

A NEW *CEANOTHUS* (RHAMNACEAE) SPECIES FROM NORTHERN
BAJA CALIFORNIA, MEXICO

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ABSTRACT

Ceanothus bolensis S. Boyd & J. Keeley is a new species in the subgenus *Cerastes* from northwestern Baja California, Mexico. It is well represented at elevations above 1000 m on Cerro Bola, a basaltic peak approximately 35 km south of the U.S./Mexican border. It is characterized by small, obovate to oblanceolate, cupped, essentially glabrous leaves with sparsely toothed margins, pale blue flowers, and globose fruits lacking horns. Principal components analysis on morphological traits shows it to be distinct from other members of *Cerastes* which are distributed away from the coast in southern California and Baja California, Mexico. These phenetic comparisons also suggest that *Ceanothus otayensis* should not be subsumed under *C. crassifolius*, as treated in the Jepson Manual, but rather should be retained at specific rank as well.

RESUMEN

Ceanothus bolensis S. Boyd & J. Keeley es una nueva especie del subgénero *Cerastes* en el noroeste de Baja California, México. Esta bien representada en altitudes por arriba de los 1000 m en el Cerro Bola, un pico basáltico, aproximadamente a 35 km de la frontera de USA/México. Esta se caracteriza por hojas pequeñas, obovadas a oblanceoladas, convexas, esencialmente glabras y con márgenes esparcidamente dentados, flores azul pálido y frutos globosos sin cornículos. El análisis de componentes principales con caracteres morfológicos la presenta como distinta de otros miembros de *Cerastes* distribuidos lejos de la costa en el sur de California y de Baja California, México. La comparación fenética también sugiere que *Ceanothus otayensis* no debe ser incluida dentro de *C. crassifolius* como en el Manual de Jepson, sino más bien debería ser retenida a nivel especie.

Key Words: *Ceanothus*, subgenus *Cerastes*, Baja California, Mexico, phenetic analysis, endemic.

Ceanothus is a diverse genus of shrubs with the center of species diversity in the Mediterranean-climate California Floristic Province (Schmitt 1993; source for nomenclature, except where indicated). It comprises approximately 60 species (van Renssalaer and McMinn 1942) more or less equally divided into two clades that have long been systematically recognized as subgenera *Ceanothus* and *Cerastes* (Harding et al. 2000).

Recent collections of a *Ceanothus* from northern Baja California, Mexico suggest a new taxon that is worthy of recognition. These collections are from Cerro Bola, a basaltic mountain, approximately 35 km south of the Tecate border crossing. At elevations between 1000 m and the peak at 1290 m, a small-leaved, erect, divaricately branched *Ceanothus* species in the subgenus *Cerastes* is frequent in chaparral dominated by

Arctostaphylos glandulosa Eastw. ssp. *adamsii* (Munz) Munz and *Chamaebatia australis* (Brandege) Abrams. It is less frequent on lower slopes from at least 500 m elevation. This *Ceanothus* shares features with several other *Cerastes* species distributed in southern California and adjacent Baja California, Mexico. The lack of fruiting horns and deeply concave, toothed leaves suggests an affinity with *Ceanothus greggii* A. Gray var. *perplexans* (Trel.) Jepson and with the relatively recently described *C. ophiophilus* Boyd, Ross, & Arnseth (Boyd et al. 1991), a rare endemic in southwestern Riverside County. The small leaf size of the Cerro Bola plants is similar to *C. ophiophilus* and *C. otayensis* McMinn (van Renssalaer and McMinn 1942), a localized endemic on two mountain peaks in southern San Diego County, California and immediately adja-

cent Baja California, ca. 30–35 km northeast of Cerro Bola. In the most recent floristic treatment *C. otayensis* is treated as a hybrid derivative of *C. crassifolius* Torr., a widespread species away from the coast in southern California and Baja California, and *C. greggii* var. *perplexans*, the principle *Cerastes* species from the interior slopes of the Peninsular Ranges (Schmitt 1993).

METHODS

Herbarium specimens of the Cerro Bola taxon and other *Ceanothus* species in subgenus *Cerastes* from southern California were used for phenetic comparisons. Because fruit morphology has more distinguishing characters than flowers, only fruiting specimens were selected. Species used for comparison were *Ceanothus greggii* var. *perplexans*, *C. greggii* var. *vestitus* (Greene) McMinn, *C. ophiophilus*, *C. otayensis*, and *C. crassifolius*.

We selected 14 characters for analysis; 6 continuous quantitative, 7 qualitative and 1 calculated ratio (Table 1). For quantitative characters, two samples were measured for each specimen and the mean was used in the analysis. For qualitative characters, characteristics were given a relative score from 1 to 5. All character states were standardized as z-scores by subtracting each observation from the mean of all individuals, and dividing by the standard deviation. A species matrix of these scores was used for ordination with principal components analysis using SYSTAT 5.05 (Evanston, IL).

RESULTS

Means values for phenetic characters for all taxa discussed above are shown in Table 1. The Cerro Bola specimens have the smallest leaves but they are not significantly different from the other two small-leaved taxa, *C. ophiophilus* and *C. otayensis*. Cerro Bola plants are similar to *C. ophiophilus* in their very deeply concave leaves, limited pubescence, and smaller fruits that lack horns, however, these two taxa differ in their leaf shape, reflected in the leaf length/width ratio. The broad leaves of Cerro Bola plants are quite unlike the nearly linear leaves of *C. ophiophilus*, which generates a length/width ratio roughly double that of all other taxa. The low apical angle on leaves of Cerro Bola plants is quite unlike *C. ophiophilus* but similar to *C. otayensis* and *C. greggii* var. *perplexans*. *Ceanothus otayensis* separates from all other taxa, except *C. crassifolius*, in having revolute leaves, well developed, often brownish pubescence on branchlets and undersides of leaves.

The principal components analysis for all taxa (Fig. 1), explained 50% of the total variance on the factor 1 axis and 20% on the factor 2 axis. *Ceanothus crassifolius* was widely separated from the other taxa on the factor 1 axis; the most important components being convex leaves, revolute margins,

TABLE 1. LEAF AND FRUIT COMPARISON OF *CEANOETHUS BOLENSIS* AND OTHER SPECIES IN SUBG. *CERASTES* (X ± SD).

Character	<i>C. bolensis</i>		<i>C. greggii</i> var. <i>perplexans</i>		<i>C. greggii</i> var. <i>vestitus</i>		<i>C. ophiophilus</i>		<i>C. otayensis</i>		<i>C. crassifolius</i>	
	n	26	9	7	12	10	12	10	12	10	12	10
Leaf length (mm)	4.9 ± 0.8	14.7 ± 2.6	10.1 ± 2.4	5.2 ± 0.8	7.1 ± 1.7	23.0 ± 4.4	5.2 ± 1.2	12.1 ± 2.6	5.2 ± 1.2	12.1 ± 2.6	1.9 ± 0.3	1.9 ± 0.3
Leaf width (mm)	3.9 ± 0.7	12.2 ± 1.9	5.9 ± 1.8	1.7 ± 0.5	1.4 ± 0.2	4.6 ± 0.7	3.2 ± 1.1	4.5 ± 0.5	3.2 ± 0.5	4.6 ± 0.7	1.0 ± 0.0	1.0 ± 0.0
Length/width ratio	1.3 ± 0.2	1.2 ± 0.1	1.8 ± 0.4	3.2 ± 1.1	3.3 ± 0.3	3.8 ± 0.8	4.5 ± 0.5	1.0 ± 0.0	3.8 ± 0.8	4.6 ± 0.7	2.8 ± 1.1	2.8 ± 1.1
Leaves concave (1 = no, 5 = extreme)	4.3 ± 0.7	2.9 ± 0.6	3.3 ± 0.3	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0
Leaves revolute (1 = no, 5 = extreme)	1.0 ± 0	1.1 ± 0.2	1.0 ± 0	1.8 ± 1.1	1.8 ± 1.1	1.8 ± 1.1	1.3 ± 0.7	2.4 ± 0.7	3.5 ± 0.4	3.5 ± 0.4	2.8 ± 1.1	2.8 ± 1.1
Teeth on leaves (1 = none, 5 = many)	3.4 ± 0.7	3.8 ± 0.6	3.8 ± 0.6	37.5 ± 11.8	37.5 ± 11.8	37.5 ± 11.8	24.2 ± 7.3	24.2 ± 7.3	5.2 ± 5.6	5.2 ± 5.6	29.5 ± 15.3	29.5 ± 15.3
Apical angle of leaves (°)	4.8 ± 5.1	6.7 ± 4.3	6.7 ± 4.3	54.6 ± 17.3	54.6 ± 17.3	54.6 ± 17.3	77.5 ± 4.1	77.5 ± 4.1	57.7 ± 7.3	57.7 ± 7.3	50.5 ± 10.3	50.5 ± 10.3
Basal angle of leaves (°)	50.1 ± 13.6	37.5 ± 20.0	37.5 ± 20.0	3.6 ± 0.5	3.6 ± 0.5	3.6 ± 0.5	2.1 ± 0.3	2.1 ± 0.3	4.4 ± 0.5	4.4 ± 0.5	5.0 ± 0.0	5.0 ± 0.0
Pubescence on branchlets (1 = glabrous, 5 = dense)	2.6 ± 0.5	3.3 ± 0.9	3.3 ± 0.9	2.7 ± 0.5	2.7 ± 0.5	2.7 ± 0.5	1.0 ± 0.0	1.0 ± 0.0	4.3 ± 0.5	4.3 ± 0.5	4.9 ± 0.3	4.9 ± 0.3
Pubescence on leaf abaxial side (1 = glabrous, 5 = dense)	1.0 ± 0.0	1.7 ± 1.0	1.7 ± 1.0	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	4.3 ± 0.5	4.3 ± 0.5	4.9 ± 0.3	4.9 ± 0.3

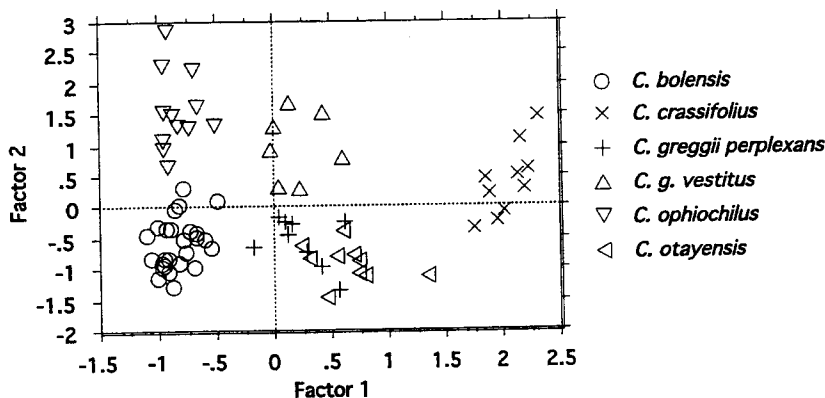


FIG. 1. Principal components analysis of *Ceanothus crassifolius*, *C. greggii* var. *perplexans*, *C. greggii* var. *vestitus*, *C. otayensis*, *C. ophiochilus*, and *C. bolensis*. Factor loading scores are in Table 2.

leaf length, pubescence characters and fruit horns (Table 2). *Ceanothus otayensis* was clearly separated from *C. crassifolius* on both the factor 1 and factor 2 axes but overlapped with *C. greggii* var. *perplexans* (Fig. 1).

Taking *C. crassifolius* out of the analysis gave greater resolution to the separation of *C. otayensis* and *C. greggii* var. *perplexans* (Fig. 2). In this analysis, factors 1 and 2 explained 36% and 21%, respectively of the total variance. *Ceanothus otayensis* was most prominently separated along the factor 1 axis, where pubescence characters and degree of leaf concavity were among the important components. On the factor 1 axis the Cerro Bola plants were distinctly intermediate to *C. otayensis* and *C. ophiochilus*. Cerro Bola plants were distinctly separated from *C. greggii* varieties on the factor 2 axis, where the important components were pedicel length, fruit horns, leaf length and apical angle (Table 2). Clearly there is a sound morphological basis for the recognition of the Cer-

ro Bola taxon (Figs. 1, 2), treated here as a new species.

SPECIES TREATMENT

Ceanothus bolensis S. Boyd and J. Keeley, sp. nov. (Fig. 3)—TYPE: MEXICO, Baja California, chaparral with *Chamaebatia australis* on NE side of Cerro Bola, S of Tecate, elevation 1000 m, 26 Apr 1996, Jon E. Keeley 27233 (RSA).

Differt a *C. ophiochilus* foliis late obovatis vel late oblanceolatis; a *C. otayensis* foliis glabris, non concavis, marginibus revolutis; a *C. greggii* var. *perplexans* foliis glabris, parvulis (sub 6 mm longis).

Erect, divaricately branched shrub, 1–1.5 m tall, lacking basal burl and not resprouting after top-killed. Older stems ashy gray, intricately branched with rigid diverging branches. Younger branches reddish gray and lightly puberulent. Stipules thick-

TABLE 2. CHARACTERS USED IN PHENETIC ANALYSIS AND FACTOR LOADINGS FOR PRINCIPAL COMPONENTS ANALYSIS FOR FIGURES 1 AND 2.

Character	Figure 1		Figure 2	
	Factor 1	Factor 2	Factor 1	Factor 2
Leaf length	0.88	0.04	0.64	0.60
Leaf width	0.78	-0.25	0.71	0.30
Length/width ratio	-0.08	0.86	-0.504	0.460
Leaves revolute	0.83	-0.06	0.66	-0.39
Leaves concave	-0.92	0.04	-0.78	-0.24
Teeth on leaves	0.11	-0.84	0.52	-0.52
Apical angle of leaves	0.35	0.77	-0.25	0.73
Basal angle of leaves	-0.22	0.70	-0.44	0.17
Pubescence on branchlets	0.88	-0.17	0.84	-0.10
Pubescence on bottom of leaves	0.88	-0.03	0.77	-0.11
Pubescence includes brown hairs	0.78	-0.13	0.66	-0.41
Pedicel length	0.67	0.31	0.36	0.81
Fruit width	0.76	0.13	0.42	0.17
Presence of fruit horns	0.82	0.27	0.49	0.63

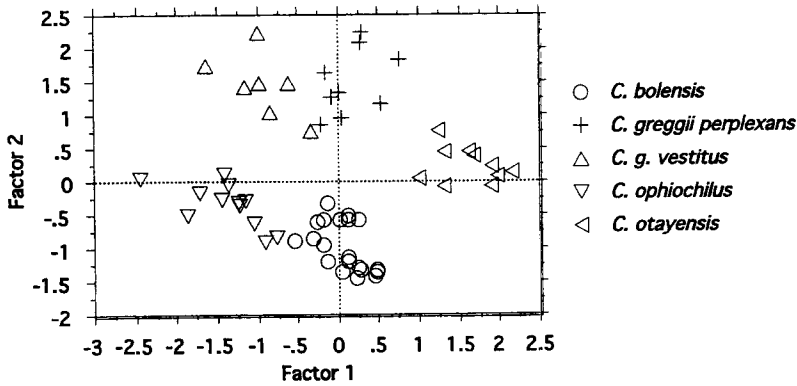


FIG. 2. Principal components analysis without *Ceanothus crassifolius*, but including all other taxa considered in Fig. 1. Factor loading scores are in Table 2.

ened and persistent, waxy or corky, dark reddish brown to purplish black. Leaves evergreen, thick, coriaceous, yellowish green, opposite, often clustered on short axillary spur branches; petioles 0.5–1 mm long, \pm 0.4 mm wide, minutely puberulent; blades broadly obovate to oblanceolate, deeply concave, (2.5)4–6(10) mm long and (3)4–7(9) mm wide, surfaces sparsely puberulent when young, glabrate in age, margins not revolute, sharply dentate distally with (1)2–3 pairs of lateral teeth and an apical tooth; midvein prominent abaxially, lateral veins obscure, 3–5 pairs. Inflorescence a subumbellate axillary raceme, peduncle \pm 2 mm long, densely short puberulent, bearing 6–8 flowers. Calyx, including receptacular disk \pm 5 mm wide at anthesis, lobes 5, pale blue, fading cream-white, 1.8–2 mm long, deltoid to ovate, apex acute. Petals 5, pale blue, fading cream-white, 1.8–2 mm long, ladle-shaped, \pm equally divided into deeply saccate distal blade and filiform proximal claw. Stamens 5, filament 1.8–2 mm long, anther \pm 0.4 mm. Ovary with style 1.8–2 mm long, 3-lobed, the lobes \pm 0.4 mm; fruit a globose to depressed globose capsule, dark green to reddish, 3–4 mm diameter, smooth, lacking apical horns, lateral valve crests absent or vestigial.

Distribution. At present, *Ceanothus bolensis* is known only from the mid- to upper slopes of Cerro Bola (>500 m), where it is locally common in the chaparral vegetation. To our knowledge, no other member of subgenus *Cerastes* is found on the mountain, and plants are uniform in overall gross morphology. Cerro Bola is noteworthy as a station for several other phylogeographically interesting taxa, such as the near-endemic *Arctostaphylos bolensis* P. V. Wells, as well as *Ceanothus papillosus* Torr. var. *roweanus* McMinn and *Lepechinia cardiophylla* Epling, two taxa considerably disjunct from their previously known occurrences in the Santa Ana Mountains of Orange and

Riverside counties, California (Boyd et al. in prep).

Paratypes. MEXICO, Baja California, chaparral with *Chamaebatia australis* on NE side of Cerro Bola, S of Tecate, elevation 1000 m, 26 Apr 1996, Jon E. Keeley 27232 (BCMEX); *ibid.*, Jon E. Keeley 27227 (CAS); *ibid.*, Jon E. Keeley 27234 (SD); *ibid.*, Jon E. Keeley 27238 (US); *ibid.*, Jon E. Keeley 27236 (MEXU); occasional in chaparral on north slope of Cerro Bola, seen to summit (1275 m), near 31°19.5'N, 116°40'W, elevation ca. 550 m, 6 Jun 1970, Reid Moran 17780 (RSA, SD).

RELATIONSHIPS

Ceanothus bolensis shows a marked morphological similarity to several other members of subgenus *Cerastes* in the southern California region. It is most distinct from the widespread *C. greggii* var. *perplexans* by having very small leaves that are deeply concave. These two leaf traits bear a strong resemblance to *C. ophiochilus*, however, leaf shape is markedly different, with the latter species being more similar in leaf shape to *C. greggii* var. *vestitus*.

Ceanothus bolensis is quite distinct from another local endemic, *C. otayensis*, a taxon restricted to a few mountain peaks about 30–35 km northwest of Cerro Bola. *Ceanothus otayensis* has been subsumed under *C. crassifolius* (Schmitt 1993) due to the presence of several shared morphological similarities (revolute leaves and dense pubescence that includes brown hairs). Munz (1959) likewise treated *C. otayensis* as *C. xotayensis* McMinn, and suggested it was probably a hybrid between *C. crassifolius* and *C. greggii* var. *perplexans*. However, principal component analysis on all 14 traits shows *C. otayensis* to be quite distinct from *C. crassifolius* (Fig. 1) and distinct from *C. greggii* (Fig. 2). Extensive exploration of both known southern California localities of *C. otayensis*, the upper slopes of Otay Mtn. (1090 m) and San Miguel Mtn. (780 m),

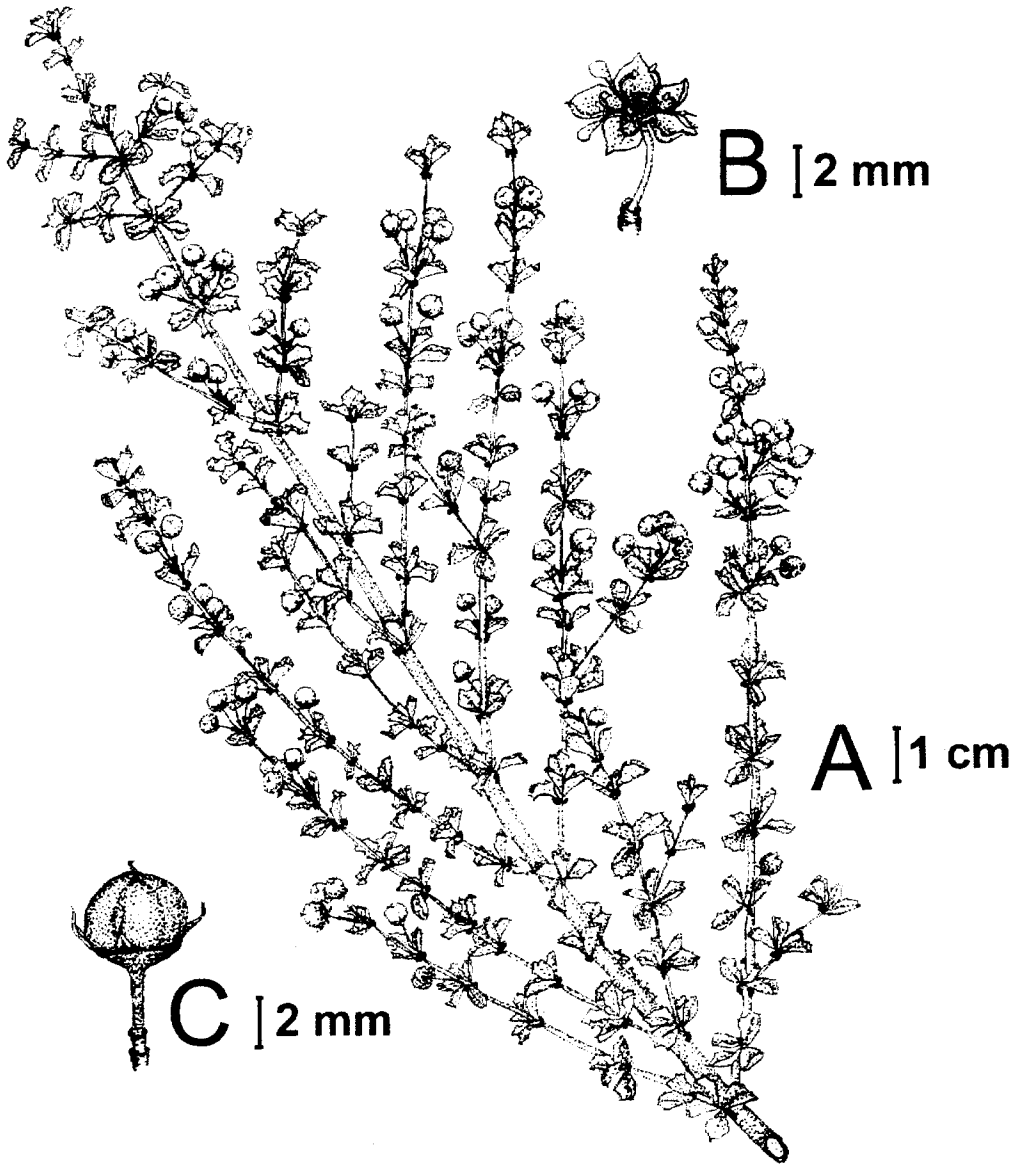


FIG. 3. *Ceanothus bolensis*. A. Fruiting branch showing characteristic small, toothed leaves, and hornless fruits on short axillary peduncles. B. Detail of individual flower. C. Detail of mature capsule showing absence of apical or lateral horns. (Illustrations by Melanie Baer-Keeley.)

failed to uncover populations of either *C. greggii* or *C. crassifolius*. *Ceanothus otayensis* forms homogenous populations that appear to be breeding true and lack any indication they are unstable hybrid swarms (J. Keeley unpublished observations). In addition to the naming of *C. bolensis*, we suggest *C. otayensis* be recognized at the specific rank as described by McMinn (van Rensselaer and McMinn 1942).

ACKNOWLEDGMENTS

Fieldwork and collections by Keeley were conducted in collaboration with Dr. Jose Delgadillo, Universidad Autonoma de Baja California, Ensenada, Baja California, Mexico (BCMEX). We wish to extend our thanks to Melanie Baer Keeley for preparing the illustration of *C. bolensis*, to Rosa Cerros Tlatilpa for kindly providing the Spanish resumen, and to Elizabeth Friar for assistance in producing figures 1 and 2.

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