currently in the final stages of pre-publication.

I am extremely pleased to be leading the next phase of the Regional Parks Botanic Garden’s ongoing native plant adventures in gardening, conservation, field work, education, and research. The Botanic Garden that we enjoy today is the physical manifestation of the 74 years of intense and dedicated effort of numerous staff and volunteers. It is most certainly a wonderful place to explore, discover, and marvel at the remarkable diversity and beauty of California’s native plants. As I delve more deeply into the Garden’s collections and history, I will be sharing some of our compelling stories with you in these pages. I am delighted to be here. 🌿



Terry Lewis

This is me with a bud mutation from a ‘Cecile Brunner’ rose that had been given to me by our former next door neighbor (Mrs. Frusetta) when we moved into the family house on Sixth Street in 1960. The flower in my hand appeared where I am pointing, and it was split down the middle: pink on one side and dark red on the other. It bloomed that way on that branch for two or three years (until my Dad accidentally pruned off that branch). My older sister, Terry, took the photo. I still have that pressed flower somewhere...

In Search of a Perfect Blue: A Brief History of *Ceanothus* Cultivation

by David Fross

Katie Hetrick



Ceanothus maritimus 'Valley Violet'

Europeans were first to recognize the garden potential of *Ceanothus*, and as early as 1713 this North American genus had found a place in French gardens. Before the discovery and exploration of California and its diverse range of species, European horticulturists began crossing New Jersey tea (*Ceanothus americanus*), native to eastern North America, and azure ceanothus (*Ceanothus caeruleus*) from Central America. French breeders developed the resulting hybrid line, *Ceanothus* x *delilianus*, and over 40 attractive blue cultivars were selected in the nineteenth century. A third species, inland Jersey tea (*Ceanothus herbaceus*), was crossed with *C.* x *delilianus* in 1840 and resulted in another hybrid line (*Ceanothus* x *pallidus*) featuring red stems and selections with pink-colored flowers. Although most of these early cultivars have been lost, they demonstrate the ease with which hybridization can occur in the genus. A few cultivar names, 'Coquette', 'Madame Furtado', or 'Sceptre d'Azur', offer the imagination a sampling of the pink to blue color range.

Horticultural interest continued as botanic luminaries such as David Douglas and Karl Hartweg explored and collected in western North America. Their collections and samples created a keen interest in the genus, and England's Veitch Nurseries sent William Lobb to California in 1849 to gather specimens and seeds for commercial production.

His steadfast dedication to this task in light of the distractions he most certainly must have encountered upon reaching San Francisco is remarkable. *Ceanothus* collections Lobb and others sent to England in the nineteenth century began a long tradition of garden use in Europe that continues to this day. A number of compelling cultivars seldom seen in the United States such as Autumnal Blue ceanothus (*Ceanothus* 'Autumnal Blue'), Trewithen Blue ceanothus (*Ceanothus arboreus* 'Trewithen Blue'), and the intersubgeneric hybrid Veitch ceanothus (*Ceanothus* x *veitchianus*) continue as popular selections in England. Although the popularity of the genus has waned in recent years, I counted 53 species and cultivars in stock at the Royal Horticultural Society garden center during my travels in 1999.

In California, recognition of the horticultural value of the genus was left to twentieth century native plant advocates such as Theodore Payne and Lester Rowntree. Their enthusiasm, followed by the 1942 publication of Howard McMinn and Maunsell Van Rensselaer's *Ceanothus*, focused attention on the rich potential the genus offered West Coast gardeners. Cultivar development followed the publication of their book and led to the selection of a number of iconic cultivars in the 1950s. Two that remain common in the California landscape are Yankee Point ceanothus (*Ceanothus thyrsiflorus* var. *griseus* 'Yankee Point') and Ray Hartman ceanothus (*Ceanothus* x 'Ray Hartman'). Horticulturists, botanic gardens, and nurseries added both garden or nursery hybrids (*Ceanothus* 'Dark Star', *C.* 'Joyce Coulter', and *C.* 'Frosty Blue') and wild-collected clones (*C. arboreus* 'Powder Blue', *C. maritimus* 'Point Sierra', and *C. gloriosus* 'Anchor Bay'), and a varied and colorful range of selections developed in the second half of the twentieth century. Today California gardeners have an array of choices that can satisfy landscape needs from shaded woodlands to hot, dry slopes.

In recent years, as many as fifteen new selections and hybrids have been introduced into the California nursery trade, continuing a horticultural exploration of the genus started by Europeans 300 years ago. The proximity of species and hybrids in nurseries and gardens provides ample opportunity for hybridization, and additional cultivars will most certainly find their way to our gardens. The three listed here offer a small sample of the promise the horticultural evolution of this genus holds for our gardens.

The garden hybrid *Ceanothus* 'Antoinetta' was selected for its vigor and triangular-shaped leaves from a group of seedlings found under a mature specimen of *Ceanothus* 'Cynthia Postan'. A nearby *Ceanothus arboreus* 'Cliff Schmidt' is believed to be the second parent. Six- to eight-inch sprays of bright blue flowers open from silver-blue buds in midspring. 'Antoinetta' is fast growing with an arching habit to 15 feet tall.

Praise for the graceful character of *Ceanothus parryi* is common in the literature of the genus, and yet this handsome species is seldom seen in the nursery trade. The recent introduction of the wild-collected clone *Ceanothus parryi* 'Benton Blue' from Benton County, Oregon, offers gardeners a chance to enjoy a species Maunsell Van Rensselaer called "one of the most beautiful of all." 'Benton Blue' features a narrow, upright habit to 15 feet tall with narrow, dark green leaves and plentiful trusses of sky-blue flowers in spring to early summer. The winter stems have a distinctive purple-blue cast and offer still another reason to consider this long-neglected species.

After years of evaluation, UC Davis released *Ceanothus maritimus* 'Valley Violet' as part of its Arboretum All-Stars program in 2008. Durable and heat tolerant, it forms stiff mounds to 2 to 3 feet tall and 4 to 5 feet wide, with leathery olive-green leaves. From mid- to late winter the foliage is covered in violet-blue flowers. 🌿

David Fross is the founder and president of Native Sons Wholesale Nursery, a grower specializing in plants from Mediterranean-climate regions of the world. He teaches horticulture at California Polytechnic University, San Luis Obispo, and is co-author of California Native Plants for the Garden, Reimagining the California Lawn, and Ceanothus.



David Fross

Ceanothus 'Antoinetta'

Wayne Roderick

Santa Barbara ceanothus (*Ceanothus impressus*) at Wisley Garden, Surrey, England, 1977

Ceanothus Diversity in California

Continued from page 6

Although recent genetic evidence does *not* support the idea that there is rampant gene flow among *Ceanothus* species in the wild, it is clear that some genes are shared and rampant exchange of DNA may only be prevented by the kind of natural selection described above, in which hybrid plants fail to succeed in either of the habitats occupied by their parents. However, in the rare case where hybrid offspring are favored, for instance in new types of habitat created by geologic and climatic change, the hybrids could be favored. What is more, such hybrids might not resemble their parents.

This phenomenon, technically known as *transgressive segregation*, can produce offspring with traits that are completely different from either of their parents. If these novel traits are advantageous in a new type of environment, then the hybrids might be expected to proliferate and to persist as a new species. Over time, the new plant would become better and better adapted to its new environment, and exchange of genes with the other species would gradually

decrease, eventually erasing the signature of the hybridization event that initiated the formation of the species. It is important to understand that this idea has not yet been tested, but it provides a potential explanation for how, over the course of just a few million years, *Ceanothus* diversified into nearly every plant habitat in the state of California. 🌿

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Beyond *Ceanothus* in the Buckthorn Family by Glenn Keator, PhD

Although *Ceanothus* is the signature genus for the buckthorn family (Rhamnaceae) in California, several other genera, particularly the buckthorns, are prominent and worthy of a place in gardens.

The Rhamnaceae, consisting of close to 900 species worldwide, is prominent in the tropics as well as temperate areas, and although it's not altogether distinctive in any one feature, it is nonetheless recognizable by a combination of traits easy to see. Besides being a family of woody shrubs and trees, the Rhamnaceae is noted for having simple, unlobed leaves; dense clusters of tiny flowers that have a nectar-secreting disc, five separate sepals, and (usually) five petals; and a fleshy capsule or drupe with just a few hard seeds. Besides ornamentals for gardens, the family is noted for edible fruits in the genus *Ziziphus* (juzube) and various sources of medicines.

Few buckthorn relatives have colorful flowers. In this character *Ceanothus* stands out in California, and down under in New Zealand and Australia, *Pomaderris* (ironically known as flowering dogwood) has yellow blossoms. Otherwise, the flowers are relatively drab, with yellow-green or white petals and small fruits that provide color as they ripen in some species, like our coffeeberry.

The most prominent native group aside from *Ceanothus* is the buckthorn clade (a group with a common ancestor), which has recently been split into two genera, *Rhamnus* and *Frangula*. *Frangula* has upright sepals and usually purple fruits, and *Rhamnus* has spreading sepals and mostly red fruits. Both are useful in gardens, providing struc-

ture and attractive foliage as well as attracting bees, and both have laxative properties in their bark and fruits.

Of these buckthorns, *Frangula californica* (coffeeberry) is most variable and most widely available for gardens. Its several variations include dark green smooth to gray-green hairy leaves, low-spreading ground covers to multitrunked trees, and adaptations to plant habitats ranging from foggy coastal scrub to desert mountains as well as many conditions in between, especially chaparral and open woodlands. The tiny, starlike, yellow-green flowers attract bees and are followed by fruits that start green, then turn from yellow to red to dark purple. Reliably drought tolerant once established, the plants can take cool to searingly hot summers and full sun to high shade.

Another *Frangula* in California is *F. purshiana*, cascara sagrada (sacred bark in Spanish), a very tall shrub to small tree living in moist north coastal forests, often on the edge of streams and wetlands. Cascara sagrada is characterized by larger, deciduous leaves and fruits like coffeeberry. Red buckthorn, *F. rubra*, completes the trio with bright red new twigs, deciduous leaves roughly the size of coffeeberry leaves, and dark purple fruits. Because it lives in mountain chaparral, where it often receives snow in winter, it's a good choice for mountain gardens but is seldom seen in the trade.

On the *Rhamnus* side of things, we have three species with bright red fruits, and thick, tough leaves. The most widespread is *R. ilicifolia* (holly-leaf redberry), a slow-growing evergreen shrub to 15 feet high with small, dark green, glossy leaves lined with teeth. The plants are usually dioecious, and on the female plant the fruits ripen to bright red and attract birds to the garden. Holly-leaf redberry is prominent in chaparral and oak woodlands over a large territory, and in the Bay Area it is especially prominent on Mount Diablo. *R. crocea* (redberry buckthorn) is closely related but generally grows as a low sprawling shrub with very small, less prickly leaves but similar flowers and fruits. It is widely scattered on rocky sites in full sun.

Our third species is *R. piriifolia*, the island redberry, which grows into a sizeable evergreen shrub with handsome, glossy, usually smooth leaves two to three times the size of the two other



Coffeeberry (*Frangula californica*) in fruit

John Rusk



Cascara sagrada (*Frangula purshiana*) in fruit



Redberry buckthorn (*Rhamnus crocea*) flowers

Alan Harper

species. Poorly known in the trade, it should prosper in coastal gardens with mild winters.

California's other rhamnaceous genera include *Ziziphus* (lote bush), *Condalia* (snakewood), *Colubrina*, and *Adolphia*, most of which are obscure desert shrubs seldom written about or grown. 🌿

Glenn Keator is the chairman of the Friends Advisory Council. He is a popular instructor of botany and field trip leader in the Bay Area, and he teaches the docent training course at the Regional Parks Botanic Garden. He is the author of a number of books on native plants.

Photos by the author except as noted.




Adolphia californica in the Sierra de San Pedro Martir, Baja California

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