

A NEWLY DESCRIBED SERPENTINE-ENDEMIC *CEANOOTHUS* (RHAMNACEAE)
FROM COASTAL MARIN COUNTY, CALIFORNIA

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ABSTRACT

Ceanothus decornutus V. T. Parker is a newly described species found on serpentine outcrops in western Marin County. This taxon has been considered as part of *C. jepsonii* Greene in recent treatments. *Ceanothus decornutus* differs in a number of ways from *C. jepsonii* and suggests relationships to other northern San Francisco Bay species. Beyond the species description and a key to similar taxa north of San Francisco Bay, an analysis of leaf characters is used to indicate possible relationships.

Key Words: *Ceanothus*, chaparral, maritime, Rhamnaceae, serpentine.

On a ridge above Platform Bridge Road, SE of Black Mountain and just south of Nicasio Reservoir, in western Marin County, I accompanied Roger Raiche and Terri Thomas on 19 April 1991 to see a *Ceanothus* found on serpentine soils along that ridge. Upon arriving, the *Ceanothus* L. was in bloom among the rocky serpentinite outcrops; Raiche asked my opinion of the species and if I thought it was *C. jepsonii* Greene. In contrast to *C. jepsonii*, the flowers ranged from light blue to white, often with pink in some of them, and those that I checked were all 5-merous in contrast to 6-merous flowers in *C. jepsonii*; that suggested it was not *C. jepsonii*, but perhaps a different species of which I was unaware.

The population currently is known to Marin County botanists and is referred to under *C. jepsonii* (Howell et al. [2007] but not mentioned in Howell [1970]). In comparison with other potential candidates in the northern San Francisco Bay region, these populations should be separated from *C. jepsonii* so that their origin and potential relationships with other North Bay species can be investigated. The newly described *Ceanothus* appears to be a part of the complex of species found mostly on serpentine and volcanic soils in Marin, Sonoma, and Napa counties.

This taxon is close to *C. jepsonii* in appearance, but differs in a few significant characters such as having 5-merous flowers and with horns (outgrowths) on the top of the fruit being usually short and rounded in contrast to the lengthy and wrinkled horns found on fruit in *C. jepsonii*. While the leaves are similar in form to *C. jepsonii*, they average fewer, shorter spines along the edges. Compared to other species in the North Bay Region, the new taxon differs by leaf or fruit characters, for example, the leaves are much shorter than *C. purpureus* Jeps. with far fewer and much shorter spines or teeth, and compared to *C. sonomensis* J. T. Howell or *C. confusus* J. T.

Howell, *C. decornutus* is much more ovate, and differs in floral color. In this paper I describe this species and compare a number of characters of this taxon with other northern San Francisco Bay region *Ceanothus* species.

TAXONOMIC TREATMENT

Ceanothus decornutus V. T. Parker, sp. nov. (Fig. 1).—TYPE: USA, California, Marin Co., serpentinite outcrops on ridge south of Black Mountain and Nicasio Reservoir, 15 April 2013, V. T. Parker 1487 (holotype: CAS; isotype: JEPS).

Plant generally erect, \pm open, < 1.5 m. **Stem:** ascending to erect, intricately branched; twigs generally brown, thick. **Leaf:** opposite, evergreen, generally reflexed at tip; stipules knob-like; petiole < 2 mm; blade 10–20 mm, 9–19 mm wide, ovate to oblong-ovate, often \pm folded lengthwise, adaxially green, glabrous, abaxially \pm short-strigose between veins, margin thick to \pm rolled under, wavy, 7–9-spine-toothed. **Inflorescence:** umbel-like, 1–2.5 cm length. **Flower:** sepals, petals 5, light blue to white, sometimes with pink. **Fruit:** 4.5–7 mm wide, 3-ridged to lacking, frequently granular-surfaced; horns 0–1.5 mm, thick, generally rounded, bulge-like. **Habitat:** Rocky, serpentinite outcrops (50) 150–290 m. Along ridge SE of Black Mountain, to the east and paralleling Bolinas Ridge, North Coast Ranges, Marin County. Center of population at 38°03'33.59"N, 122°44'25.82"W. Mar–Apr.

METHODS

Collections of *Ceanothus decornutus* were made multiple times. Data in this paper reflect collections made 22 March 1991 (V. T. Parker 1474), 14 June 1991 (V. T. Parker 1475), 24 May 2011 (V. T. Parker 1486), and 15 April 2013 (V. T.

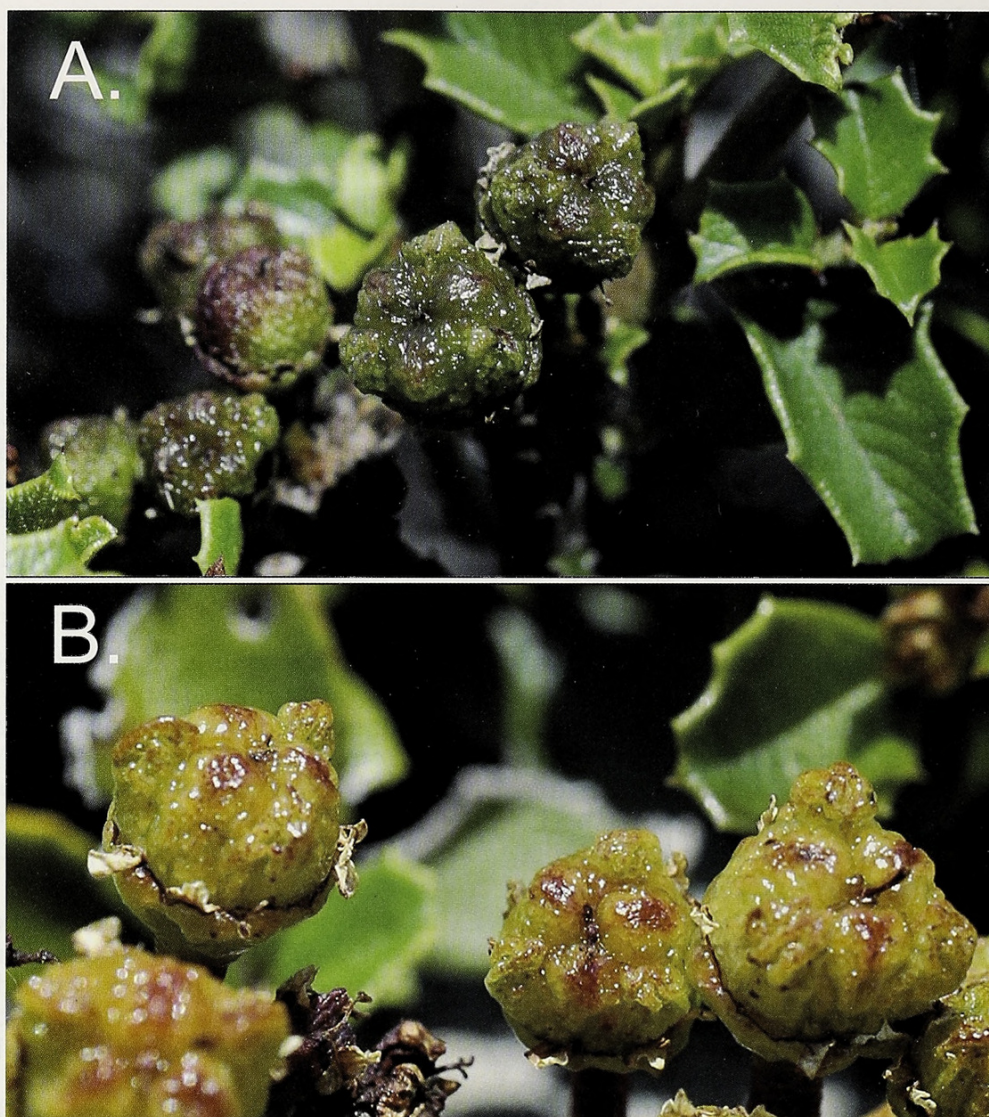


FIG. 1. Fruits and leaves of *Ceanothus decornutus*. 1A) typical fruits illustrating the thickened mounds for horns at the top of the fruit, leaves folded with significant spines; 1B) example of a plant with fruit having small horns, and granular to papillate surfaces.

Parker 1487). Other collections were *C. sonomensis* J. T. Howell, Sonoma County, 1 July 1991, near Sugar Loaf along Adobe Canyon Road (V. T. Parker 1478); *C. gloriosus* J. T. Howell var. *exaltatus* J. T. Howell, Marin County, Bolinas Ridge north of Bolinas-Fairfax Road, 18 July 1991 (V. T. Parker 1479); *C. purpureus* Jeps., Napa County, Soda Canyon Road, near Chimney Rock Road, 18 July 1991 (V. T. Parker 1482); *C. jepsonii* var. *jepsonii*, Marin County, Pine Mountain Fire Road, near the Azalea Hill parking area, 18 July 1991 (V. T. Parker 1481); *C. jepsonii* var. *albiflorus* J. T. Howell, Napa County, North of Hwy 121 about 6–8 mi N of Napa, 18 March 1994 (V. T. Parker 1475). I did not include *C. confusus* nor *C. divergens* in the following analyses because of the presence of horns on their fruit and the typical leaf only having spines near the tip of the leaf.

Measurements of leaves and fruit were made with digital calipers; measurements of fruit used

freshly collected fruit. For *C. decornutus* and *C. jepsonii* var. *jepsonii*, 15 individuals were used, for the other species, ten individuals. For leaf measurements, a mature branch from current years growth was selected arbitrarily and the largest leaf on that branch was measured. Similarly, the largest fruit on an arbitrarily chosen branch was measured for *C. decornutus* and *C. jepsonii* var. *jepsonii*.

Analyses were made using R (R Core Team 2012), and consisted of simple descriptive statistics and Principal Components Analysis. The data used in the PCA included leaf length, leaf width, spine number, spine length, and both with and without floral merosity. The results shown are PCA analyses without including floral merosity.

RESULTS

This species is variable in floral color and fruit morphology. Generally flowers are light blue but

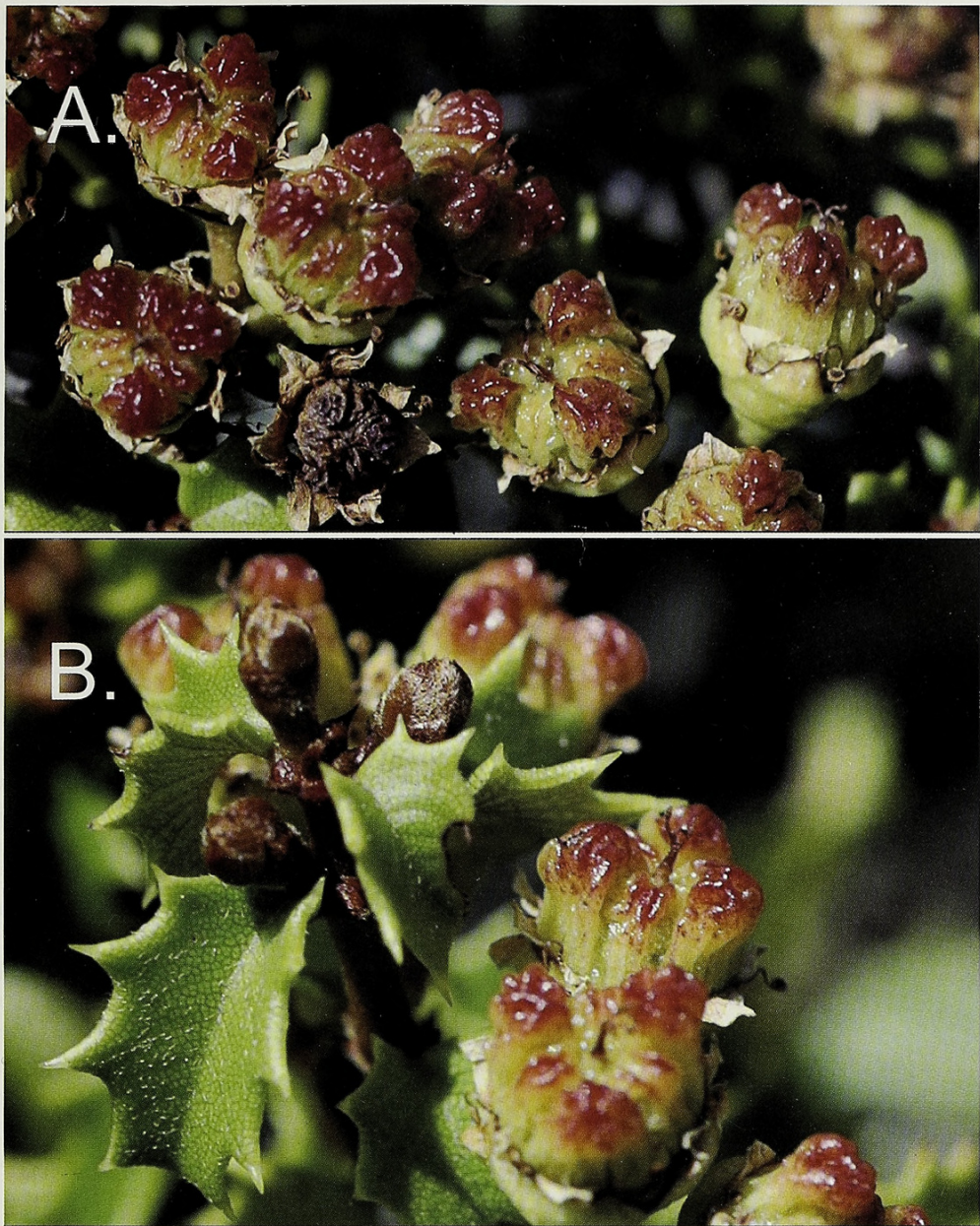


FIG. 2. Fruits and leaves of *Ceanothus jepsonii* var. *jepsonii*. 2A) fruits illustrating the prominent and wrinkled horns. Fruits typically display prominent and wrinkled ridges. 2B) close-up of fruits also illustrating typical leaves, folded with significant spines.

frequently there are white flowers; additionally, in some instances pink occurs as part of the floral tube. Similarly, fruit are usually quite similar, with a rounded bulge or thickened horn that is short and lacking prominent ridges, although the fruit are often somewhat granular to papillate on the surface (Fig. 1A). If one searches through the population, fruit with more prominent horns and sometimes wrinkled ridges do occur (Fig. 1B) similar to but shorter and not as pronounced as in *C. jepsonii* (Fig. 2).

Distribution and Habit

This taxon is found among rocky, serpentinite outcrops generally along a ridge parallel to and east of Platform Bridge Road, south of

Black Mountain and Nicasio Creek. The ridge is principally serpentine grassland (Fig. 3A) with serpentinite outcrops in some places among soils that are clay-dominated Henneke Series serpentine soils (calsoilresource.lawr.ucdavis.edu). Most of the population is along the upper portions of the ridge, above 200 m, but serpentinite outcrops with clusters of *Ceanothus* plants continue on the northern side of the ridge down to Nicasio Reservoir. The vegetation containing *Ceanothus decornutus* is essentially a nearly monospecific maritime chaparral stand, within which are occasional other woody species (e.g., *Baccharis pilularis* DC. and *Umbellularia californica* [Hook. & Arn.] Nutt.) intermixed with or surrounded by serpentine grassland (Fig. 3B).

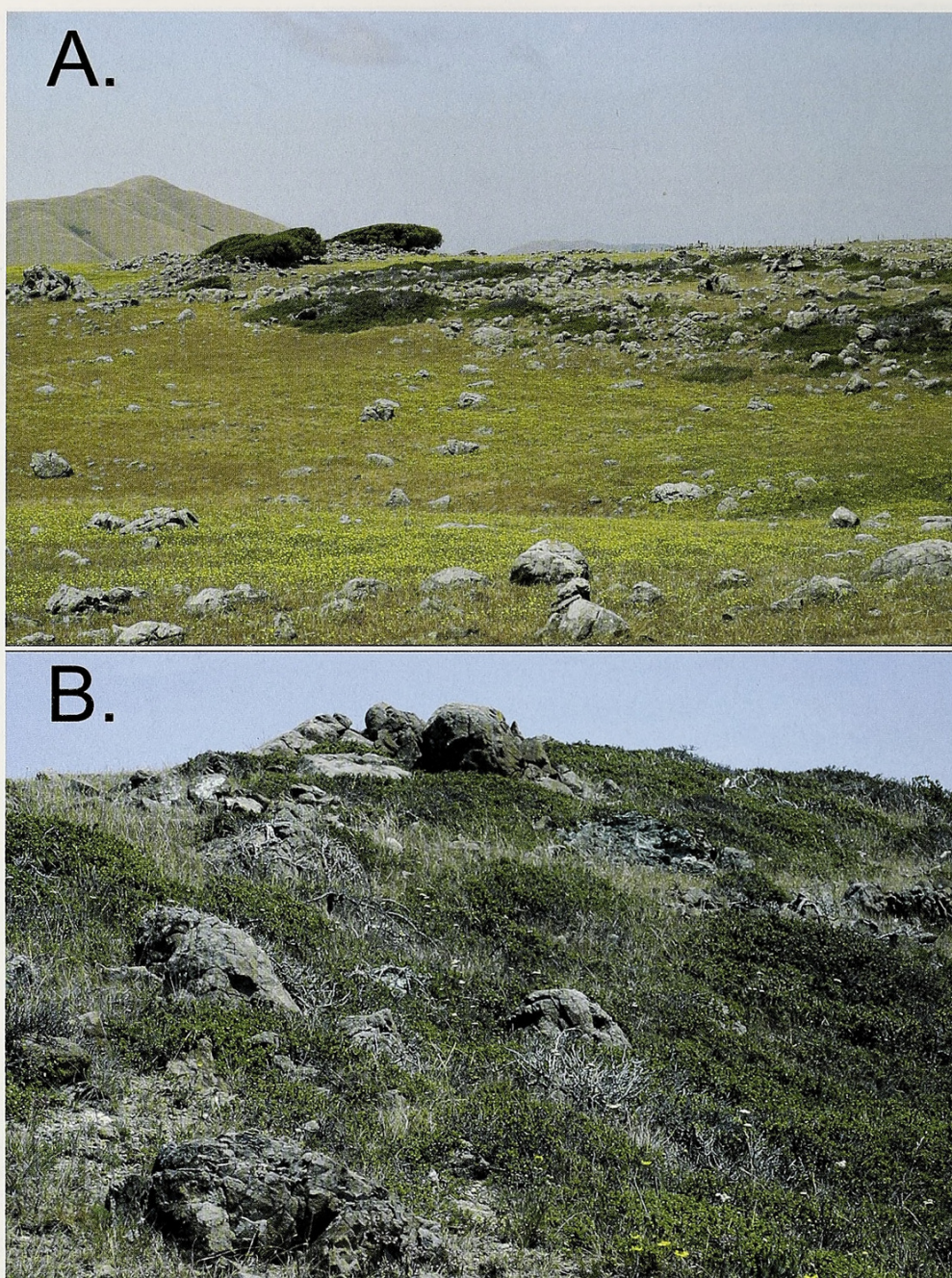


FIG. 3. Habitat of *Ceanothus decornutus*. 3A) Generally the populations are on exposed serpentinite outcrops along a ridge above Nicasio Reservoir. They are visible as the darker grey areas along the top of the ridge. Salt spray/wind-sculpted *Umbellularia* (Nees) Nutt. are visible toward the back of the photo along the ridge. 3B) *Ceanothus* individuals are found within the rock outcroppings, usually as the only woody species.

Taxonomic Relationships

Ceanothus decornutus differs from *C. jepsonii* by the flowers being 5-merous while *C. jepsonii* are 6-merous, and by reduced length of horns on the fruit (hence the name 'decornutus' to reflect the fruit being 'unhorned' or 'dehorned') (Table 1). Additionally, in Marin County, *C. jepsonii* is dark blue-purple in flower color (var. *jepsonii*), while flowers of *C. decornutus* range from white to light blue, sometimes with pink. While there is some variation in flower color and fruit characteristics in *C. decornutus*, other morphological characteristics

are generally quite consistent within the population, e.g., leaf morphology and branching patterns.

Although located within a similar geographic region, *C. decornutus* deviates more from *C. jepsonii* and *C. gloriosus* varieties than expected. When superficially examining the leaf and stem morphology, *C. decornutus* appears to be related to *C. jepsonii*. Both have spiny, 'holly-like' leaves, often with the apical spine bent under, with leaves slightly folded along the midrib (Figs. 1A, 2B). Similarly, stems found on both are rather stout. Variation in the fruit suggests the potential for a relationship with *C. jepsonii*.

TABLE 1. FRUIT CHARACTERS (MEAN AND STANDARD DEVIATION) FOR *CEANOTHUS DECORNUTUS* AND *C. JEPSONII* (N = 15).

Taxon	Fruit width (mm) (SD)	Height to rim (mm) (SD)	Length of horn (mm) (SD)
<i>C. decornutus</i>	5.77 (0.63)	3.82 (0.61)	0.58 (0.39)
<i>C. jepsonii</i> var. <i>jepsonii</i>	5.34 (0.49)	3.26 (0.58)	2.05 (0.48)

At the same time, other morphological characters of *Ceanothus decornutus* are more consistent with the two serpentine and/or volcanic-soil endemics *C. sonomensis* and *C. purpureus*. For example, when considering leaf and fruit characters, *C. decornutus* often falls allometrically more with *C. sonomensis* or *C. purpureus*, depending on the character, than with either *C. jepsonii* var. *jepsonii* or *C. jepsonii* var. *albiflorus* (Table 2). Measurements of leaf length (Fig. 4A), leaf width (Fig. 4B), number of teeth on leaves (Fig. 4C), and the length of the teeth (Fig. 4D) suggest that *C. gloriosus* does not share leaf characters with *C. decornutus*. The new taxon is close to *C. purpureus* in leaf length and width characters, while closer to *C. sonomensis* in number of teeth and their length (Figs. 4C, 4D). Combining these characters in a PCA analysis also indicates that *C. decornutus* variation is centered as much within *C. sonomensis* and *C. purpureus* than with either *C. jepsonii* variety for this combination of characters and that *C. gloriosus* is quite distinct from the other taxa as expected (Fig. 5). The first two axes of the PCA account for 70% of the variation, with leaf length and leaf width loaded more on the first axis, and tooth length and number loaded more on the second axis.

Fruit morphology also varies among these species. All the species have similar sized fruit, but *C. decornutus* differs from *C. gloriosus*, *C. purpureus* and *C. sonomensis* in often having a roughened, granular surface of the fruit and, short, thickened or highly reduced horns (if they are present at all). Although the fruit horns are thickened similar to *C. jepsonii*, in *C. decornutus* most often they are reduced to absent and almost always lack the significant wavy ridges. Finally, *C. decornutus* fruit differs *C. jepsonii* fruit in another way; *C. jepsonii* fruit generally go through a significant reddish color phase prior to fruit ripening (Howell 1970; Howell et al. 2007) while *C. decornutus* fruit lack that reddish phase.

The origin of *C. decornutus* is not clear, for example, and recent molecular genetic research in *Ceanothus* frequently does not help to define closely related species boundaries (Jeong et al. 1997; Hardig et al. 2000; Burge and Manos 2011). The combined history of research in *Ceanothus* suggests several hypotheses. *Ceanothus decornutus* could be a taxon that simply has arisen allopatrically from a common ancestor with, for example, *C. jepsonii*; serpentine endemics have arisen more than once in section *Cerastes* S. Watson, so that is a possibility. The North San Francisco Bay spiny-leaved section *Cerastes* species represent a collection of closely related taxa (Hardig et al. 2002), and given that some of the mosaic of characters in *C. decornutus* are similar to *C. jepsonii* and others similar to *C. sonomensis* or *C. purpureus*, *C. decornutus* also could have arisen from incomplete lineage sorting (Burge et al. 2011). Not that many characters were examined in this study, so all of these are a possibility. Another hypothesis is that taxa have genetically hybridized and introgressed; this has been the principal model for *Ceanothus* since early studies showed little reproductive barriers among species (e.g., Nobs 1963). Nobs (1963) conducted considerable experimental work with *Ceanothus* taxa and was impressed with the ability of taxa within sections to hybridize, particularly in section *Cerastes* occurring in the north coast ranges (p. 50, Nobs 1963). Nobs (1963, p. 82) also thought that new forms could arise by natural selection working on recombination swarms of different taxa brought together by environmental change, selecting among phenotypes arising post-fire from persistent soil seed banks.

Recent research confirms that these section *Cerastes* taxa in the North Bay are closely related (Hardig et al. 2002). While hybridization may be possible and hybrids can be seen in the field, other hypotheses are just as or more likely in the

TABLE 2. LEAF CHARACTERS (MEAN AND STANDARD DEVIATION) FOR SELECT *CEANOTHUS* SPECIES (N = 15 FOR THE FIRST TWO, N = 10 FOR THE REST) FROM THE NORTHERN SAN FRANCISCO BAY REGION.

Taxon	Leaf length (mm) (SD)	Leaf width (mm) (SD)	Teeth #/side (SD)	Length of teeth (mm) (SD)
<i>C. decornutus</i>	14.65 (2.91)	14.56 (2.80)	3.73 (0.46)	1.43 (0.40)
<i>C. jepsonii</i> var. <i>jepsonii</i>	11.96 (1.63)	10.13 (1.82)	4.27 (0.80)	2.02 (0.54)
<i>C. jepsonii</i> var. <i>albiflorus</i>	14.28 (1.29)	10.46 (1.43)	4.80 (0.63)	2.09 (0.45)
<i>C. sonomensis</i>	13.09 (1.80)	8.38 (1.15)	3.30 (0.48)	1.30 (0.39)
<i>C. purpureus</i>	17.51 (2.37)	16.76 (3.07)	5.30 (0.68)	2.50 (0.45)
<i>C. gloriosus</i> var. <i>exaltatus</i>	14.31 (2.80)	10.48 (1.62)	7.50 (0.97)	0.90 (0.18)

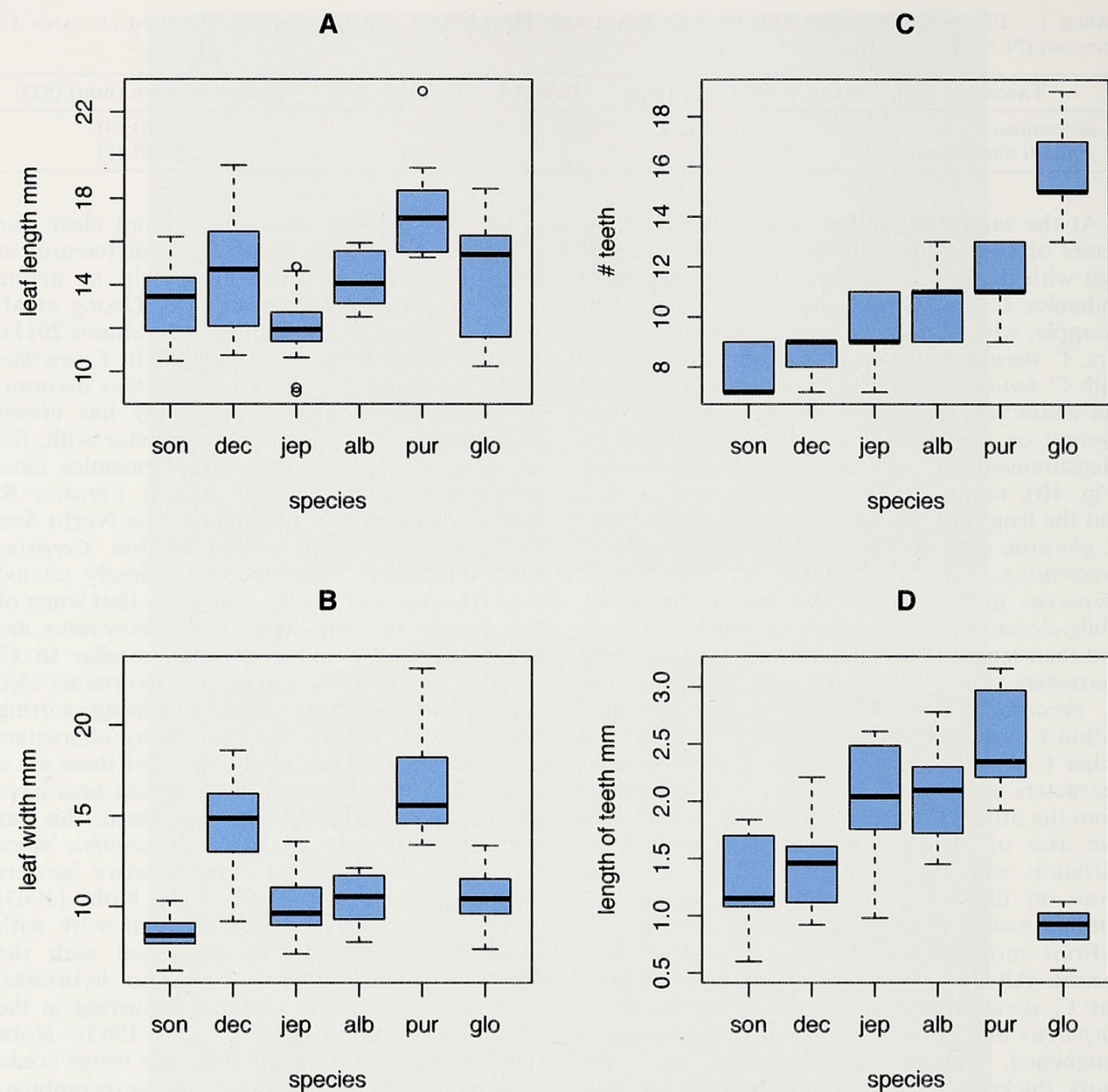


FIG. 4. Comparison of leaf characteristics among select *Ceanothus* species from the northern San Francisco Bay region. 4A) leaf length and standard errors; 4B) leaf width and standard errors; 4C) number of teeth per side of leaf with standard errors; 4D) length of teeth with standard errors. Species include son = *C. sonomensis*; dec = *C. decornutus*; jep = *C. jepsonii* var. *jepsonii*; alb = *C. jepsonii* var. *albiflorus*; pur = *C. purpureus*; glo = *C. gloriosus* var. *exaltatus*.

origin of these taxa (Hardig et al. 2002; Burge and Manos 2011; Burge et al. 2011, 2013). For example, Hardig et al. (2002) investigated two *Ceanothus* taxa of presumed hybrid origin and their putative parents but concluded the possibility of allopatric speciation was just as likely. Burge et al. (2011, 2013) also could not genetically fully separate two closely related *Ceanothus* taxa on adjacent but different soil types and concluded that soil or other abiotic processes were driving species boundaries.

Thus, while the variable floral color and fruit morphology in *C. decornutus* may suggest a history of hybridization or introgression, equally

likely scenarios are allopatric speciation or incomplete lineage sorting. Currently, determining the exact origin of this entity may be difficult, but this study “opens the way for further studies and observations” of these North Bay taxa as suggested by Howell (1939) when he originally described several of them. Further studies should incorporate more taxa (e.g., *C. confusus* and *C. divergens*) and morphological characters, as well as including molecular or other data. *Ceanothus* taxa in the North Bay region represent a potentially ideal set of species to understanding patterns and modes of evolution within California’s radiation of species in this genus.

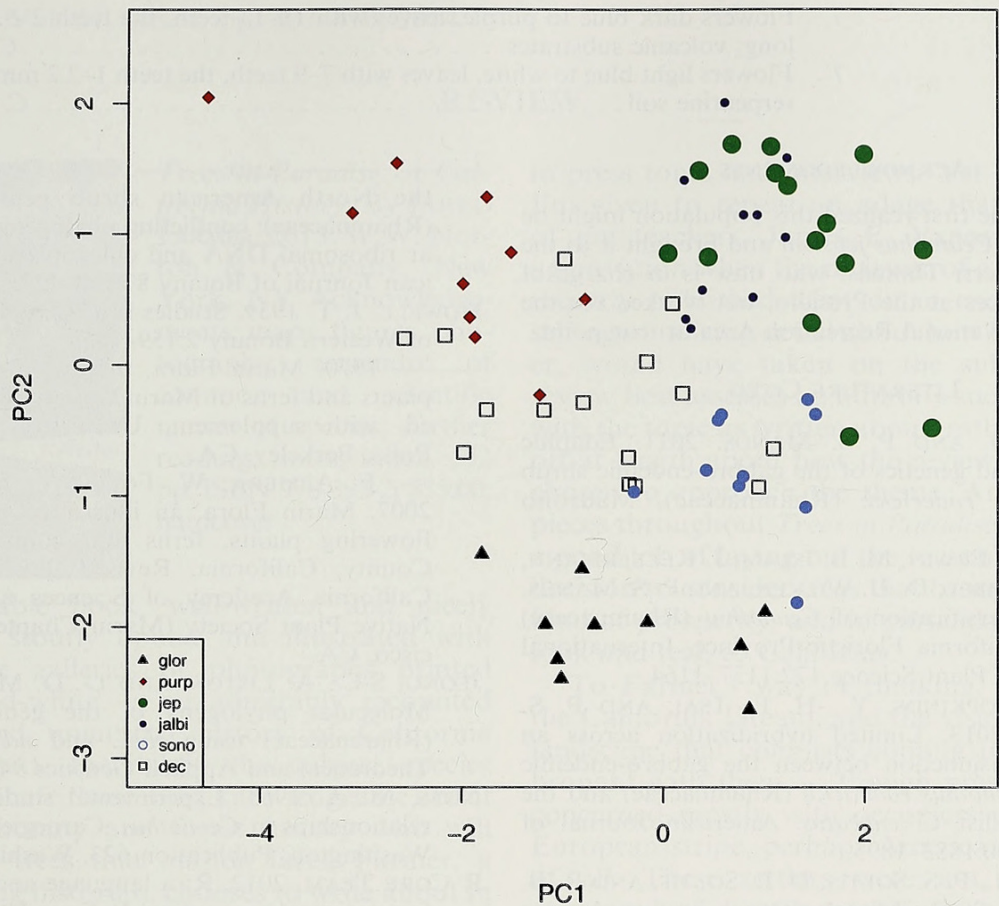


FIG. 5. Principal components analysis of leaf characters for select *Ceanothus* species from the northern San Francisco Bay region. Legend abbreviations as in Figure 4.

Special Status Consideration

Many of the stands of *C. decornutus* are found on property owned by the Golden Gate National Recreation Area and managed by Pt. Reyes National Seashore. The total area occupied by *Ceanothus* patches overall is under 0.25 km² and the majority of populations are on other adjacent property and some are within a development to the north end of the ridge. Currently, these populations do not seem at risk except within the development should

the development expand in the future. Historic cattle management practices in the area have preserved this taxon as well as other rare species co-occurring at the same site both on public lands as well as on private lands nearby. At the same time, this is a rare species with relatively limited distribution, and it should be accorded special status. This will potentially be one of the rarest and most endangered of all the *Ceanothus* species. Purchasing lands or development rights from willing sellers might be a consideration.

KEY TO *C. DECORNUTUS* and SPINY-LEAVED ERECT *CEANOOTHUS* SHRUBS OF NORTHERN SF BAY REGION

- 1. Leaves alternate, stipules thin and deciduous (*Ceanothus* section *Ceanothus*)
- 1'. Leaves generally opposite, stipules thick, corky and persistent (*Ceanothus* section *Cerastes*)
- 2. Leaf blade generally flat or convex to concave adaxially, leaf margin entire or teeth \pm sharp, but not spine-like
- 3. Leaves broadly ovate to widely elliptic, base round, edge not revolute, usually 13–17 small teeth well distributed along the edge *C. gloriosus* (several varieties)
- 3'. Leaves narrowly ovate to oblong, base usually cuneate, edge slightly revolute, 3–5 teeth generally above the middle of the leaf. *C. confusus*
- 2'. Leaf blade \pm wavy to \pm folded lengthwise, leaf margin with spiny teeth
- 4. Leaf blade elliptic to narrowly obovate *C. divergens*
- 4'. Leaf blade widely elliptic to \pm round
- 5. Leaves \pm spreading, margin 3–5-toothed *C. sonomensis*
- 5'. Leaves generally reflexed, margin 7–15-toothed
- 6. Sepals, petals 6(–8); fruit with prominent wavy ridges, horns wrinkled, 1.5–3 mm; generally rocky serpentine soils *C. jepsonii*
- 6'. Sepals, petals 5; fruit generally smooth, ridges, if present, generally straight, horns 1–1.3 mm; multiple soil types

- 7. Flowers dark blue to purple, leaves with 11–13 teeth, the teeth 2–3.2 mm long; volcanic substrates *C. purpureus*
- 7'. Flowers light blue to white, leaves with 7–9 teeth, the teeth 1–2.2 mm long; serpentine soil. *C. decornutus*

ACKNOWLEDGMENTS

Roger Raiche first realized this population might be different from *Ceanothus jepsonii* and brought it to the attention of Terri Thomas, who now is in charge of natural resources at the Presidio, but worked for the Golden Gate National Recreation Area at that point.

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