ARCTOSTAPHYLOS INCOGNITA, A NEW SPECIES AND ITS PHENETIC RELATIONSHIP TO OTHER MANZANITAS OF BAJA CALIFORNIA

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ABSTRACT

Arctostaphylos incognita Keeley, Massihi, Delgadillo & Hirales is a new diploid, burl-forming manzanita endemic to rhyolitic soils in the northern coast range of Baja California. The intensely glaucous and glabrous foliage, coupled with highly reduced bracts on nascent panicles, bears remarkable resemblance to that of another Baja California manzanita, *A. peninsularis*, which is restricted to granitic soils in the interior ranges of the Sierra San Pedro Mártir and Sierra Juárez. The extreme differences in fruit structure, however, readily distinguish these two species. Unlike the round fruits with leathery pericarp and solid endocarp stones of *A. peninsularis*, the new *A. incognita* has depressed fruits with mealy pericarp and separable nutlets, indistinguishable from those of *A. glandulosa*. Principal components analysis based on 57 phenetic characters showed that the widespread *A. glandulosa* and *A. glauca* were clearly separable from the five species endemic to Baja California; *A. incognita*, *A. peninsularis*, *A. australis*, *A. bolensis*, and *A. moranii*. Principal components analysis on the endemic species alone showed that *A. incognita* was closest to *A. peninsularis* and further analysis showed that *A. australis* and *A. moranii* overlapped a great deal in their morphology. Also we report here chromosome numbers for *A. incognita* (n=13), for the first time for *A. australis* (n=13), and *A. moranii* (n=26).

RESUMEN

Arctostaphylos incognita Keeley, Massihi, Delgadillo & Hirales, es una nueva especie de manzanita diploide que forma nudos y es endémica de las cordilleras costeras del norte de Baja California. Su folláje intensamente glauco y glabro, con brácteas reducidas en panículas nacientes, tienen una notable semejanza a *A. peninsularis*, una especie restringida a las cordilleras interiores de Sierra Juárez y Sierra San Pedro Mártir. La estructura del fruto en *A. incognita* es muy diferente a las de *A. peninsularis*, en cambio frutos depresos y aplanados con pericarpo granuloso y nuecesillas separables son indistinguibles en *A. glandulosa*. Un análisis de componentes principales basado en 57 caractéres fenéticos, nostró claramente una separación de mayormente endémicas a Baja California; *A. incognita*, *A. peninsularis*, *A. australis*, *A. bolensis* y *A. moranii*. Por otra parte, el análisis de componentes principales de sólo las especies endémicas mostraron que *A. incognita* esta proxima a *A. pen-*

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insularis, y *A. australis* y *A. moranii* al traslaparse una gran parte de sus caracteristicas morfológicas. También, se reporta el número cromosómico de *A. incognita* (n=13), *A. australis* (n=13), y *A. moranii* (n=26).

The manzanita flora of northern Baja California comprises nine shrub species, four of which are endemic to the state; three are restricted to the coast ranges and one to the interior ranges. The coast ranges species include *Arctostaphylos australis* Eastwood, a non-burl-forming species distributed in widely disjunct populations, mostly south of Ensenada (latitude 31°50′). *Arctostaphylos bolensis* Wells is another non-burl-forming species, which was described recently from a single population at about 600 m elevation on the north side of Cerro Bolo, 25 km south of Tecate (Wells 1992). Although apparently not widespread, it also occurs at about the same elevation on Cerro Italia, approximately 10 km south of the type locality (*J. E. Keeley 2337* RSA). Another localized endemic is the burl-forming *A. moranii* Wells, which is restricted to north of Ensenada, between Cerro Ensenada and El Tigre.

In the interior ranges, *A. peninsularis* Wells is the only manzanita endemic to Baja Calfornia; early reports of this species in coastal San Diego County were in error and represent *A. rainbowensis* Keeley & Massihi and interior San Diego Country reports of this species (Keeley and Massihi 1994) are based on specimens that require further study. In the northern part of *A. peninsularis's* range, in the Sierra Juárez, it is a non-burl-forming single-stemmed arborescent shrub (*A. peninsularis* ssp. *juarezensis* Keeley, Massihi, & Goar 1992, Keeley and Massihi 1994). Farther south, largely in the Sierra San Pedro Mártir, it is a low-growing, multi-stemmed resprouting shrub. Although the other Baja manzanitas are very widespread outside of Mexico, within Baja California they too are restricted to either the coast or the interior ranges. *Arctostaphylos glandulosa* Eastw. with one of the widest ranges in the genus, is a burl-forming shrub restricted to the coast ranges, extending inland only to the foothills east of Ensenada. The non-burl-forming *A. pungens* Kunth, *A. pringlei* Parry, and *A. patula* Greene are restricted to high elevations in the interior ranges, and are widespread in southwestern North America. The only species not restricted to coastal or interior ranges is the widespread non-burl-forming *A. glauca* Lindl., occurring on the interior sides of the coast ranges and well into the inteior ranges.

Recent collections have uncovered a new manzanita species endemic to the coast range north of Ensenada, Baja California. This taxon is described here and a multivariate phenetic comparison is made between it and associated *Arctostaphylos*.

Species Treatment

Arctostaphylos incognita J. Keeley, A. Massihi, J. Delgadillo, & S. Hirales. sp. nov. (Fig. 1)—TYPE: MEXICO, Baja California,

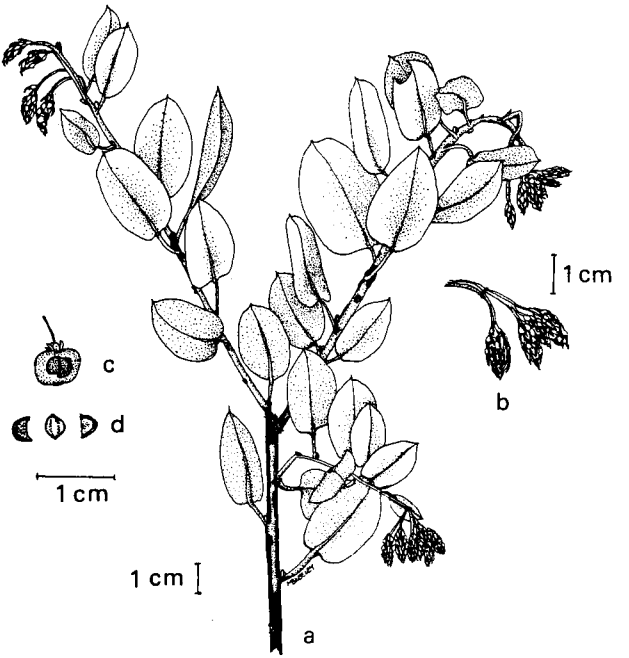

FIG. 1. *Arctostaphylos incognita* (J. Keeley 24108). a. Branchlet with nascent inflorescences. b. Nascent inflorescence. c. Whole fruit. d. Pyrenes. By Melanie Baer Keeley.

NE slope of Cerro Italia, W of Carmen Serdán, elevation 620 m, 9 August 1993, *J. E. Keeley 24108* (holotype, RSA; isotypes, BCUGX,CAS,SD,MO).

Frutices erecti aut arbores, 1–4 m alti; caudex tumescens, repullulans post combustum; cortex laevus rufus; ramuli glabris; laminae isofaciales, numero stomatarum adaxiales et abaxiales aequalis, ellipticae, glaucae, apices rotundi, basis acuti-rotundi, petioli 4–6 mm longi; inflorescentiae nascens descendens, paniculate, ramuli 5–6, glabrati; bracteae 1–2 mm longae, subulatae, acuminatate, glabrae; pedicelli 5–7 mm longi, glabri; corolla urceolatae, 5–6 mm longae, 4–5 mm latae, albae; ovaria glabra; drupae depressae, 5–6 mm longae, 8–9 mm latae, glabrae, rubrae, mesocarpia crassa, separabiles.

Erect shrub or arborescent, 1–4 m high, with large globose burl on unburned shrub or platform-like on resprouted shrubs. Bark red-brown, smooth. Branchlets glabrous and glaucous. Leaves isofacial with equal number of stomata on adaxial and abaxial sides, blades 35–40 mm long, 25–30 mm wide, elliptic, glabrous, and heavily glaucous, base acute to rounded with rounded apex, petioles 4–6 mm. Panicle with 5–6 branches; bracts 1–2 mm, overlapping, del-

toid-subulate, keeled, upper-half early marcescent; rachis glabrous. Corolla urceolate, 5-lobed, white, pubescent inside, 5–6 mm long, 4–5 mm wide; inflated filaments bases densely hairy; ovary glabrous; pedicel glabrous; sepals reflexed. Fruit depressed, 5–6 mm long, 8–9 mm wide, glabrous, red; mesocarp thick and mealy, nutlets separable. Flowering January–February. n=13 (J. Keeley & A. Massihi). The epithet was inspired by the fact that, although populations of this species are easily visible from one of the two major highways in northern Baja California, it has long been overlooked by botanists. The arborescent stature and glaucous foliage of *A. incognita* provide a perfect disguise as it resembles *A. glauca,* which is common near the highway.

Distribution. In addition to the type locality on the NE side of Cerro Italia and surrounding hills, we have made additional collection of this species approximately 15 km SW, along a dirt road W of San Jose de la Zorra. All of these collections were from rhyolite soils between 300 and 700 m. North of the type locality, at about 600 m on basaltic soil on the N side of Cerro Bolo there are populations of manzanitas very similar to *A incognita,* however, as one ascends to the peak this taxon intergrades morphologically with *A. glandulosa.* Wells (1987) describes the intensely glaucous population at the top of Cerro Bolo Peak (1200 m) as *A. glandulosa* ssp. *adamsii* forma *wieriana* Wells.

Paratypes. MEXICO, Baja California, 24.5 km NE of La Misión on road to San Jose de la Zorra, 340 m, 30 August 1993, *J. Keeley 24210* (RSA); 22 km NE of La Misión on road to San Jose de la Zorra, 30 August 1993, 370 m, *J. Keeley 24256* (RSA); SE of Ejido Carmen Serdán, 530 m, 27 July 1993, *Massihi, Hirales, & J. Keeley 23520* (RSA); 2 km SE of Carmen Serdán, 550 m, 19 February 1994, *J. Keeley 25237* (RSA).

Phenetic Analysis of *A. incognita* and Other Baja California Manzanitas

Phenetic data were collected from herbarium specimens and used to compare *A. incognita* with other species from Baja California. Extensive collections of this new species and other Baja California manzanitas were made during late summer, when both fruits and nascent inflorescences were available (specimens are housed at RSA and BCUGX).

Methods

Species. The phenetic analysis included the Baja California species most similar to *A. incognita* (sample sizes and collection locations are in Table 1). Sample sizes were in part a function of

TABLE 1. SPECIES, SAMPLE SIZES AND LOCATION OF *ARCTOSTAPHYLOS* USED IN THE PHENETIC ANALYSIS. Letter codes used in Figures 2–4 are included.

Species	(Code)	Specimens sampled	Collecting locations
A. australis	(A)	25	South of Ensenada
A. bolensis	(B)	26	Type locality, North side of Cerro Bolo
A. incognita	(I)	70	Throughout its range (see text)
A. glandulosa	(g)	30	Southern San Diego County
A. glandulosa var. *adamsii* forma *wieriana*	(C)	22	Cerro Bolo Peak
A. glauca	(G)	30	Southern San Diego County North Baja California
A. moranii	(M)	22	Type locality, near San Jose de las Minas
A. peninsularis	(P)	80	Sierra Juárez & Sierra San Pedro Mártir

TABLE 2. CHARACTERS USED IN PRINCIPLE COMPONENTS ANALYSIS AND FACTOR LOADINGS FOR FIGURES 2, 3, AND 4. Characters lacking scores were dropped due to zero variance.

	Figure 2		Figure 3		Figure 4	
Character	Factor 1	Factor 2	Factor 1	Factor 2	Factor 1	Factor 2
Presence or absence of burl	0.46	−0.38	−0.19	−0.68	−0.06	0.82
Leaf blade length	0.24	−0.22	0.12	−0.67	0.01	−0.26
Leaf blade width	−0.05	−0.11	0.14	−0.50	−0.16	−0.32
Ratio leaf length/width	0.21	0.01	−0.42	−0.19	0.12	−0.76
Basal angle	0.38	−0.32	−0.01	−0.31	0.14	0.35
Apical angle	0.39	−0.10	−0.05	−0.24	0.07	0.13
Blade shape	0.26	−0.08	−0.10	−0.04	−0.11	−0.11
Petiole length	−0.17	−0.10	0.24	−0.24	0.43	−0.25
Leaf color	0.09	−0.03	0.11	−0.16	−0.03	−0.06
Leaf glaucousness	0.63	−0.08	0.55	−0.36	0.24	0.21
Leaf scabrousness	0.91	0.26	0.36	0.08	0.17	−0.06
Density of abaxial stomata	0.50	0.46	−0.07	−0.34	−0.84	0.04
Density of adaxial stomata	−0.01	0.47	0.02	−0.27	−0.85	−0.07
Abaxial stomata/adaxial stomata	0.68	0.15	−0.14	−0.09	0.20	0.26
Branchlet pubescence	0.89	0.13	0.87	0.25	0.56	0.11
Petiole pubescence	0.90	0.14	0.86	0.24	0.44	0.29
New leaf blade pubescence	0.84	0.17	0.81	0.15	−0.26	0.35
Old leaf blade pubescence	0.64	0.10	0.66	0.10	−0.63	0.47
Rachis pubescence	0.88	0.10	0.78	0.16	0.77	−0.07
Pedicel pubescence	0.73	0.59	0.68	0.26	0.46	0.22
Fruit pubescence	0.51	0.19	—	—	—	—
Branchlet glandularity	0.90	0.21	0.42	0.22	0.67	−0.20
Petiole glandularity	0.71	0.17	0.24	0.14	0.36	−0.09
New leaf blade glandularity	0.81	0.25	0.07	−0.02	−0.16	−0.07
Old leaf blade glandularity	0.51	0.12	−0.02	−0.07	—	—
Rachis glandularity	0.87	0.22	0.50	0.27	0.86	−0.37
Pedicel glandularity	0.48	0.79	0.48	0.21	0.45	0.11
Fruit glandularity	−0.06	0.89	−0.07	0.13	—	—
Inflorescence length	−0.18	−0.02	0.16	0.09	−0.04	0.31
Number of rachis branches	−0.09	−0.33	0.40	−0.16	−0.17	0.13
Nascent orientation	0.07	−0.14	0.64	0.04	−0.88	0.21
Bract spacing	−0.56	0.38	0.31	0.02	−0.81	0.07
Bract keel	−0.66	−0.03	−0.61	−0.44	0.14	0.32
Bract shape	−0.77	−0.19	−0.05	−0.16	−0.74	−0.10
Bract marcescence	−0.34	−0.64	−0.23	0.70	−0.14	0.03
Bract reflexed	−0.24	0.76	0.31	0.05	−0.10	−0.24
Bract length						
(subtending inflorescence)	0.79	0.35	0.20	0.53	0.87	−0.30
(subtending flower buds)	0.67	0.47	0.43	0.07	0.71	0.23
Pedicel length	−0.16	−0.02	−0.20	0.26	0.58	−0.13
Sepal shape	−0.41	−0.61	0.48	−0.53	0.22	−0.29
Sepal reflexed	0.48	−0.36	0.09	−0.11	0.43	−0.36
Fruit color	−0.39	0.26	−0.02	−0.25	0.29	−0.11
Fruit length	−0.52	0.76	−0.30	0.79	0.03	0.70
Fruit width	−0.14	0.74	−0.67	0.09	0.13	0.68
Fruit width/fruit length	0.58	−0.19	−0.26	−0.77	0.16	−0.03
Fruit weight	−0.41	0.84	−0.70	0.44	0.38	0.78
Pericarp weight	−0.26	0.68	−0.63	0.02	0.29	0.48
Endocarp weight	−0.44	0.83	−0.59	0.59	0.32	0.74

TABLE 2. CONTINUED

Character	Figure 2		Figure 3		Figure 4	
	Factor 1	Factor 2	Factor 1	Factor 2	Factor 1	Factor 2
Fruit weight/endocarp weight	−0.40	0.28	0.18	0.49	−0.04	0.06
Mesocarp texture	−0.12	0.06	0.06	0.09	−0.01	0.16
Endocarp segments	0.44	−0.33	−0.23	−0.79	0.09	0.09
Endocarp lateral ridges	0.51	−0.29	−0.82	−0.16	0.08	0.28
Endocarp sculpturing	0.34	−0.17	−0.87	0.02	−0.10	0.08
Endocarp apiculate	−0.71	0.33	−0.46	0.70	0.58	−0.21
Stone height	−0.56	0.74	−0.43	0.83	0.33	0.65
Stone width	−0.34	0.83	−0.53	0.67	0.48	0.60
Stone width/stone height	0.65	0.03	−0.10	−0.48	0.17	−0.10

availability of complete specimens, which included both nascent inflorescences and mature fruits. Three Baja California species, *A. pungens*, *A. pringlei*, and *A. patula* were not included in our comparison because they differ markedly from the other manzanitas, both morphologically and ecologically, and do not occur within the range of *A. incognita*.

Analysis. We used 57 characters in this study; 16 continuous quantitative, 2 meristic, 33 qualitative, and 6 calculated ratios (Table 2). Qualitative characters were given a ranking on a scale from 1 to 5. For quantitative characters, two samples were measured or weighted for each specimen and the mean was used in the analysis. As in previous studies (Keeley and Massihi 1994), patterns of variation suggested that more sampling of the same specimen was of less value than sampling more individuals in the population. In other words, despite the differences in sample size, the within specimen variance was seldom greater than the between specimen variance. Additionally, for most reproductive characters, a sample size of 2 was all that was available on each herbarium sheet. All character states were standardized by transforming each variable with a z-score calculated by subtracting each observation from the mean of all individuals, and dividing by the standard deviation. This matrix was used for ordination with principal components analysis using SYSTAT for Windows, Version 5.05 (Evanston, IL).

Stomatal distribution was determined from epidermal peels (2 × 2 cm) made with clear polish and examined at 25×. The mean of five different sections of a peel were recorded for each specimen. Chromosome counts were made from buds collected in February for one population of *A. incognita* (*J. Keeley 25237* RSA) and for a single population of two other Baja California manzanitas lacking published counts: *A. australis* (*J. Keeley 25239* RSA) and *A. moranii* (*J. Keeley 25238* RSA). Developing anthers were squashed in

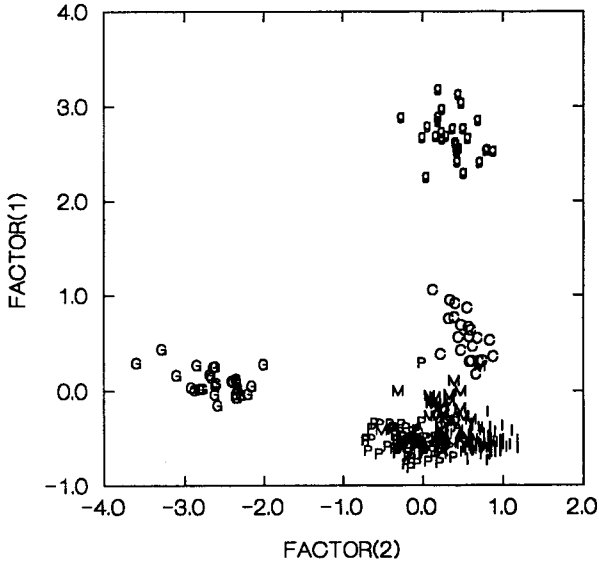

FIG. 2. Principal components analysis with all species listed in Table 1. Species are designated by letter codes listed in Table 1. Factor loading scores are in Table 2.

acetocarmine and viewed at 100×. This character was not used in the principal components analysis because *A. peninsularis* and *A. bolensis* have not been counted.

RESULTS

The first two components or factors of the principal components analysis for 261 specimens, including *A. incognita*, and the six other Baja California species distributed within its range, are shown in Figure 2. *Arctostaphylos incognita* and the other four Baja California endemic species are clearly differentiated from the widespread *A. glandulosa* on the factor 1 axis and from the widespread *A. glauca* on the factor 2 axis. The first factor explained 29% of the variance and the second factor explained 17% of the variance.

The factor loadings indicate the extent to which each character used in this analysis contributes to the variance in its respective plane and are shown in Table 2. Based on the component loadings for factor 1, it is apparent that the characters most important in distinguishing *A. glandulosa* from the five endemic species (and from *A. glauca*) are leaf and stem indument, and inflorescence bract length and shape. Component loadings for factor 2 indicated that fruit size and bract characters are most responsible for distinguishing *A. glauca* from the endemics (and from *A. glandulosa*). In this analysis, the Cerro Bolo Peak population of *A. glandulosa* (Wells 1987

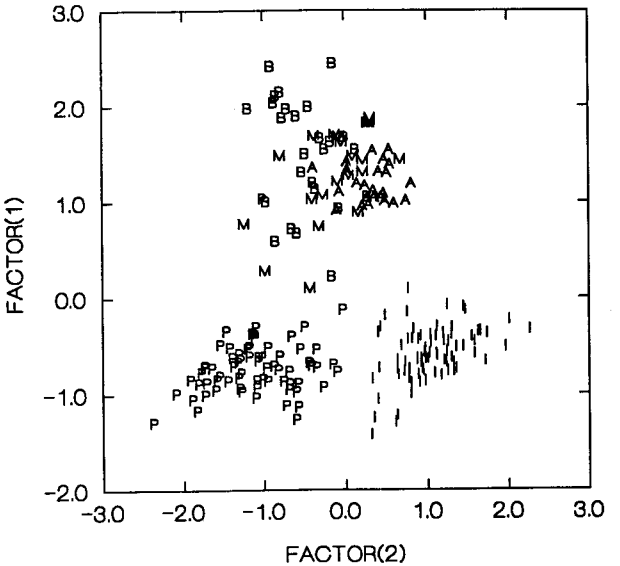

FIG. 3. Principal components analysis with *Arctostaphylos incognita* (I), *A. peninsularis* (P), *A. australis* (A), *A. bolensis* (B), and *A. moranii* (M). Factor loading scores are in Table 2.

refers these plants to ssp. *adamsii* forma *wieriana* Wells), is morphologically more similar to the Baja endemic species than to San Diego County *A. glandulosa* (Fig. 2). Although the Cerro Bolo *A. glandulosa* overlap with *A. bolensis*, which is also from Cerro Bolo, it is well separated from *A. incognita* (Fig. 2).

Principal components analysis for the five endemic species alone showed *A. incognita* and *A. peninsularis* can be distinguished readily from *A. australis*, *A. bolensis*, and *A. moranii* (Fig. 3). The first factor explained 20% of the variance and was the primary axis along which *A. incognita* and *A. peninsularis* separated from the other three endemic species. The component loading scores indicated that indument and a few fruit and leaf characters were most important in separation on the factor 1 axis (Table 2). *Arctostaphylos incognita* separated from *A. peninsularis* along the factor 2 axis and, based on the component loading scores, separation was largely due to fruit characters (Table 2).

Although *A. australis*, *A. bolensis*, and *A. moranii* are not differentiated in either of the above principal components analyses, they can be distinguished when analyzed alone (Fig. 4 and Table 2). *Arctostaphylos bolensis* separated clearly along the factor 1 axis, and this factor explained 19% of the variance. Factor 2 accounted

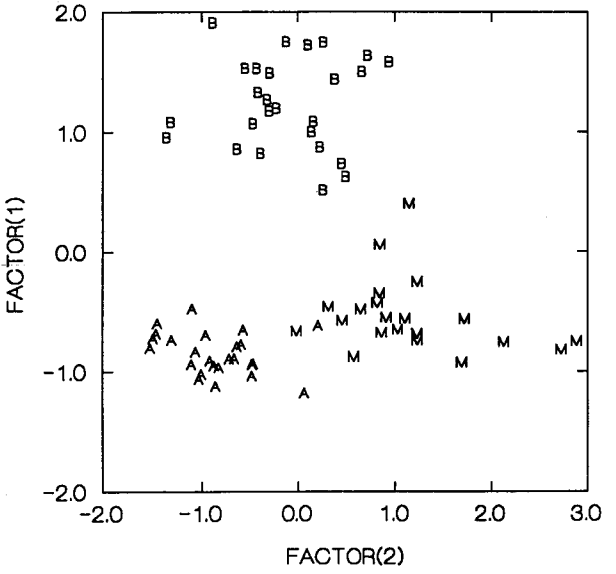

FIG. 4. Principal components analysis with *Arctostaphylos australis* (A), *A. bolensis* (B), and *A. moranii* (M). Factor loading scores are in Table 2.

for only 10% of the variance and still left some overlap between *A. australis* and *A. moranii.*

Chromosome counts were made on several individuals of *A. incognita* from one population (n=13), and for a single individual of *A. australis* (n=13) and *A. moranii* (n=26).

DISCUSSION

Based on the patterns of morphological similarity (Figs. 2 and 3), we hypothesize that *A. incognita* is related to *A. peninsularis.* Indeed, in the absence of reproductive structures, these species are remarkably similar and not readily distinguished. They have a similar leaf shape and similar foliage indument; leaves and branchlets are intensely glaucous and glabrous (Table 3). The only measurable differences in vegetative characteristics are larger leaves with a more acute base in *A. incognita.* Even the presence of nascent inflorescences would not assist in separating these two taxa as both have panicles with highly reduced bracts, although *A. incognita* panicles are more highly branched than those of *A. peninsularis.* However, fruit characteristics are radically different between these species (Table 3). The flattened or depressed fruits with mealy endocarp and separable nutlets of *A. incognita* contrasts sharply with the larger round fruits, leathery to papery pericarp, and solid stone of fused nutlets of *A. peninsularis.* The fact that these taxa differ in the struc-

ture of the exocarp, mesocarp, and endocarp, differences that nearly span the range of variation in the genus, supports their recognition as separate species.

A comparison of fruit characteristics (Table 3) reveals that *Arctostaphylos incognita* shares nearly identical fruit characteristics with *A. glandulosa,* suggesting the hypothesis that this species also has played a role in the ancestry of *A. incognita.* Tests of this hypothesis should include *A. glandulosa* ssp. *adamsii* forma *wieriana* from Cerro Bolo Peak, as it closely resembles *A. incognita* in its intensely glaucous leaves and reduced nascent inflorescence bracts.

Of course a phenetic analysis such as this can not unequivocally rule out convergence in accounting for the similarity of these taxa, but hybridization should be given serious consideration. There are countless cases of apparent hybridization in the genus and, although all are suggested by patterns of phenetic variation, a few have been supported with genetic evidence (Ellstrand et al. 1987; Nason et al. 1992). Based on the vegetative similarity between *A. incognita* and *A. peninsularis,* and the fruit similarity between *A. incognita* and *A. glandulosa,* it is tempting to hypothesis that the origin of this newly described species may involve an ancient hybridization between these two well known species.

Other scenarios, however, are possible, particularly since such parentage can not explain all characteristics associated with this new species. For example, Ball et al. (1983; see also Ellstrand et al. 1987 for genetic confirmation) showed that tolerance to water stress in *Arctostaphylos* hybrids was intermediate between a lower elevation species and a higher elevation species. *Arctostaphylos incognita* occupies a more arid habitat than either *A. peninsularis* or *A. glandulosa. Arctostaphylos peninsularis* is restricted to the interior ranges, above 1000 m on granitic soils (with one rare occurrence on an unusual slate outcrop in the Sierra San Pedro Mártir (*J. Keeley 23181–23191* LOC). In contrast, *A. incognita* is restricted to much lower elevations on rhyolitic soils in the interior side of the coast ranges. Although, *A. glandulosa* is widespread on rhyolitic soils, in the interior part of the coast ranges it is distributed at higher elevations than *A. incognita.* The arid habitat occupied by *A. incognita* is shared by *A. glauca* and thus, if we had included physiological and ecological characters in our principal components analysis we may have found a closer relationship between these two species than is evident in Figure 2.

Our comparison of *A. incognita* with the other Baja California *Arctostaphylos* raises a question about distinctness of *A. australis* and *A. moranii* (Fig. 4). Both *A. australis* and *A. moranii* have relatively thin nascent inflorescences that stand erect, with buds relatively widely spaced, characteristics heavily weighted in *Arctostaphylos* taxonomy and found in more northerly distributed species

TABLE 3. COMPARISON OF CHARACTERISTICS OF SELECTED BAJA CALIFORNIA *ARCTOSTAPHYLOS*. Mean ± standard error. Glaucous scale: 1 = intensely glaucous–5 = non-glaucous and lustrous. Bract marcescence scale: 1 = tips never withered–5 = tips always withered. Bract spacing scale: 1 = bracts strongly overlapping–5 = bracts very widely spaced.

Character	*A. incognita*	*A. peninsularis*	*A. glandulosa*	*A. glauca*	*A. australis*	*A. moranii*	*A. bolensis*
Sample size:	80	70	30	30	25	22	26
Chromosome #:	$n = 13$	?	$n = 26$	$n = 13$	$n = 13$	$n = 26$	?
Burl:	Yes	Yes & no	Yes (no)*	No	No	Yes	No
Leaves							
Length (mm):	39.5 ± 0.6	29.0 ± 0.5	37.3 ± 1.0	33.5 ± 1.2	35.2 ± 1.3	32.8 ± 1.3	34.3 ± 0.8
Ratio length/width:	1.6 ± 0.0	1.6 ± 0.0	1.8 ± 0.1	1.4 ± 0.0	1.5 ± 0.1	1.6 ± 0.1	1.6 ± 0.0
Basal angle (°):	27.7 ± 1.1	19.6 ± 1.3	31.4 ± 1.7	9.7 ± 1.5	18.7 ± 2.3	25.1 ± 2.4	19.7 ± 2.9
Glaucous (1–5 scale):	2.0 ± 0.0	1.1 ± 0.0	3.3 ± 0.1	1.5 ± 0.1	2.2 ± 0.1	2.4 ± 0.1	2.5 ± 0.1
Scabrous:	No	No	Yes	No	No	No	No
Stomata							
Abaxial density (#/mm^2):	24.2 ± 0.3	22.2 ± 0.8	40.6 ± 1.6	31.5 ± 1.2	29.3 ± 0.7	22.4 ± 0.5	16.1 ± 0.3
Ratio (ab-/adaxial):	1.0 ± 0.0	1.0 ± 0.0	1.6 ± 0.1	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0
Branchlet indument:	Glabrous & glaucous	Glabrous & glaucous	Pubescent to glandular-hispid	Glabrous & glaucous	Glabrous	Pubescent	Glandular-hispid
Inflorescences							
Nascent orientation:	Descending	Descending	Descending (erect)**	Descending	Erect	Erect	Descending to ascending
Branches (#):	6.0 ± 0.1	2.2 ± 0.1	2.0 ± 0.2	2.1 ± 0.2	4.0 ± 0.3	4.6 ± 0.3	3.4 ± 0.3
Basal bract lengths (mm):	0.1 ± 0.1	1.9 ± 0.3	12.4 ± 0.4	2.2 ± 0.5	0.0 ± 0.0	0.7 ± 0.4	5.3 ± 0.3
Bract marcescence (1–5 scale):	4.9 ± 0.1	2.8 ± 0.1	1.0 ± 0.0	1.8 ± 0.2	3.0 ± 0.2	3.0 ± 0.2	2.6 ± 0.2
Bract spacing (1–5 scale):	1.9 ± 0.1	2.0 ± 0.0	1.0 ± 0.0	3.9 ± 0.1	3.6 ± 0.2	2.5 ± 0.2	1.5 ± 0.1

TABLE 3. CONTINUED

Character	*A. incognita*	*A. peninsularis*	*A. glandulosa*	*A. glauca*	*A. australis*	*A. moranii*	*A. bolensis*
Fruits							
Ratio width/height:	1.5 ± 0.0	1.0 ± 0.0	1.7 ± 0.1	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0
Mass (mg):	198.6 ± 7.9	292.0 ± 10.5	184.5 ± 10.4	924.0 ± 38.7	81.9 ± 6.9	197.6 ± 19.0	142.7 ± 11.1
Endocarp segments:	3.6 ± 0.1	1.0 ± 0.0	3.4 ± 0.1	1.0 ± 0.0	1.0 ± 0.0	1.1 ± 0.1	1.1 ± 0.1
Coloration:	Red	Orange-red	Orange-red	Brown	Tan-red	Red	Red
Mesocarp:	Mealy	Papery	Mealy	Papery	Leathery	Leathery	Leathery

* Although a vigorous burl-forming resprouter throughout its entire range, a single non-burl-forming, non-sprouting population of *A. glandulosa* is known from south of Ensenada (*J. Keeley 24150–24163* RSA).

** Several *A. glandulosa* populations in Baja California have erect nascent inflorescences (*J. Keeley 17860–17931* RSA).

such as *A. stanfordiana* Parry. This similarity between *A. australis* and *A. moranii* likely contributed to Knight (1984) originally describing this latter taxon as *A. australis* var. *sericea* Knight, a name apparently ignored by Wells (1992) in naming *A. moranii.* If chromosome number had been included in our principal components analysis, the tetraploid *Arctostaphylos moranii* likely would have separated more distinctly from the diploid *A. australis* (cf. Fig. 4). In light of the ease with which *Arctostaphylos* hybridize (and arguments presented by Schierenbeck et al. 1992), it seems likely that *A. moranii* represents an allopolyploid. We hypothesize that its origin involves a cross between *A. australis* and the tetraploid, burl-forming *A. glandulosa*; the latter species possesses all of the characteristics that distinguish *A. moranii* from *A. australis*; a burl, foliage pubescence and leaf coloration differences. Indeed, in the chaparral E of El Tigre, there are populations with intermediate characteristics and recombinations between *A. glandulosa* and *A. moranii* (*J. Keeley 17087–17203* RSA)

Conclusions

In light of the apparent ease of hybridization and introgression in *Arctostaphylos,* it may prove difficult to test any hypothesis on the origin of *A. incognita.* It seems evident that the apparently high incidence of hybridization in the genus has led to a reticulate pattern of variation, and this is supported by the pattern of species recombining different combinations of traits as seen in Table 3.

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