Analysis of infraspecific taxa within Cylindropuntia acanthocarpa using multivariate analysis of morphological characters

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ABSTRACT: The circumscription of infraspecific taxa of *Cylindropuntia acanthocarpa* was evaluated using multivariate analysis of morphological characters, with *C. echinocarpa* as the outgroup. Our primary objectives were to sample and analyze sufficient morphological data to determine: 1) how populations within *C. acanthocarpa* might be best grouped, 2) whether means for certain character values differ significantly among groups, and 3) whether these groups of populations correlate with geography and/or habitat type. A review of the literature indicated that the basionym *Opuntia acanthocarpa* var. *major* was incorrectly interpreted by L. Benson and that southeastern populations of *C. acanthocarpa* should instead fall under the name *C. acanthocarpa* var. *ramosa*. Our analyses did not support the recognition of *C. acanthocarpa* var. *coloradensis* as a separate taxon from *C. acanthocarpa* var. *acanthocarpa* but supported the recognition of *C. acanthocarpa* var. *thornberi*. Although individuals of *C. acanthocarpa* var. *ramosa* were more weakly defined, their morphology was correlated with geography, and therefore the name retains some usefulness and should be maintained. A new neotype is selected for *Opuntia echinocarpa* var. *major,* and a lectotype is designated for *O. acanthocarpa* var. *ramosa*.

INTRODUCTION

Six basionyms have been published for the *Cylindropuntia acanthocarpa* complex and two for *C. echinocarpa* as they are presently circumscribed, and several new combinations within both species have been proposed. The limits of infraspecific taxa within *C. acanthocarpa* have not been clear, and it has been the purpose of this morphometric study to clarify these limits as much as possible. The nomenclature of

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this group is complex and often confusing. We believe that mistakes have been made in the past, and we try to correct some of these in the nomenclature discussion following the morphometric analysis.

Most recent treatments have divided *Cylindropuntia acanthocarpa* into four varieties: *C. acanthocarpa* var. *acanthocarpa, C. acanthocarpa* var. *coloradensis, C. acanthocarpa* var. *major,* and *C. acanthocarpa* var. *thornberi* (Benson 1982, Pinkava 2003). Distinguishing among these varieties is ambiguous because of a large degree of morphological variability within and among populations and because some type localities occur within areas of morphological intermediacy between two varieties. These problems have been exacerbated by an injudicious choice of neotypes. The extent of this taxonomic confusion is readily apparent from an herbarium database search of the Southwestern Environmental Information Network (SEINet 2014). Of 758 georeferenced *C. acanthocarpa* specimens, only 173 (22.8%) are identified to the variety or subspecies level. Guzmán et al. (2003) made numerous recombinations in the Cactaceae, primarily changing varieties to subspecies, with little explanation. Although we have no strong opinions regarding the use of variety versus subspecies, we treat infraspecific taxa within *C. acanthocarpa* as varieties, which is traditional for the genus.

In order to apply the names correctly, it is necessary to circumscribe recognizable entities, and that has been the purpose of this morphometric analysis. We evaluated morphological characters for populations of *Cylindropuntia acanthocarpa* throughout its range and for selected populations of the outgroup, *C. echinocarpa. Cylindropuntia echinocarpa* was selected as an outgroup because it is morphologically similar to and often sympatric with *C. acanthocarpa*, though there is no assumption of close evolutionary relatedness. Chromosome number determinations of $n = 11$ (diploid) have been made numerous times for both species, including those at all of the type localities (Baker et al. 2009; Pinkava et al. 1985, 1992, 1998). Our primary objectives were 1) to sample and analyze sufficient morphological data to define how populations within *C. acanthocarpa* are best grouped, 2) to discover whether means for certain character values differ significantly among groups, and 3) to discover whether these groups of populations correlate with geography and/or habitat type.

METHODS

Twenty-two populations were sampled, 19 for *Cylindropuntia acanthocarpa* and three for the outgroup, *C. echinocarpa*. Populations were chosen from across the ranges of the species and included type localities. An attempt was made to sample at least 30 individuals within each population. A total of 571 individuals were sampled for *C. acanthocarpa* and 89 for *C. echinocarpa* (Figure 1, Table 1). Characters measured are presented in Table 2. Except for individual height and width, each character was measured three times from separate areas on the trunk or from separate stems. Plant height and width were not used for the multivariate analyses because, although useful for taxonomic descriptions, values for these characters are age-dependent. Statistical analyses were performed using SPSS 22® (IBM 2013).

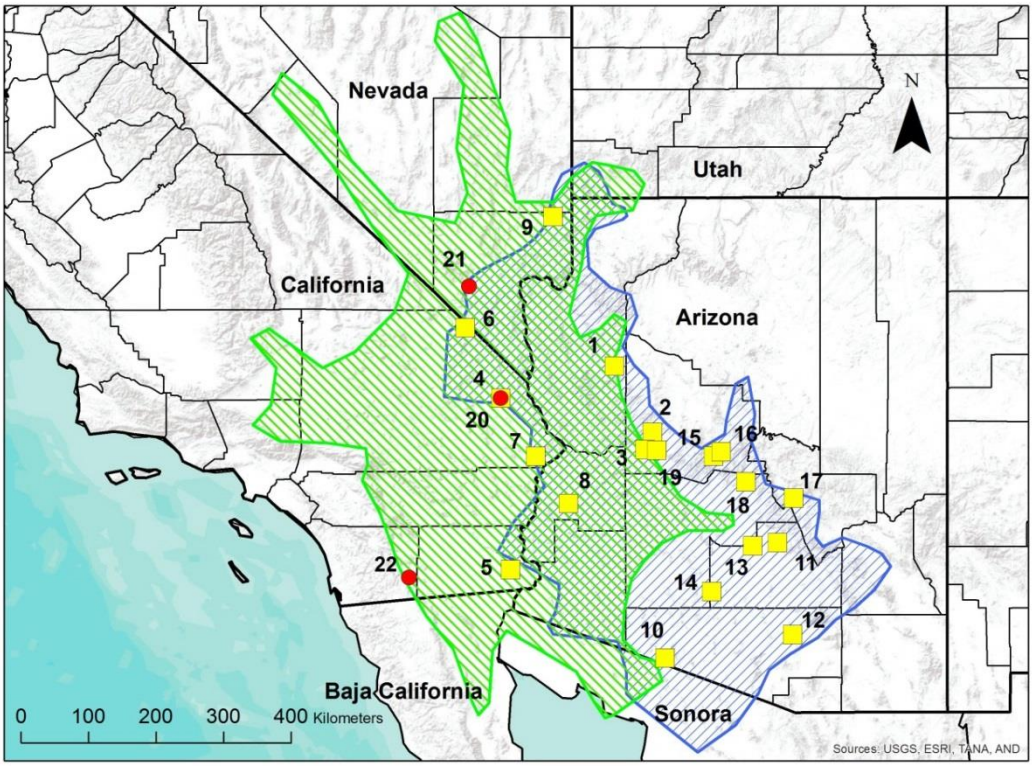

Figure 1. Locations of populations sampled for the morphological analysis of *Cylindropuntia acanthocarpa* and *C. echinocarpa*. Note that populations 4 and 20 occur in the same locality and represent the type locality for *C. acanthocarpa* var. *coloradensis* (as *Opuntia acanthocarpa* var. *coloradensis*) and the neotype locality for *C. echinocarpa* (as *O. echinocarpa*), respectively. Yellow squares = *C. acanthocarpa*, red circles = *C. echinocarpa*. Green hash-marks = known distribution of *C. echinocarpa*, blue hash-marks = known distribution of *C. acanthocarpa*.

For our initial analysis, discriminant function analysis (DFA) was used to place clusters of populations with morphological affinities into potential taxonomic groups (PTGs) by defining population as the dependent (grouping) variable (Tabachnick & Fidell 1996). We chose populations that appeared to be morphologically uniform in that there was no apparent hybridization and assumed that all individuals within each population site were of the same taxon. The one exception to this rule was the site from which both the holotype of *Opuntia acanthocarpa* var. *coloradensis* and the neotype for *O. echinocarpa* had been collected by L. Benson. At this site, individuals were selected as representatives of either taxon based on their general morphology, including habit. Potential taxonomic groupings of populations were then chosen by the proximity of their centroids (Figure 2) and to a lesser extent by the proximity of their geographical distribution. Iterations of DFA were then used to compare the significance of various taxonomic arrangements. Once the PTG with the highest percent of correct classification of individuals was ascertained, multiple analyses of variance (MANOVA) were used to

determine which characters were significantly different among the newly-defined taxonomic grouping.

Table 1. Locations, sample sizes, and herbarium vouchers of populations sampled for the morphological analysis of *Cylindropuntia acanthocarpa*.

Site no.	Taxon	Locality	N	Latitude, longitude	Elev. (m)	Voucher(s) collector and number
1	*C. acanthocarpa*	Arizona, Mohave County, vicinity of Cactus Pass, 50 km east of Kingman; **type locality for *Opuntia acanthocarpa***	30	35.1880º -113.4779º	1465	*MAB 11813* (ASU)
2	*C. acanthocarpa*	Arizona, Yavapai County, McCloud Mountains, 5.5 km WNW of Hillside, **near neotype locality for *Opuntia acanthocarpa***	31	34.4664º -112.9684º	1110	*MAB 17671* (ASU), *L. Benson 10874* (RSA, ARIZ, CAS)
3	*C. acanthocarpa*	Arizona, Yavapai County, 17.5 km SE of the summit of Ives Peak, 2 km north of Date Creek, just west of the Date Creek Mountains, 65 km SW of Prescott	30	34.2771º -113.0710º	887	*MAB 17673* (ASU)
4	*C. acanthocarpa*	California, San Bernardino County, 9 km WSW of South Pass, 32 km due west of Needles, just south of Interstate 40, **type locality for *Opuntia acanthocarpa* var. *coloradensis***	30	34.8375º -114.9848º	670	*L. Benson 10375* (RSA, ARIZ) *Baker 16724.1* (ASU)
5	*C. acanthocarpa*	California, Imperial County, 5 km NW of the north end of the Cargo Muchacho Mountains, 32 km NW of Yuma, Arizona	30	32.9452° -114.8558°	190	*MAB 17541.1* (ASU)
6	*C. acanthocarpa*	California, San Bernardino County, Ivanpah Valley, 13 km NNE of the summit of Clark Mountain, 67 km SE of central Las Vegas	30	35.6040° -115.4600°	900	*MAB 17660* (ASU)
7	*C. acanthocarpa*	California, San Bernardino County, 5 km ENE of Vidal Junction, 8 km south of Savahia Peak, lower bajada to the SW of the Whipple Mountains	30	34.1994° -114.5216°	295	*MAB 17718* (ASU, RSA)
8	*C. acanthocarpa*	Arizona, La Paz County, Plomosa Mountains, 13 km east of Quartzsite	30	33.6821° -114.0865°	440	*MAB 17718* (ASU, RSA)
9	*C. acanthocarpa*	Nevada, Clark County, Mormon Mesa, 103 km NE of central Las Vegas	30	36.7993° -114.2928°	655	*MAB18670, 18671* (ASU, UNLV)
10	*C. acanthocarpa*	Arizona, Pima County, Headquarters, Organ Pipe Cactus National Monument, **neotype locality for *Opuntia echinocarpa* var. *major* as designated by L. Benson**	30	31.9545º -112.8005º	513	*W. F. Steenbergh 5-2662-1* (RSA)

Table 1. Locations, sample sizes, and herbarium vouchers of populations sampled for the morphological analysis of *Cylindropuntia acanthocarpa*.

Site no.	Taxon	Locality	N	Latitude, longitude	Elev. (m)	Voucher(s) collector and number
11	*C. acanthocarpa*	Arizona, Pinal County, 3 km ESE of Florence Junction; ca. 40 km NE of Sacaton**, approximate type locality for *Opuntia acanthocarpa* var. *ramosa***	30	33.2488º -111.3043º	600	*MAB 17654* (ASU)
12	*C. acanthocarpa*	Arizona, Pima County, 500m SSW of Gates Pass, 16 km WNW of downtown Tucson	30	32.2176º -111.1027º	910	*MAB 8114* (ASU)
13	*C. acanthocarpa*	Arizona, Pinal County, 13 km NNE of Sacaton, Goldmine Mountain, 4 km north of Rock Peak	30	33.1720º -111.6404º	524	*MAB 18667* (ASU)
14	*C. acanthocarpa*	Arizona, Pinal County,1.9 km WNW of Summit of Little Tabletop, 60 km ESE of Gila Bend	30	32.7110º -112.1598º	694	*MAB 18665* (ASU)
15	*C. acanthocarpa*	Arizona, Yavapai County, Black Canyon, 600 m NW of Bumble Bee, **epineotype locality for *Opuntia thornberi***	30	34.2063º -112.1567º	835	*MAB 16147* (ASU, RSA)
16	*C. acanthocarpa*	Arizona, Yavapai County, along Bloody Basin Road, 850 m east of the Agua Fria River, 50 km SE of Prescott	30	34.2514º -112.0552º	1015	*MAB 17657* (ASU)
17	*C. acanthocarpa*	Arizona, Gila County, 9.4 km NNE of Roosevelt between Dagger Wash and Salome Creek, 48 km NNW of Globe	30	33.7427º -111.0889º	800	*MAB 17681* (ASU)
18	*C. acanthocarpa*	Arizona, Maricopa County, 7 km SSW of Horseshoe Dam, 50 km NNE of downtown Phoenix	30	33.9201º -111.7249º	915	*MAB 17870 (*ASU)
19	*C. acanthocarpa*	Arizona, Yavapai County, 50 km SW of Prescott, 16 km SSW of Hillside,	30	34.2761º -112.9053º	1001	*MAB 18269.1* (ASU)
20	*C. echinocarpa*	California, San Bernardino County, 9 km WSW of South Pass, 32 km west of Needles, just south of Interstate 40, **neotype locality for *Opuntia echinocarpa***	30	34.8375º -114.9848°	670	*MAB 13838* (ASU), *L. Benson 10374* (RSA)
21	*C. echinocarpa*	Nevada, Clark County, just north of the town of Blue Diamond, 23 km SW of central Las Vegas	29	36.0517º -115.4082º	1035	*MAB 13670* (ASU)
22	*C. echinocarpa*	California, San Diego County, Carrizo Valley, 1 km SE of Egg Mountain, 90 km east of central San Diego	30	32.8584º -116.2078º	210	*MAB 7531* (ASU)

Table 2. Description of characters measured in the morphological analysis of *Cylindropuntia acanthocarpa*. Node is used here in reference to where branches originate from trunks or larger branches, not a stem node or areole. Except for individual height and width, characters were measured three times, each from separate areas on the trunk or from separate stems. Central spines were those centermost in the areole and were characterized by notably greater diameters of both the spines themselves and their sheaths, in comparison to those of the outermost or radial spines.

Character	Description
plant height	height of the individual from ground level to the tip of the tallest stem, excluding spines
plant width	width of the plant at its widest point, excluding spines
branch angle	angle between trunk and primary branch, divaricate branches equaling 90º
distance between trunk branches (cm)	mean length of three inter-branch spaces along the main trunk or, if unavailable, those along primary branches
branches per trunk node	mean number of branches at each of three trunk nodes or, if unavailable or not easily visible, those along primary branches. Trunk nodes with 0 branches were not included.
stem length (mm)	mean length of three ultimate mature stem segments
stem diameter (mm)	mean diameter at widest portion of three ultimate mature stem segments
tubercle length (mm)	mean length of top-most penultimate tubercle from three stem segments
tubercle width (mm)	mean width of top-most penultimate tubercle from three stem segments
tubercle height (mm)	mean height of top-most penultimate tubercle from three stem segments
central spine number	mean number of central spines per areole from tubercles as described above
radial spine number	mean number of radial spines per areole from tubercles as described above
central spine length (mm)	mean length of longest central spine per areole from tubercles as described above
radial spine length (mm)	mean length of longest radial spine per areole from tubercles as described above
central spine diameter (0.01 mm)	mean diameter of longest central spine per areole from tubercles as described above
central spine sheath diameter (0.01 mm)	mean diameter of the sheath of the longest central spine per areole from tubercles as described above

RESULTS

Discriminant Function Analysis.—Discriminant Function Analysis was first used to assess the groupings of populations. Figure 2 is a scatterplot of population centroids for functions 1 and 2, which represent 68% of the total variation. Populations 1 through 3 are the most representative of what has been classified under typical *Cylindropuntia acanthocarpa*. The population centroid for the type locality at Cactus Pass (population 1) falls close to those of traditionally defined as *C. acanthocarpa* var. *thornberi* (populations 15-19), and the centroid for the neotype locality (population 2) west of Hillside falls close to those of *C. acanthocarpa* var. *ramosa* (populations 10-14). The population centroid for the type locality for *C. acanthocarpa* var. *coloradensis* (population 4) is close to those of *C. acanthocarpa* var. *acanthocarpa* and *C. acanthocarpa* var. *ramosa*. Populations 5 through 9 also fall within the geographical distribution of what has been traditionally classified under *Cylindropuntia acanthocarpa* var. *coloradensis*. Group centroids for population 4 and the neotype population of *C. echinocarpa* (population 20) are in close proximity, indicating that introgression may be influencing one or both populations. Populations 21 and 22 also represent *C. echinocarpa*. In general, results from the first DFA indicated that the most supportable PTG of populations appeared to align with the recognition of three subspecific taxa: *C. acanthocarpa* var. *acanthocarpa*, *C. acanthocarpa* var. *ramosa*, and *C. acanthocarpa* var. *thornberi* (Table 7).

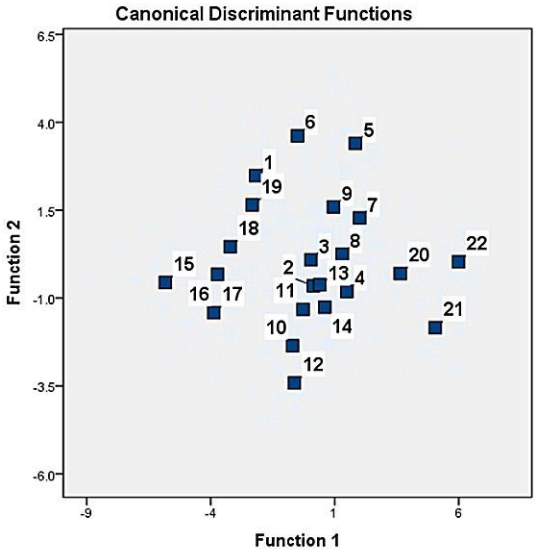

Figure 2. Scatterplot of population centroids for DFA function 1 vs. function 2 defining groupings as populations. Functions 1 and 2 represent 68% of the total variation. Each symbol represents a population.

A discriminant function analysis was then run placing populations within groupings or potential taxa (PTGs). The PTGs were based on the grouping of population centroids from the first DFA and geographic distribution. Because of the lack of morphological correlation between populations of *C. acanthocarpa* var. *acanthocarpa* and those of traditional *C. acanthocarpa* var. *coloradensis*, individuals of the two taxa were combined. This DFA resulted in an overall correct classification of 88.2%, with correct classification for individuals of *C. acanthocarpa* var. *acanthocarpa* of 86.7% (Table 3). As expected, individuals of the outgroup *C. echinocarpa* were well-assembled, with only a single individual misclassified as *C. acanthocarpa* var. *acanthocarpa* and another as *C. acanthocarpa* var. *ramosa*. For individuals of the expanded *C. acanthocarpa* var. *acanthocarpa* group, 8.1% were misclassified as *C. acanthocarpa* var. *ramosa* and 4.4% were misclassified as *C. acanthocarpa* var. *thornberi*. The *C. acanthocarpa* var. *ramosa* group was the weakest, with 84.7% correctly classified individuals and all misclassified individuals being placed within the *C. acanthocarpa* var. *acanthocarpa* group. The *C. acanthocarpa* var. *thornberi* group had the highest percentage of correctly classified individuals (88.7%), with misclassified individuals being more evenly placed between the other two *C. acanthocarpa* groups. Figure 3 is a scatterplot of DFA function 1 vs. 2; the weighting of the characters is presented in Table 4. There was good separation among individuals of *C. acanthocarpa* var. *acanthocarpa, C. acanthocarpa* var. *thornberi,* and *C. echinocarpa* and rather poor separation between individuals of *C. acanthocarpa* var. *acanthocarpa* and *C. acanthocarpa* var. *ramosa*. However, when function 3 was added, resulting in a three-dimensional plot (Figure 4), separation of individuals between the two taxa became more apparent. Function 3 represented another 10% of the total variation.

A DFA with *Cylindropuntia acanthocarpa* var. *coloradensis* included as a group, along with the other currently accepted taxa based on Benson's (1982) taxonomy, resulted in an 83.6% overall correct classification among the four varieties of *C. acanthocarpa*. Individuals within the *C. acanthocarpa* var. *acanthocarpa* group were only 42.9% correctly classified (Table 5).

Because of the low correct classification for individuals of *Cylindropuntia acanthocarpa* var. *ramosa,* with all of the misclassified individuals classified as *C. acanthocarpa* var. *acanthocarpa*, a final DFA was run with individuals of *C. acanthocarpa* var. *ramosa* and *C. acanthocarpa* var. *coloradensis* pre-classified as *C. acanthocarpa* var. *acanthocarpa*. In this DFA, individuals of *C. acanthocarpa* var. *acanthocarpa* were 97.1% correctly classified and those of *C. acanthocarpa* var. *thornberi* were 86.0% correctly classified (Table 6).

Table 7 summarizes the definitions of taxa, by study population, for the DFA using populations as the grouping variable and the resulting DFA of taxa as defined by population centroids; for the DFA using taxa as circumscribed by recent taxonomic treatments, which follow Benson (1982); and for the DFA lumping both *C. acanthocarpa* var. *coloradensis* and *C. acanthocarpa* var. *ramosa* into *C. acanthocarpa* var. *acanthocarpa*.

Table 3. Classification results of discriminant function analysis: predicted group membership by number of individuals correctly classified and by percentage of individuals correctly classified (bold); the dependent (grouping) variable defined as taxa with traditional populations of *C. acanthocarpa* var. *coloradensis* included within *C. acanthocarpa* var. *acanthocarpa*.

Taxon	Predicted group membership				Total
	var. *acanthocarpa*	var. *ramosa*	var. *thornberi*	*C. echinocarpa*	
	By number of individuals				
var. *acanthocarpa*	235	22	12	2	271
var. *ramosa*	23	127	0	0	150
var. *thornberi*	9	7	133	1	150
C. echinocarpa	1	1	0	87	89
	By percentage of individuals				
var. *acanthocarpa*	**86.7**	8.1	4.4	0.7	100.0
var. *ramosa*	15.3	**84.7**	0.0	0.0	100.0
var. *thornberi*	6.0	4.7	**88.7**	0.7	100.0
C. echinocarpa	1.1	1.1	0.0	**97.8**	100.0
88.2% overall correct classification					

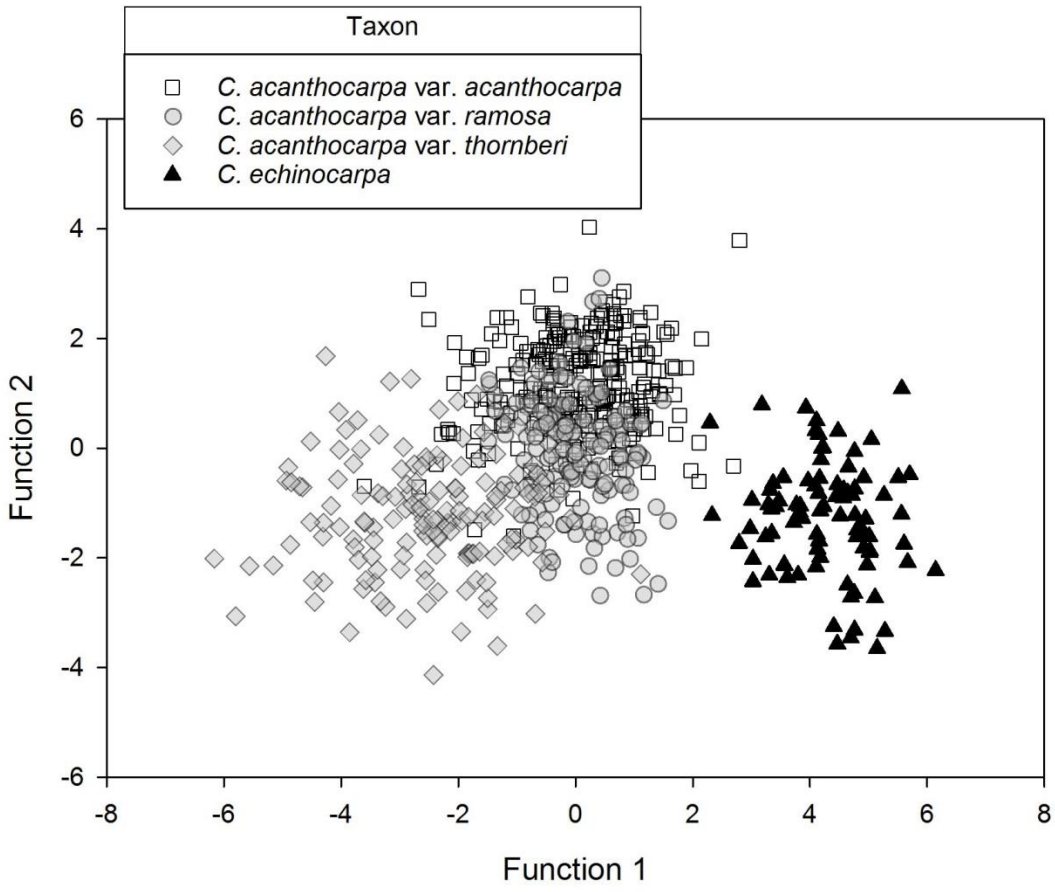

Fig. 3. Scatterplot of functions 1 and 2 for DFA defining populations into four groupings (taxa), *Cylindropuntia acanthocarpa* var. *acanthocarpa*, *C. acanthocarpa* var. *ramosa*, *C. acanthocarpa* var. *thornberi*, and *C. echinocarpa.* Each symbol represents an individual.

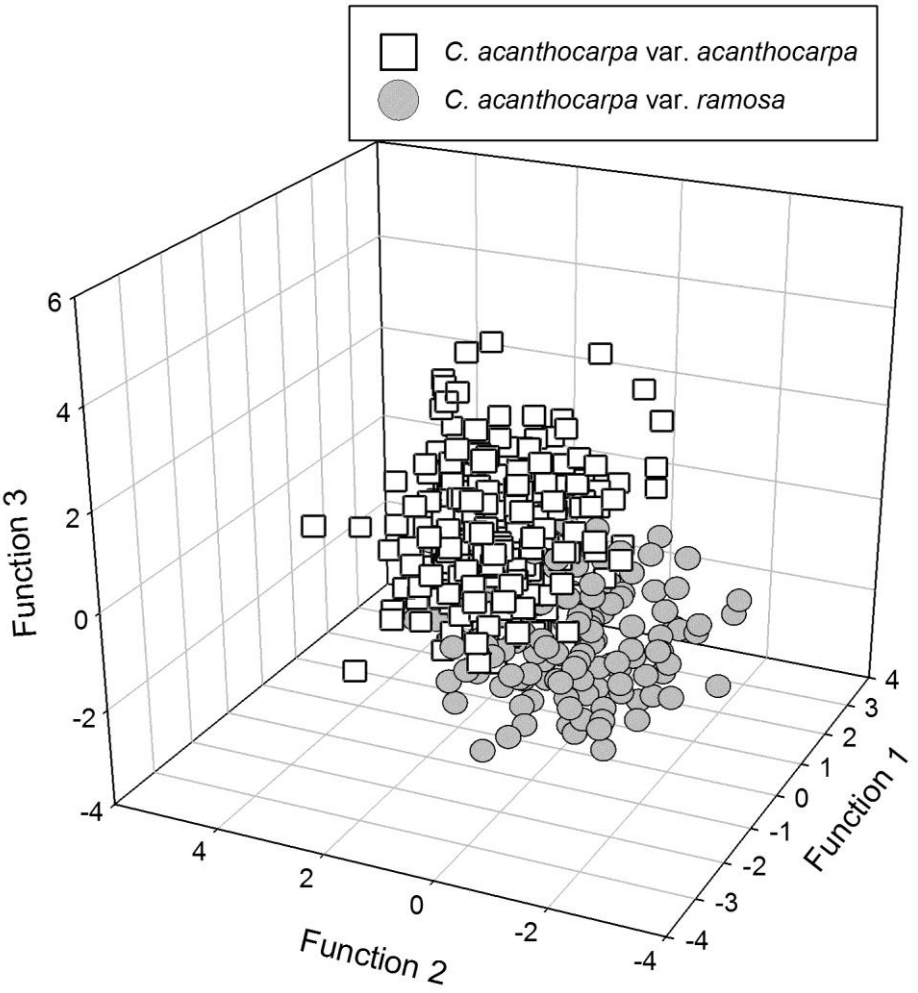

Figure 4. Scatterplot of functions 1, 2, and 3 for DFA defining populations into four groupings (taxa), only individuals of *Cylindropuntia acanthocarpa* var. *acanthocarpa* and *C. acanthocarpa* var. *ramosa* shown. Each symbol represents an individual.

Table 4. Weighting of characters for DFA functions 1 and 2. Numbers represent standardized canonical discriminant function coefficients. Weighting is represented by the absolute value of the difference between the coefficients of F1 and F2. Those with the greatest weighting figure most prominently in the analyses.

Character	F1	F2	Absolute value of (F1-F2)
Tubercle length	-0.83	0.354	1.184
Central spine number	0.547	-0.049	0.596
Central spine sheath diameter	-0.097	0.329	0.426
Central spine diameter	0.019	-0.299	0.318
Tubercle width	0.069	0.366	0.297
Branch angle	-0.003	-0.24	0.237
Branches per trunk internode	0.227	0.003	0.224
Central spine length	0.33	0.119	0.211
Stem length	-0.139	-0.332	0.193
Stem diameter	0.245	0.406	0.161
Tubercle height	-0.014	0.144	0.158
Radial spine number	0.109	0.264	0.155
Radial spine length	-0.091	-0.217	0.126
Distance between trunk branches	-0.041	0.013	0.054

Table 5. Classification results of discriminant function analysis: predicted group membership by number of individuals correctly classified and by percentage of individuals correctly classified (bold); the dependent (grouping) variable defined as taxa according to Benson's (1982) taxonomy with the exception that his *C. acanthocarpa* var. *major* is under the name *C. acanthocarpa* var. *ramosa*.

	Predicted group membership					
Taxon	var. *acanthocarpa*	var. *coloradensis*	var. *ramosa*	var. *thornberi*	*C. echinocarpa*	Total
	By number of individuals correctly classified					
var. *acanthocarpa*	39	21	19	12	0	91
var. *coloradensis*	9	161	9	0	1	180
var. *ramosa*	4	13	133	0	0	150
var. *thornberi*	11	1	6	132	0	150
C. echinocarpa	0	1	1	0	87	89
	By percentage of individuals correctly classified					
var. *acanthocarpa*	**42.9**	23.1	20.9	13.2	0.0	100.0
var. *coloradensis*	5.0	**89.4**	5.0	0.0	0.6	100.0
var. *ramosa*	2.7	8.7	**88.7**	0.0	0.0	100.0
var. *thornberi*	7.3	0.7	4.0	**88.0**	0.0	100.0
C. echinocarpa	0.0	1.1	1.1	0.0	**97.8**	100.0

83.6% overall correct classification

Table 6. Classification results of discriminant function analysis: predicted group membership by number of individuals correctly classified and by percentage of individuals correctly classified (bold); the dependent (grouping) variable defined as taxa with populations of *C. acanthocarpa* var. *coloradensis* and *C. acanthocarpa* var. *ramosa* included within *C. acanthocarpa* var. *acanthocarpa*.

	Predicted group membership			
Taxon	var. *acanthocarpa*	var. *thornberi*	*C. echinocarpa*	Total
	By number of individuals			
var. *acanthocarpa*	409	10	2	421
var. *thornberi*	21	129	0	150
C. echinocarpa	2	0	87	89
	By percentage of individuals			
var. *acanthocarpa*	**97.1**	2.4	0.5	100.0
var. *thornberi*	14.0	**86.0**	0.0	100.0
C. echinocarpa	2.2	0.0	**97.8**	100.0

94.7% correct classification

Multiple Analysis of Variance.—Duncan's multiple range test showed that 12 of the 14 stem characters were significantly different at $P < 0.001$ for one or more of the four taxa. Selected homogeneous subsets for stem characters are presented in Table 8. As expected, the outgroup *Cylindropuntia echinocarpa* possessed the greatest number of significantly different mean values, with 10 of the 14 characters being significantly different from any of the *C. acanthocarpa* taxa.

The most significant differences among the infraspecific taxa in *C. acanthocarpa* were associated with tubercle morphology and spine number. The branch angles were narrowest in *C. acanthocarpa* var. *acanthocarpa*, including populations originally classified as *C. acanthocarpa* var. *coloradensis*, and widest in *C. acanthocarpa* var. *ramosa*. Stem diameter was also diagnostic among the three infraspecific taxa, with *C. acanthocarpa* var. *acanthocarpa* having the thickest stems and *C. acanthocarpa* var. *ramosa* the thinnest. Individuals of *C. acanthocarpa* var. *acanthocarpa* had the longest central spines, while central spine and spine sheath diameters were smallest in *C. acanthocarpa* var. *ramosa*. Spine length data from our samples supports that the type description of *O. echinocarpa* var. *major* belongs within *C. acanthocarpa* var. *acanthocarpa*.

DISCUSSION AND CONCLUSIONS

Our analysis did not provide sufficient evidence for a morphological distinction between *Cylindropuntia acanthocarpa* var. *acanthocarpa* and *C. acanthocarpa* var. *coloradensis*; we therefore combined them under *C. acanthocarpa* var. *acanthocarpa*. The data provide the strongest support for preserving *C. acanthocarpa* var. *thornberi* and reasonable support for the preservation of *C. acanthocarpa* var. *ramosa*, populations of which have been under the name *C. acanthocarpa* var. *major* in recent treatments. There is an 85% correct classification for sampled individuals of *C. acanthocarpa* var. *ramosa*, and there are five characters that possess mean values that are significantly different from all other taxa.

The taxonomy of this group is complicated by the location of the type populations, with both the original and neotype populations for *Opuntia acanthocarpa* occurring at the edge of the geographic range for the typical variety, near where these individuals intergrade morphologically with *Cylindropuntia acanthocarpa* var. *thornberi*. The choice of type locality for *O. acanthocarpa* var. *coloradensis* was also unfortunate because it was also the neotype locality for *Opuntia echinocarpa*, and putative hybrids (*C.* ×*deserta* [Griffiths] F. M. Knuth), as indicated by intermediate morphology, have been documented in the areas of sympatry between *C. acanthocarpa* and *C. echinocarpa* (Baker 2016, Baker et al. 2012, Pinkava 1999, Pinkava & Baker 2012).

Although there is some confusion with respect to morphology and taxonomy for the original type and neotype localities of *Opuntia acanthocarpa*, Engelmann's original description of *Opuntia acanthocarpa* fits best with our group of populations we define as *Cylindropuntia acanthocarpa* var. *acanthocarpa*. Engelmann used the French metric system (Trelease and Gray 1887), for which at the time a "line" was ca. 2.3 mm (Hallock and Wade 1906). Using this conversion, Engelmann's description of stem diameter for *O. acanthocarpa* was 25.4 mm, and the central spine length was

between 25.4 and 31.8 mm, which most closely match the mean values for those of *C. acanthocarpa* var. *acanthocarpa* as defined in our analyses. The tubercle length (20.7- 23 mm) in the original description is far too short for *C. acanthocarpa* var. *thornberi*, which is the other variety that occurs in or near the areas of both the original type and the neotype localities.

It may be prudent to maintain only two infraspecific taxa within *Cylindropuntia acanthocarpa*, but we have chosen to be conservative in the redefinition of taxa. It is of interest that our current taxonomic position reflects that of Benson's original edition of the Cacti of Arizona (1940), although he placed chollas (*Cylindropuntia*) within *Opuntia* and gave species rank to *O. ramosa* Peebles.

Table 7. Definition of *Cylindropuntia* taxa, by study population, as circumscribed by recent taxonomic treatments, which follow Benson (1982); and by our assessment of the literature and DFA analyses.

Site no.	Taxa as defined by DFA analyses of populations and for the subsequent grouping of centroids	Taxa as defined by Benson (1982)	Taxa as defined by DFA analysis that lumped both *C. acanthocarpa* var. *coloradensis* and *C. acanthocarpa* var. *ramosa* into *C. acanthocarpa* var. *acanthocarpa*
1	*C. acanthocarpa* var. *acanthocarpa*	*C. acanthocarpa* var. *acanthocarpa*	*C. acanthocarpa* var. *acanthocarpa*
2	*C. acanthocarpa* var. *acanthocarpa*	*C. acanthocarpa* var. *acanthocarpa*	*C. acanthocarpa* var. *acanthocarpa*
3	*C. acanthocarpa* var. *acanthocarpa*	*C. acanthocarpa* var. *acanthocarpa*	*C. acanthocarpa* var. *acanthocarpa*
4	*C. acanthocarpa* var. *acanthocarpa*	*C. acanthocarpa* var. *coloradensis*	*C. acanthocarpa* var. *acanthocarpa*
5	*C. acanthocarpa* var. *acanthocarpa*	*C. acanthocarpa* var. *coloradensis*	*C. acanthocarpa* var. *acanthocarpa*
6	*C. acanthocarpa* var. *acanthocarpa*	*C. acanthocarpa* var. *coloradensis*	*C. acanthocarpa* var. *acanthocarpa*
7	*C. acanthocarpa* var. *acanthocarpa*	*C. acanthocarpa* var. *coloradensis*	*C. acanthocarpa* var. *acanthocarpa*
8	*C. acanthocarpa* var. *acanthocarpa*	*C. acanthocarpa* var. *coloradensis*	*C. acanthocarpa* var. *acanthocarpa*
9	*C. acanthocarpa* var. *acanthocarpa*	*C. acanthocarpa* var. *coloradensis*	*C. acanthocarpa* var. *acanthocarpa*
10	*C. acanthocarpa* var. *ramosa*	*C. acanthocarpa* var. *major*	*C. acanthocarpa* var. *acanthocarpa*

Table 7. Definition of *Cylindropuntia* taxa, by study population, as circumscribed by recent taxonomic treatments, which follow Benson (1982); and by our assessment of the literature and DFA analyses.

Site no.	Taxa as defined by DFA analyses of populations and for the subsequent grouping of centroids	Taxa as defined by Benson (1982)	Taxa as defined by DFA analysis that lumped both *C. acanthocarpa* var. *coloradensis* and *C. acanthocarpa* var. *ramosa* into *C. acanthocarpa* var. *acanthocarpa*
11	*C. acanthocarpa* var. *ramosa*	*C. acanthocarpa* var. *major*	*C. acanthocarpa* var. *acanthocarpa*
12	*C. acanthocarpa* var. *ramosa*	*C. acanthocarpa* var. *major*	*C. acanthocarpa* var. *acanthocarpa*
13	*C. acanthocarpa* var. *ramosa*	*C. acanthocarpa* var. *major*	*C. acanthocarpa* var. *acanthocarpa*
14	*C. acanthocarpa* var. *ramosa*	*C. acanthocarpa* var. *major*	*C. acanthocarpa* var. *acanthocarpa*
15	*C. acanthocarpa* var. *thornberi*	*C. acanthocarpa* var. *thornberi*	*C. acanthocarpa* var. *thornberi*
16	*C. acanthocarpa* var. *thornberi*	*C. acanthocarpa* var. *thornberi*	*C. acanthocarpa* var. *thornberi*
17	*C. acanthocarpa* var. *thornberi*	*C. acanthocarpa* var. *thornberi*	*C. acanthocarpa* var. *thornberi*
18	*C. acanthocarpa* var. *thornberi*	*C. acanthocarpa* var. *thornberi*	*C. acanthocarpa* var. *thornberi*
19	*C. acanthocarpa* var. *thornberi*	*C. acanthocarpa* var. *thornberi a*	*C. acanthocarpa* var. *thornberi*
20	*C. echinocarpa*	*C. echinocarpa*	*C. echinocarpa*
21	*C. echinocarpa*	*C. echinocarpa*	*C. echinocarpa*
22	*C. echinocarpa*	*C. echinocarpa*	*C. echinocarpa*

Table 8. Character means by *Cylindropuntia* taxon. Means in bold are significantly different ($p < 0.001$) from means of all other taxa. Standard deviations are given in parentheses.

Character	Taxon			
	C. acanthocarpa var. *acanthocarpa*	*C. acanthocarpa* var. *ramosa*	*C. acanthocarpa* var. *thornberi*	*C. echinocarpa*
Plant height (cm)	116.5 (33.5)	121.7 (34.0)	83.0 (33.3)	82.2 (29.2)
Plant width (cm)	151.1 (54.2)	168.6 (53.4)	132.2 (53.1)	86.5 (36.9)
Branch angle (°)	**36.2** (9.2)	44.1 (11.8)	44.5 (12.7)	**60.5** (15.0)
Distance between trunk branches (cm)	16.6 (5.7)	16.9 (6.1)	15.4 (5.3)	**9.4** (2.9)
Branches per trunk node	1.7 (.53)	1.6 (.51)	1.5 (.46)	**2.6** (.83)
Stem length (mm)	105.2 (25.4)	102.3 (28.4)	**125.6** (33.6)	**57.5** (14.0)
Stem diameter (mm)	**24.7** (3.9)	**19.6** (2.5)	**21.3** (3.2)	**23.4** (3.0)
Tubercle length (mm)	**27.5** (5.2)	**22.8** (3.0)	**35.6** 6.5()	**12.1** (2.6)
Tubercle width (mm)	**6.6** (1.3)	**4.9** (0.8)	6.0 (1.4)	6.1 (0.9)
Tubercle height (mm)	6.7 (1.2)	**5.3** (0.8)	6.4 (1.3)	**5.8** (1.2)
Central spine number	**7.0** (1.8)	**5.4** (1.3)	**3.5** (1.5)	**7.8** (1.8)
Radial spine number	**9.0** (1.7)	7.5 (1.4)	**5.7** (1.5)	7.9 (1.8)
Central spine length (mm)	25.7 (5.8)	19.3 (5.7)	19.1 (7.2)	24.6 (7.3)
Radial spine length (mm)	16.9 (3.7)	17.1 (3.9)	**14.5** (3.3)	**12.6** (3.1)
Central spine diameter (mm)	0.62 (0.129)	0.48 (0.106)	0.64 (0.160)	0.52 (0.152)
Central spine sheath diameter (mm)	**1.02** (0.196)	**0.72** (0.191)	**0.94** (0.238)	**0.84** (0.166)

NOMENCLATURAL SUMMARY

Types are cited using the numbering system of each herbarium, and in brackets the JSTOR Global Plants Initiative numbering system of images online is given (Global Plants Initiative 2017).

1. ***Cylindropuntia acanthocarpa*** (Engelmann & J. M. Bigelow) F. M. Knuth, Kaktus-ABC [Backeberg & F. M. Knuth] 124. 1936.

Opuntia acanthocarpa Engelmann & J. M. Bigelow, Proc. Amer. Acad. Arts 3: 308. 1856. TYPE. Arizona, Mohave County, "mountains of Cactus Pass," January 1854, *J. M. Bigelow s. n.* (all original material lost). NEOTYPE designated by Benson, (1982). Arizona, Yavapai County, 9.5 miles west of Hillside, *L. Benson 10874*, (NEOTYPE: POM274024! [=RSA-0008890]; ISONEOTYPES: CAS500838! [=CAS-0006948], ARIZ 74828! [=ARIZ-BOT-0005737]).

The original material of *Opuntia acanthocarpa* was collected in January 1854 by J. M. Bigelow near Cactus Pass, Mohave County, Arizona, during the Whipple expedition to survey for a railroad route from the Mississippi River to the Pacific Ocean (Engelmann 1856a, 1856b; Engelmann & Bigelow 1856). To date, the original material has not been found. The name was first published in Engelmann's Synopsis of the Cactaceae of the territory of the United States (Engelmann 1856a), which was reprinted, apparently in the same year, by Metcalf and Company (Engelmann 1856b). Although within the Synopsis, Engelmann ascribes the name *Opuntia acanthocarpa* to the report on the botany of the Whipple expedition (Engelmann & Bigelow 1856), the report was not published prior to the Synopsis. This is evident in Engelmann's own words in the Synopsis, page 260:

> "Most of the materials brought together by these different explorers have come into the hands of the writer; but few of the discoveries made since 1847 and 1848 have been given to the public;—partly because the material on hand very often was incomplete, and partly because it seemed desirable to publish the whole in an elaborate form with the Reports of the Boundary Commission and those of the Pacific Railroad Surveys. These reports are now in preparation; but the splendid plates which are to illustrate the natural history of these plants cannot be finished for some time; it is therefore deemed advisable now to publish short descriptions of the new species, and systematically to arrange them with those before known."

The significance of the chronological order of these publications is in the designation of the type. As mentioned above, there are no original specimens, and the "splendid plates" that were referred to by Engelmann were not finished and not included in the Synopsis and therefore cannot serve as types. Thus the lectotypifications of *Opuntia acanthocarpa* and *O. echinocarpa* Engelmann & J. M. Bigelow by Crook and Mottram (1995, 1996) with illustrations from Engelmann and Bigelow (1856) have no standing (Holmgren et al. 2012).

1A. *Cylindropuntia acanthocarpa* var. *acanthocarpa*. Autonym based on same type as the species (Figures 5A; 6A, B, C).

Opuntia echinocarpa* var. *major Engelmann, Proc. Amer. Acad. Arts 3: 305 1856. TYPE. Arizona, California or Sonora, Mexico, "In the valley of the Lower Colorado" river, *Schott s. n.*. (no original material has been found). Engelmann (1859) elaborated on the type as "In the deserts on both sides of the Colorado, and in Sonora, *Schott*."

Because all original material is missing and because we believe that a previously designated neotype was done erroneously, we designate a new neotype here.

United States, California, Imperial County, Picacho State Recreation Area, south of Colorado River, Taylor Lake Overlook, 16 April 2005, *Larry Hendrickson et al. 3223,* (NEOTYPE designated here: NEOTYPE: ASU0089312! [=ASU-293568]; ISONEOTYPE: SD191490). We have chosen this specimen because it has both flowers and branching stems and comes from the approximate type locality as specified by Engelmann.

We reject Benson's choice of a neotype (Benson 1969, pg. 20): Arizona. Pima County, near border of northwestern Sonora [Mexico]," *W. F. Steenbergh 5-2552-1*, 26 May 1962, Headquarters of the Organ Pipe Cactus National Monument, Arizona (POM306088! [=RSA-008882]). The spine length data from our samples indicate that the type description of *O. echinocarpa* var. *major* belongs within *C. acanthocarpa* var. *acanthocarpa*. Benson's neotype falls within the morphological description of *C. acanthocarpa* var. *ramosa*. In addition, Schott collected the material, from which Engelmann originally described that taxon, from the area around the Colorado River, where only *C. acanthocarpa* var. *acanthocarpa* occurs.

Opuntia echinocarpa* var. *robustior J. M. Coulter, Contr. U. S. Natl. Herb. 3(7): 446. 1896. A superfluous new name proposed by Coulter for *Opuntia echinocarpa* var. *major* Engelmann. The rules of nomenclature as we now use them were not in effect at that time. Coulter seems to have believed that because the epithet "*major*" had been used for a variety of *O. phaeacantha* it could not be used again in another species in the genus. Coulter does list specimens he examined, only the first of which represents *Cylindropuntia acanthocarpa*: Arizona (G. R. Vasey of 1881, Yuma) (US3046040!), annotated by J. M. Coulter as *Opuntia echinocarpa* [var.] *major*). The other specimens listed by Coulter represent *Cylindropuntia echinocarpa*: Newberry, 1858 [Mojave Valley, Camp 60, 23 March 1858] (MO-5254054!); Lemmon, 1878 [California desert] (MO-5254055!); with no collector given, 1880 [White Water Desert to San Gorgonio Pass, California, 10 Nov 1880], almost certainly collected by Charles Parry, who was at the locality on the same date. (MO5254053!); Parish Bros.,1882 [S. B. & W. F. Parish, San Bernardino, Vallecito] (MO5234057!)

Opuntia acanthocarpa* var. *coloradensis L. D. Benson, Cacti Ariz. ed. 3. 20. 1969. TYPE. California, 23 miles west of Needles, 14 July 1940, *L. Benson 10375* (HOLOTYPE: POM244022! [=RSA0008891]; ISOTYPE: ARIZ137142!) (Figure 6).

Opuntia acanthocarpa* var. *major (Engelmann & J. M. Bigelow) L. D. Benson, Cacti Ariz. ed. 3. 20. 1969.

Cylindropuntia acanthocarpa* var. *coloradensis (L. D.Benson) Pinkava, Ariz.-Nev. Acad. Sci. 32(1):42. 1999.

Cylindropuntia acanthocarpa* var. *major (Engelmann) Pinkava, Ariz.-Nev. Acad. Sci. 32(1): 42. 1999.

Cylindropuntia acanthocarpa* subsp. *major (Engelmann & J. M. Bigelow) U. Guzmán, Cactaceae Syst. Init. 16: 16. 2003.

Cylindropuntia acanthocarpa* subsp. *coloradensis (L. D. Benson) U. Guzmán, Cactaceae Syst. Init. 16: 16. 2003.

1B. *Cylindropuntia acanthocarpa* var. *ramosa* (Peebles) Backeberg, Cactaceae (Backeberg) 1: 181. 1958 (Figures 5B, 6D).

Opuntia acanthocarpa Engelmann & J. M. Bigelow **var. *ramosa*** Peebles, Cact. Succ. J. (Los Angeles) 9: 37. 1937. TYPE. Arizona, Pinal County, near Sacaton, cultivated, 1920, *A. R. Leding SF* 2. (TYPE SHEET: US 1699996! [=US-00115774]) The type sheet has specimens collected on more than one date and thus represents multiple gatherings: Mounted stem with single dry flower, is here designated as LECTOTYPE; ISOLECTOTYPE: stems with flowers (ARIZ 94443! [=ARIZ-Bot-0005731]). The lectotype material apparently collected in 1920 and the additional material (fruits, flowers and seeds) collected 22 March 1927, June 1934, and 30 April 1937 has been added in three separate packets.

1C. *Cylindropuntia acanthocarpa* var. *thornberi* (Thornber & Bonker) Backeberg, Cactaceae (Backeberg) 1: 184. 1958 (Figures 5C, 6E).

Opuntia thornberi Thornber & Bonker, Fantastic Clan: 133, 148. 1932. TYPE. upper illustration on page 135 of Thornber & Bonker (1932) [Note that Thornber & Bonker (1932) stated that the name had recently been published but no such publication has been found]; no type locality given, but Thornber & Bonker (1932) described populations as occurring on arid, sandy, or gravelly and rocky soils along the foothills and broad desert mesas in south central Arizona. EPITYPE designated by Crook & Mottram (1995): "Arizona, Yavapai County, Bumblebee, 2700 ft, June 16, 1939", *Lyman Benson 9671*, POM 274081! [= RSA-0008883, labelled "neotype"]; ISOEPITYPE: ARIZ 158257!).

Opuntia acanthocarpa* var. *thornberi (Thornber & Bonker) L. D. Benson, Proc. Calif. Acad. Sci. ser. 4, 25: 247. 1944.

Cylindropuntia acanthocarpa* subsp. *thornberi (Thornber & Bonker) Lodé, Cact.-Avent. Int. 98 (Suppl.): 3. 2013.

2. *Cylindropuntia echinocarpa* (Engelmann & J. M. Bigelow) F. M. Knuth, Kaktus-ABC [Backeberg & F. M. Knuth] 124. 1936 (Figures 5D, 6F).

Opuntia echinocarpa Engelmann & J. M. Bigelow, Syn. Cact. U. S. 49. 1856. TYPE. Apparently Arizona, near mouth of Bill Williams River at Colorado River, *Bigelow s.n.* (original material not found). NEOTYPE designated by Benson (1982). California, San Bernardino County, 23 miles west of Needles, 1200 feet elevation, (in fruit) *Lyman Benson 10374* (NEOTYPE: POM274071! [=RSA-008845]).

Opuntia wigginsii L. D. Benson, Cacti Ariz. ed. 3, 19, 32. 1969. TYPE. Arizona, Yuma County [probably now La Paz County], south of Quartzite, 900 feet elevation, *Lyman & Evelyn L. Benson 16465*, March 30, 1965 (HOLOTYPE: POM-296264! [=RSA-008930]) [a sheet composed of mature stems typical for *C. echinocarpa*, with some immature new growth]

Cylindropuntia wigginsii (L. D. Benson) H. Robinson, Phytologia 26:175. 1973.

EXCLUDED NAMES (accepted synonyms are preceded by "=")**:**

1. ***Opuntia acanthocarpa* subsp. *ganderi*** C. B. Wolf**,** Occas. Pap. Rancho Santa Ana Bot. Gard. 1(2): 75. 1938. TYPE. California, San Diego County, 3 mi. below the old Vallecito Stage Station, June 12, 1938, *C. B. Wolf 9424*, (HOLOTYPE: RSA- 18631! [=RSA-008893]).
   Opuntia acanthocarpa* var. *ganderi (C. B. Wolf) L. D. Benson, Cact. Succ. J. (Los Angeles) 41: 33. 1969.
   = ***Cylindropuntia ganderi* (C. B. Wolf) Rebman & Pinkava var. *ganderi*** J. Arizona-Nevada Acad. Sci. 33: 150. 2001**.**

2. ***Opuntia echinocarpa* var. *parkeri*** J. M. Coulter, Contr. U.S. Natl. Herb. 3(7): 446. 1896. TYPE. California, San Diego County, "east side of mountains facing desert," Sept 1879, *C.F. Parker s. n.* (HOLOTYPE: two sheets, apparently from the same gathering, MO-39397! [=MO-178063] with young fruits; and MO-39396! [=MO-178062] with stems.
   = ***Cylindropuntia californica* (Torrey & A. Gray) F. M. Knuth var. *parkeri* (J. M. Coulter) Pinkava**, J. Arizona-Nevada Acad. Sci. 33: 150. 2001.

3. ***Opuntia echinocarpa* var. *nuda*** J. M. Coulter, Contr. U.S. Natl. Herb. 3(7): 446. 1896. Holotype. "in Herb. Brandegee, Lower California, near San Gregorio ([*T. S.*] *Brandegee of 1889*)". (Holotype: UC 110317!)
   = ***Cylindropuntia alcahes* var. *alcahes* (F. A. C. Weber) F. M. Knuth**, Kaktus-ABC [Backeb. & Knuth] 127. 1936.

4. ***Opuntia echinocarpa* var. *wolfii*** L. D. Benson. Cact. Succ. J. (Los Angeles) 41: 33. 1969. Nom. Inval.

KEY TO THE TAXA

Because of overlapping character states, we recommend examining a number of individuals within a population in order to obtain an approximate average for key characters.

1. Branches generally two or more per trunk node, with trunk branch internodes mostly less than 10 cm in length; stem tubercles mostly less than 12 mm long; central spines averaging greater than seven in number. Primarily Mojave Desert but occurring sporadically southward into the Sonoran Desert to Baja California and Sonora, Mexico. .....……***C. echinocarpa*** (Figures 5D, 6F)

1’ Branches generally one to two per trunk node, with trunk branch internodes mostly greater than 15 cm in length; stem tubercles mostly greater than 23 mm long; central spines averaging fewer than seven in number

2. Plants mostly less than 1 m tall and generally 50% or broader than tall; stem tubercles averaging 36 mm long; longest radial spines averaging 15 mm long. Endemic to the central highlands of Arizona..... .....***C. acanthocarpa*** var. ***thornberi*** (Figures 5C, 6E)

2’ Plants mostly more than 1 m tall and generally less than 50% broader than tall; stem tubercles averaging 27.5 mm or less in length; longest radial spines averaging greater than 17 mm in length

3. Branches mostly spreading less than 40° from the trunk; stem diameter mostly more than 20 mm; tubercles averaging 27.5 mm in length and 6.6 mm in width; spines generally more than 15 in number; central spine sheaths about 1 mm in diameter. Western Mojave Desert and eastern Sonoran Deserts of California, Nevada, Arizona, and northernmost Sonora. ..... ***C. acanthocarpa*** var. ***acanthocarpa*** (Figures 5A; 6A, B, C)

3’ Branches mostly spreading more than 40° from the trunk; stem diameter mostly less than 20 mm; tubercles averaging 22.8 mm in length and 4.9 mm in width; spines generally fewer than 13 in number; central spine sheaths about 0.7 mm in diameter. Western Sonoran Desert of Arizona and northernmost Sonora. ..***C. acanthocarpa*** var. ***ramosa*** (Figures 5B, 6D)

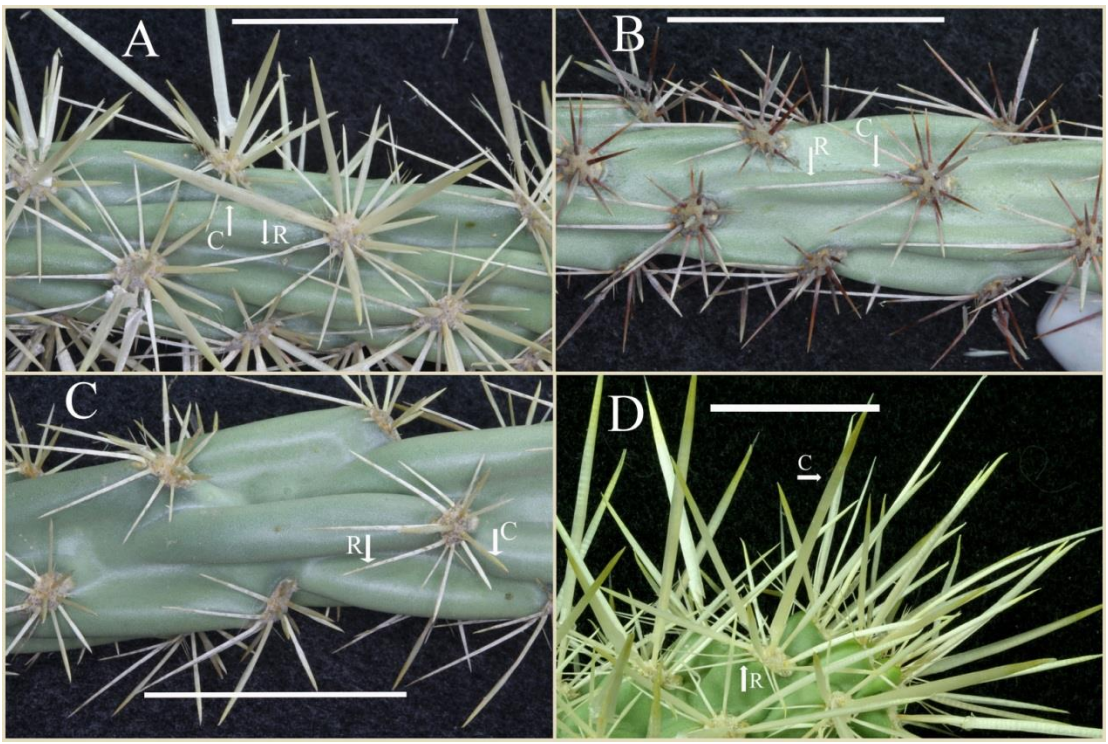

Figure 5. Representative ultimate stem segments of *Cylindropuntia acanthocarpa* and *C. echinocarpa*. A. *C. acanthocarpa* var. *acanthocarpa*. B. *C. acanthocarpa* var. *ramosa*; C. *C. acanthocarpa* var. *thornberi*. D. *C. echinocarpa*. Arrow with "C" = central spine, arrow with "R" = radial spine. Bars = 3 cm.

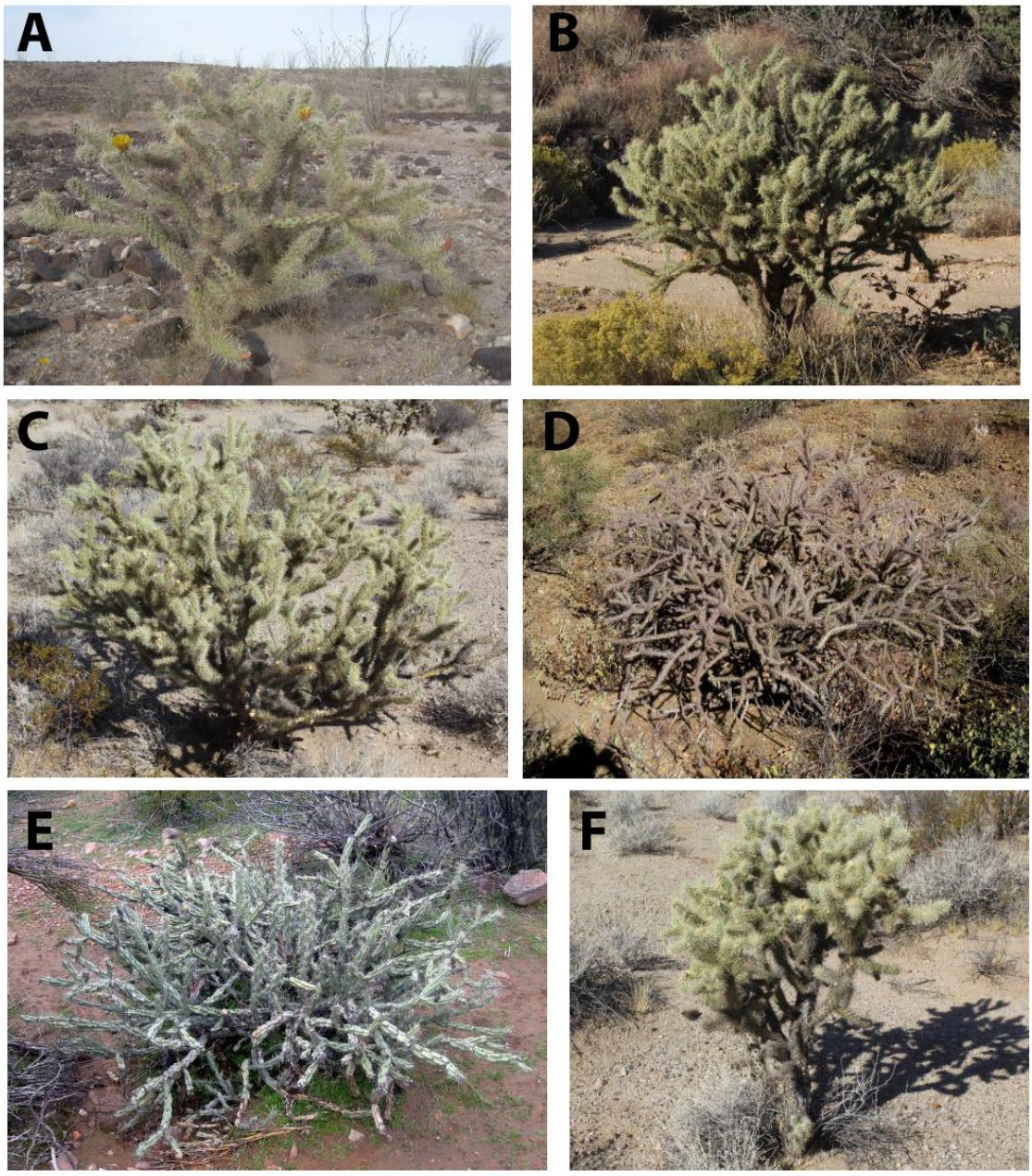

Figure 6. A. *Cylindropuntia acanthocarpa* var. *acanthocarpa* from Imperial County, California; B. *C. acanthocarpa* var. *acanthocarpa* from Mojave County, Arizona, near the original type locality (Cactus Pass); C. *C. acanthocarpa* var. *acanthocarpa* from San Bernardino County, California, at the type locality for *C. acanthocarpa* var. *coloradensis*; D. *C. acanthocarpa* var. *ramosa* from Pima County, Arizona; E. *C. acanthocarpa* var. *thornberi* from Gila County, Arizona; F. *C. echinocarpa* from San Bernardino County, California, neotype locality for the species.

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This paper is dedicated to Dr. Donald J. Pinkava, who passed away 25 July 2017. He was beloved by all of his students and colleagues and provided an unfaltering example of hard work, dedication, and an insatiable curiosity about all things, especially those concerning the evolution and taxonomy of the Cactaceae. Known affectionately as "the Nipper," he habitually insisted of students and colleagues, "Show me the data".

LITERATURE CITED

BAKER, M. A. 2016. Morphological and cytological analyses in C*ylindropuntia* (Cactaceae): the taxonomic circumscription of *C. echinocarpa, C. multigeniculata,* and *C. whipplei*. Journal of the Botanical Research Institute of Texas 10:325-343.

BAKER, M. A., D. J. PINKAVA, J. P. REBMAN, B. D. PARFITT, & A. D. ZIMMERMAN. 2009. Chromosome numbers in some cacti of western North America. VIII. Haseltonia 15:117–134.

BAKER, M. A., B. D. PARFITT, and J. P. REBMAN. 2012. *Cylindropuntia*. pp. 580-582. In: The Jepson Manual. B. G. Baldwin, D. H. Goldman, D. J. Keil, R. Patterson, T. J. Rosatti, and D. H. Wilken (eds.). University of California Press, Berkeley, California.

BENSON, L. 1940. The Cacti of Arizona. University of Arizona Biological Sciences Bulletin 5 (21):1-134.

BENSON, L. 1969. Cacti of Arizona. ed. 3. University of Arizona Press, Tucson, Arizona.

BENSON, L. D. 1982. The Cacti of the United States and Canada. Stanford University Press, Stanford, California.

COULTER, J. M. 1896. Preliminary revision of the North American species of *Echinocactus*, *Cereus*, and *Opuntia*. Contributions from the U. S. National Herbarium 3:355-462.

CROOK, R. and R. MOTTRAM. 1995. *Opuntia* index, part 1: introduction and A–B. Bradleya 13:89-118.

CROOK, R. and R. MOTTRAM. 1996. *Opuntia* index, part 2: introduction and C–E. Bradleya 14:99-144.

ENGELMANN, G. 1856a. Synopsis of the Cactaceae of the territory of the United States and adjacent regions. Proceedings of the American Academy of Arts and Science 3:.259-314.

ENGELMANN, G. 1856b. Synopsis of the Cactaceae of the territory of the United States and adjacent regions (reprinted from the Proceedings of the American Academy of Arts and Science 3:259-314, with additional errata). Metcalf and Company, Cambridge, Massachusetts.

ENGELMANN, G. 1859. Cactaceae of the Boundary. in Emory, W. H., Report on the United States and Mexican boundary survey: made under the direction of the Secretary of the Interior. Vol 2, part 1. 34th Cong., 1st sess. House. Ex doc. 135. Cornelius Wendell, Printer, Washington, DC.

ENGELMANN, G. and J. M. BIGELOW. 1856. Description of the Cactaceae. pp. 27-53. In: Reports of explorations and surveys to ascertain the most practicable and economical route for a railroad from the Mississippi River to the Pacific Ocean. Vol. 4, The Report of the botany of the expedition. 33d Cong., 2nd sess., House Exec. doc. 91 and Senate Ex. doc. No. 78. A. O. F. Nicholson, Printer, Washington, DC.

GLOBAL PLANTS INITIATIVE. 2017. http://plants.jstor.org/. (Accessed November 2017).

GUZMAN, U., B. VASQUEZ-BENITEZ, and M. DEL C. M. SANCHEZ. 2003. Combinaciones and estatus nuevos de Cactáceas Mexicanas. Cactaceae Systematic Initiatives 16:16-18.

HALLOCK, W. and H. T. WADE. 1906. Outlines of the evolution of weights and measures and the metric system. Macmillan Co. New York.

HOLMGREN, N. H., P. K. HOLMGREN, and J. L. REVEAL (eds.). 2012. Intermountain Flora.Vol. 2 (part A). New York Botanical Garden Press, Bronx, New York.

IBM CORP. (2013). IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY: IBM Corporation.

PINKAVA, D. J. 1999. Cactaceae Part Three. *Cylindropuntia*. Journal of the Arizona Nevada Academy of Science 32:32–47.

PINKAVA, D. J. 2003. *Cylindropuntia*. pp. 102–118. In: Flora of North America Editorial Committee (eds.), Flora of North America North of México. Vol. 4: Magnoliophyta: Caryophyllidae, Part 1. Oxford University Press, New York, NY.

PINKAVA, D. J. and M. A. BAKER. 2012. *Cylindropuntia*. pp.637-644. In: Intermountain Flora. N. H. Holmgren, P. K. Holmgren, and J. L. Reveal (eds.). Vol. 2 (part A). New York Botanical Garden Press, Bronx, New York.

PINKAVA, D. J., M. A. BAKER, B. D. PARFITT, M.W. MOHLENBROCK, and R. D. WORTHINGTON. 1985. Chromosome numbers in some cacti of western North America-V. Systematic Botany 10: 471–483.

PINKAVA, D. J., B. D. PARFITT, M. A. BAKER, and R. D. WORTHINGTON. 1992. Chromosome numbers in some cacti of western North America-VI. Madroño 39:98–113.

PINKAVA, D. J., J. P. REBMAN, and M. A. BAKER. 1998. Chromosome numbers

in some cacti of western North America-VII. Haseltonia No. 6:32–41.
PEEBLES, R. H.1937. Comments on the dry-fruited cylindric Opuntias of Arizona. Cactus and Succulent Journal (US) 9:35-38. Correction: Cactus and Succulent Journal (US) 9:50.
SEINet (SOUTHWEST ENVIRONMENTAL INFORMATION NETWORK) Arizona Chapter. 2014. http//:swbiodiversity.org/seinet/index.php. (Accessed November 2017).
TABACHNICK, B. O. and L. S. FIDELL. 1996. Using multivariate statistics. Harper Collins, New York, NY.
THORNBER, J. J. and F. BONKER. 1932. The fantastic clan: The cactus family. Macmillan Company; New York.
TRELEASE, W. and A. GRAY [eds]. 1887. The botanical works of the late George Engelmann. Collected for Henry Shaw, Esq. John Wilson & Son, University Press, Cambridge, Massachusetts.