Phenetic analysis of *Coryphantha*, section *Robustispina* (Cactaceae), part 1: stem characters.

Final report

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Abstract

A preliminary phenetic analysis was done to evaluate the taxonomic relationships within *Coryphantha*, section *Robustispina*, which includes *C. robustispina* ssp. *robustispina*, *C. robustispina* ssp. *uncinata, C. robustispina* ssp. *scheeri,* and *C. poselgeriana*. ANOVA, PCA, and DA procedures were performed on ten continuous stem characters for 14 populations and 447 individuals. Of primary concern was the taxonomic validity of the subspecific taxa within *C. robustispina*, with *C. poselgeriana* serving as out-group comparison. Data indicated that populations of *C. robustispina* ssp. *scheeri* represent a separate taxon and possibly a distinct species. Populations of both *C. robustispina* ssp. *uncinata* and *C. robustispina* ssp. *robustispina* are morphologically coherent within their respective taxa and are allopatric between the two taxa, thus indicating that they deserve taxonomic recognition. Individuals of *C. poselgeriana* were morphologically discrete from those of *C. robustispina*.

Introduction

The purpose of the on-going study is to ascertain whether any of the known populations of *Coryphantha robustispina* are morphologically distinct from one another and whether any such distinction, if significant, reflects geographical range. This information is important for the assessment of the taxonomy of the species.

Nomenclature within *Coryphantha (Engelm.) Lemaire*, section *Robustispina* Dicht & A. Lüüthy is confusing. A comparison of various taxonomic treatments is given in Table 1. For simplicity, the taxonomy of Taylor (1998) will be used here for *C. robustispina* (Engelm.) Britton & Rose, which recognizes three subspecies, *C. robustispina* ssp. *robustispina*, *C. robustispina* ssp. *uncinata* (L. D. Benson) N. P. Taylor, and *C. robustispina* ssp. *scheeri* (Lemaire) N. P. Taylor. These three subspecies are roughly equivalent to the varieties of Benson (1982) with the notable exception that Benson's *C. scheeri* var. *valida* is not recognized.

The geographic range of the three subspecies is a matter of dispute. Roughly, populations of *C. robustispina* ssp. *robustispina* occur in Pima County, Arizona and northern Sonora, Mexico; those of *C. robustispina* ssp. *uncinata* occur from Cochise County, Arizona, east to Doña Ana County, New Mexico, northern Chihuahua, and El Paso County, Texas; and *C. robustispina* ssp. *scheeri* occurs from Eddy and Chaves Counties of New Mexico, south through Texas into Chihuahua and Coahuila (Figure 1).

The foremost goal of the present study was to provide an adequate sample size for the objectives sought. Recommendations of adequate sample size for multivariate statistics vary widely among authors and there is no specific rule that applies. In our studies within Cactaceae (Baker & Johnson 2000, Baker unpublished data) measurement for most characters of 30 individuals accounts for about 90% of the variation within a single population and at least three populations are chosen to account for the variation across the geographic range. Most authors agree that the minimum number of samples (OTU's) for comparing two trials (taxa) is 100 and that for each population is 20, while others recommend a minimum of three to a preferred ten times

the amount of individuals to characters (Huberty 1994, Lawley & Maxwell 1971, Marascuilo & Levin 1983, Tabachnick & Fidell 1996, 2001).

Table 1. Cross-reference of classifications for *Coryphantha robustispina*.

Taylor (1998)	*C. robustispina* ssp. *robustispina*	*C. robustispina* ssp. *uncinata*	*C. robustispina* ssp. *scheeri*
Anderson (2001)	Same as Taylor	Same as Taylor but defines this ssp. as having only "strongly curved or hooked spines"	Same as Taylor
Benson (1982), Bravo-Hollis (1991)	*C. scheeri* var. *robustispina*	*C. scheeri* var. *valida* and *C. scheeri* var. *uncinata*	*C. scheeri* var. *scheeri*
Dicht & Lüüthy (2001)	Same as Taylor	*C. robustispina* ssp. *scheeri*	*C. robustispina* ssp. *scheeri*
Britton & Rose (1920)	*C. robustispina*	*C. muehlenpfordtii*	*C. muehlenpfordtii*
New Mexico Rare Plant Technical Council (1999)	Not discussed	*C. scheeri* var. *valida*	*C. scheeri* var. *scheeri*

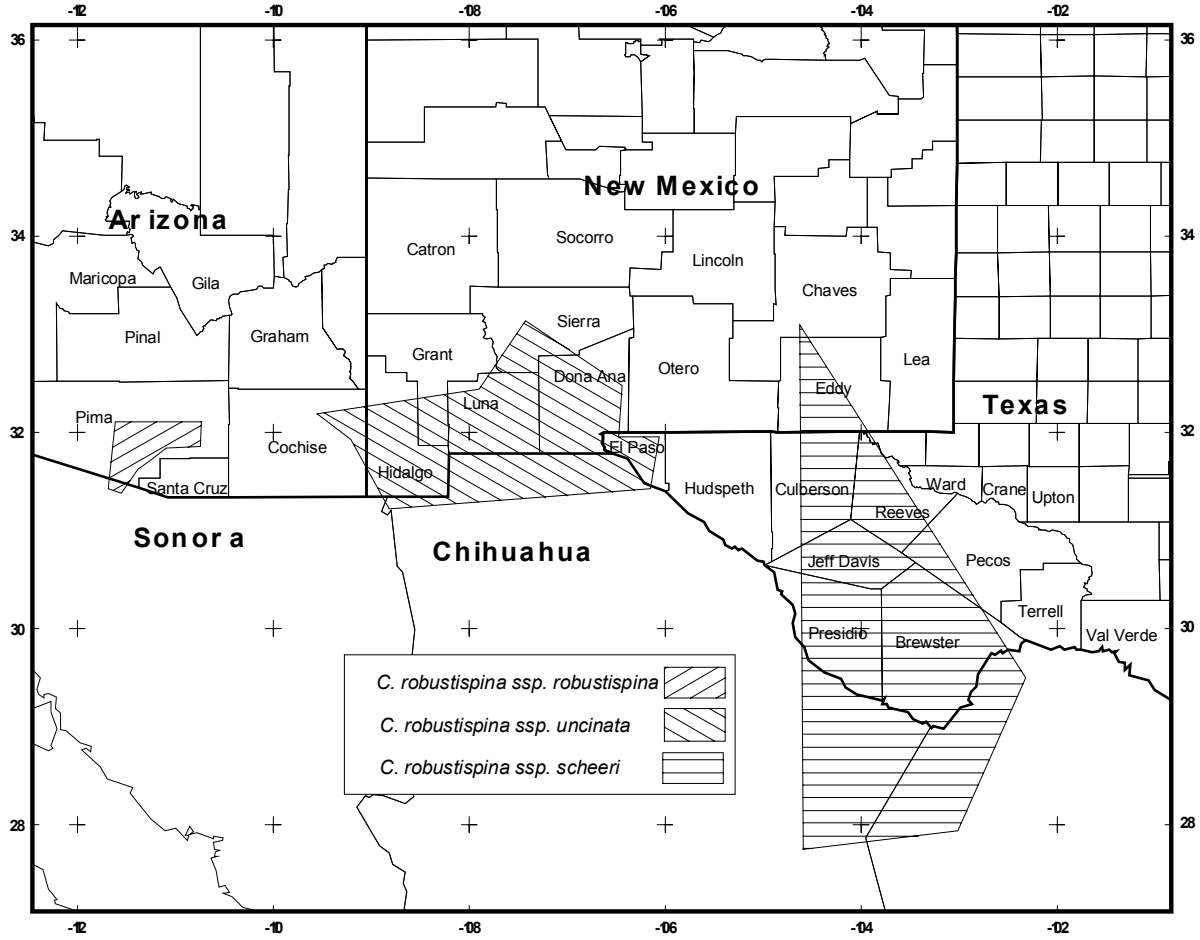

Figure 1. Approximate distribution of *Coryphantha robustipina* based on literature.

Methods

Fieldwork

Fieldwork was conducted 24-28 July 24-28 2000, 2-6 & 11 September 2003, and 9-14 & 22 October 2003. Locations of individuals were recorded as NAD27 CONUS UTM grid coordinates using a Garmin™ 12XL GPS unit with an accuracy of 8m. Figure 2 presents an overview of the study sites. Descriptions of sites are presented in Table 2. Three supplementary sites, Gray Ranch, Vanar, and the junction of I-40 and Hwy 191 are not shown in figure 2 or listed in Table 2.

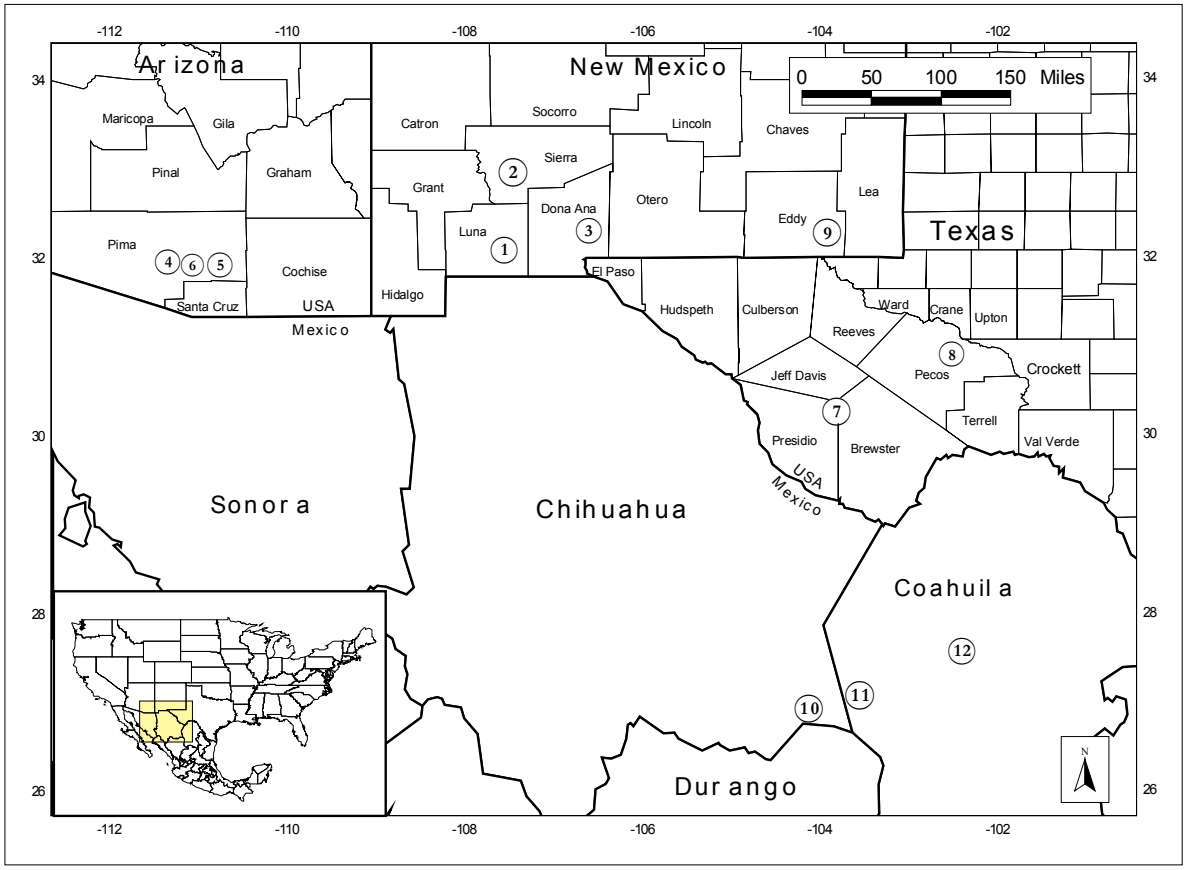

Figure 2. Locations of study sites.

Table 2. Location and description of sites. (UTM = NAD27, CONUS)

Site	Taxon/voucher	Location	Habitat
1	*C. robustispina* ssp. *uncinata* *Baker 15561*	13S 02 55 082mE 35 54 983mN; N32º 06.38' W107º 35.73, 1465m (4800ft) elev. Gym Peak 7.5' USGS topographic quadrangle, Luna Co., New Mexico, along Lobo Draw, 3.3km SE of Florida Peak; Florida Mtns.; 25km SE of Deming	Shallowly dissected upper bajada of granitic silt, gravel, and cobble; disclimax Bouteloua eriopoda/Pleuraphis mutica grassland with *Cylindropuntia spinosior, Dasylirion wheeleri, Echinocereus fendleri, Ephedra trifurca, Erioneuron pulchellum, Ferocactus wislizenii, Gutierrezia sarothrae, Juniperus coahuilensis, Krameria erecta, Echinomastus intertexta, Opuntia engelmannii, Prosopis glandulosa,* and *Yucca elata*.
2	*C. robustispina* ssp. *uncinata* *Baker 15561*	13S 02 67 860mE 36 49 369mN; N32º 57.58' W107º 29.01, 1555m (5100ft) elev., Stone Arroyo 7.5' USGS topographic quad., Sierra Co., NM along Hwy 90, 10km east of Hillsboro, between Greyback and Greenhorn Arroyos, north of Percha Creek	Disclimax *Pleuraphis mutica* grassland with *Acourtia nana, Cylindropuntia leptocaulis, Echinocereus fendleri, Ephedra trifurca, Erioneuron pulchellum, Flourensia cernua, Gutierrezia sarothrae, Larrea tridentata, Lycium pallidum, Muhlenbergia porteri, Opuntia macrocentra, O. phaeacantha, Parthenium incanum, Prosopis glandulosa, Rhus microphylla, Yucca elata,* and *Zinnia acerosa*.

Table 2. Location and description of sites. (UTM = NAD27, CONUS)

Site	Taxon/voucher	Location	Habitat
3	*C. robustispina* ssp. *uncinata* *Baker 15568*	13S 03 48 368mE 35 84 446mN; N32º 23.3' W106º 36.72, 1485-1615m (4875-5300ft) elevation, west slope of the Organ Mtns., Organ Peak 7.5' USGS topographic quadrangle, Doña Ana Co., NM east of Las Cruces, below Baylor Canyon, 3.5km west of Baylor Pea	*Prosopis glandulosa/Flourensia cernua* scrub with *Bouteloua eriopoda, Condalia warnockii, Coryphantha macromeris, Echinocereus rosei, Ephedra trifurca, Ericameria laricifolia, Eriogonum wrightii, Erioneuron pulchellum, Ferocactus wislizenii, Gutierrezia sarothrae, Larrea tridentata, Mimosa biuncifera, Muhlenbergia porteri, Echinomastus intertexta, Opuntia engelmannii, O. macrocentra, O. phaeacantha, Parthenium incanum, Pleuraphis mutica, Yucca baccata, Yucca elata,* and *Zinnia acerosa*
4	*C. robustispina* ssp. *robustispina* no voucher	12S 04 65 100-04 72 700mE 35 33 500-35 43 900mN; N31º 56.0-32º 01.9' W111º 17.4'-W111º 22.1', 840-975m (2750-3200 ft) elev., Three Points and Stevens Mtn. USGS topographic quads., Pima Co., Arizona, Alter Valley, 40km SW of Tucson, south of Three Points	Habitat variable: low ridges, areas adjacent to shallow ravines, and deep alluvium of wide drainages. *Larrea tridentata* scrub, Arizona Upland-disclimax grassland transition, and disclimax grassland with *Acacia constricta, Carnegiea gigantea, Celtis pallida, Cercidium microphyllum, Cylindropuntia arbuscula, C. fulgida, C. leptocaulis, C. spinosior, Ephedra torreyana, Erioneuron pulchellum, Ferocactus wislizenii, Gutierrezia sarothrae, Isocoma tenuisecta, Larrea tridentata, Muhlenbergia porteri, Opuntia engelmannii, Prosopis velutina, Yucca elata,* and *Zinnia acerosa*

Table 2. Location and description of sites. (UTM = NAD27, CONUS)

Site	Taxon/voucher	Location	Habitat
5	*C. robustispina* ssp. *robustispina* no voucher	12S 05 21 150mE 35 35 420mN, N31º 57.4' W110º 46.6', 1015m (3325 ft) elev., Corona De Tucson USGS topographic quad., Pima Co., Arizona, 9km NNW of Mount Fagan, 30km SSW of Tucson	Level area of silt and gravel, disclimax grassland with *Ambrosia psilostachya, Aristida purpurea, A. ternipes, Ayenia pusilla, Bouteloua rothrockii, Calliandra eriophylla, Cylindropuntia fulgida, Echinocereus fendleri, Eragrostis lehmanniana, Ferocactus wislizenii, Isocoma tenuisecta, Opuntia engelmannii, O. phaeacantha, Prosopis velutina, Solanum elaeagnifolium,* and *Zinnia acerosa*
6	*C. robustispina* ssp. *robustispina* no voucher	12S 04 93 200mE 35 35 750mN, N31º 57.6' W111º 04.3', 1080m (3550 ft); Pima Co., Arizona, 10km west of the Santa Cruz R., 1,100m SSE of the summit of Helmet Peak, 30km SSW of Tucson.	Low ridges of silt and gravel; Arizona upland with *Acacia constricta, Acourtia nana, Ayenia pusilla, Calliandra eriophylla, Celtis pallida, Cercidium floridum, C. microphyllum, Coryphantha vivipara, Cylindropuntia fulgida, C. spinosior, Digitaria californica, Echinocereus fasciculatus, Ephedra trifurca, Erioneuron pulchellum, Ferocactus wislizenii, Fouquieria splendens, Gutierrezia microcephala, Heteropogon contortus, Hibiscus denudatus, Janusia gracilis, Krameria erecta, Larrea tridentata, Lycium berlandieri, Lycium exertum, Mammillaria grahamii, Menodora scoparia, Muhlenbergia porteri, Opuntia engelmannii, O. phaeacantha, O. santaritensis, Parthenium incanum, Prosopis velutina, Scleropogon brevifolia, Setaria macrostachya, Tridens muticus,* and *Zinnia pumila*

Table 2. Location and description of sites. (UTM = NAD27, CONUS)

Site	Taxon/voucher	Location	Habitat
7	*C. robustispina* ssp*. scheeri* *Baker 15642*	13R 06 05 656mE 33 56 437mN; N30º 20.21' W103º 54.05', 1540m (5050ft) elev., Nopal 7.5' USGS topographic quadrangle, Presidio Co., TX, between Colquitt and Long Draws; 15km ENE of Marfa	Mixed grassland with *Aristida purpurea, A. ternipes, Bothriochloa barbinodis, Bouteloua curtipendula, B. eriopoda, B. gracilis, B. hirsuta, Condalia warnockii, Cylindropuntia imbricata, Ephedra trifurca, Lesquerella fendleri, Machaeranthera pinnatifida, Muhlenbergia arenicola, Opuntia phaeacantha, Panicum hallii, P. obtusum,* and *Yucca elata*.
8	*C. robustispina* ssp*. scheeri* *Baker 15645*	13R 07 42 525-43 115mE 34 18 545-900mN; N30º 52' W102º 27', 0810m (2660ft) elev., Bootleg Canyon 7.5' USGS topographic quad., Pecos Co., TX, just south of Big Mesa, 40km east of Fort Stockton, along I-10 at interchange	Areas of various levels of disturbance with *Cylindropuntia imbricata, C. leptocaulis, Larrea tridentata, Muhlenbergia arenicola, Opuntia engelmannii, O. phaeacantha, Prosopis glandulosa, P. velutina, Scleropogon brevifolius, Setaria macrostachya,* and *Tiquilia canescens*.
9	*C. robustispina* ssp*. scheeri* *Baker 15646.2*	13S 06 00 800mE 35 78 115mN; N32º 20.23' W103º 55.73', 0915m (3000ft) elev., Remuda Basin 7.5' USGS topographic quadrangle, Eddy Co., NM, along Hwy 128, 30 km ESE of Carlsbad	Gypsum flats with *Aristida purpurea, Bouteloua breviseta, Coryphantha macromeris, Cylindropuntia leptocaulis, Ephedra torreyana, Larrea tridentata, Opuntia phaeacantha, Prosopis glandulosa, Setaria macrostachya, Sporobolus airoides, Sporobolus nealleyi, Tiquilia hispidissima,* and *Yucca angustissima*

Table 2. Location and description of sites. (UTM = NAD27, CONUS)

Site	Taxon/voucher	Location	Habitat
10	*C. poselgeriana Baker 15663*	13R 05 86 120-05 86 350mE 29 71 190-29 71 320mN (NAD 27); 26º 52'N 104º 07.5ºW; 1220m elev.; 1km east of Mercurio; 25km NE of Escalón; 2km NNW of the summit of Cerro Piloncilla; Chihuahua; Mecurio 1:50,000 Centenal topographic quadrangle.	*Larrea tridentata* scrub with *Acacia constricta, Agave scabra, Coryphantha macromeris, Cylindropuntia leptocaulis, C. imbricata, Echinocereus stramineus, Echinomastus unguispinus, Euphorbia antisyphilitica, Ferocactus hamatacanthus, Flourensia cernua, Fouquieria splendens, Grusonia grahamii, Jatropha dioica, Krameria grayi, Mammillaria heyderi, Opuntia engelmannii, O. macrocentra, Prosopis velutina,* and *Yucca faxoniana*.
11	*C. poselgeriana Baker 15669*	13R 06 34 840mE 29 93 630mN (NAD 27); 27.05987ºN 103.64029ºW; 1120m elev.; 20km west of Laguna del Rey; 1km NE of El Milagro; Coahuila, Laguna del Rey Cetenal 1:50,000 topographic quadrangle.	*Larrea tridentata* scrub with *Coryphantha macromeris, Cylindropuntia leptocaulis, C. imbricata, Echinocereus stramineus, Echinocactus horizonthalonius, Ferocactus hamatacanthus, Euphorbia antisyphilitica, Flourensia cernua, Fouquieria splendens, Jatropha dioica, Mammillaria heyderi, Opuntia rufida,* and *Parthenium incanum*.

Table 2. Location and description of sites. (UTM = NAD27, CONUS)

Site	Taxon/voucher	Location	Habitat
12	*C. poselgeriana* *Baker 15671*	13R 07 58 140-390mE 30 48 820-49 500mN (NAD 27); 27º 32'N 102º 23'W; 1195m elev.; north of Ocampo, 1km NE of Guadalupe, east of Sierra del Mula; nearly level valley floor of fine pale brown silt; Coahuila, Charcos de Figueroa Cetenal 1:50,000 topographic quadrangle.	*Flourensia cernua* scrub with *Acacia constricta, Acacia greggii, Coryphantha macromeris, Cylindropuntia leptocaulis, Echinocereus stramineus, Flourensia cernua, Grusonia grahamii, Koeberlinia spinosa, Larrea tridentata, Mammillaria heyderi, Parthenium incanum, Prosopis glandulosa, Tiquilia canescens,* and *Yucca faxoniana*.

Phenetic analysis

Characters measured for the 2003 sites are presented in Table 3. Two characters, vertical central spine thickness and upper tubercle width, were not measured in 2000.

Table 3. Morphological characters

Character	Explanation
Stem height	Height of the tallest stem from ground level to tip of highest tubercle, excluding spines
Stem diameter	Maximum diameter of the same stem used for height measurements, tubercle tip to tubercle tip, excluding spines.
No. mature stems	The number mature stems. Those possessing tubercles with a complete ventral groove.
No. immature stems	The number of immature shoots. Those not possessing tubercles with a complete ventral groove.
For the following characters, measurements were made from three separate areoles from the first mature ring of tubercles near the stem apex.	
Central spine no.	Number of central spines per areole.
Radial spine no.	Number of radial spines per areole.
Central spine length	Length of the longest central spine in a spine cluster.
Radial spine length	Length of the longest radial spine in a spine cluster.
Central spine thickness (vertical)	The vertical (dorsal-ventral) thickness just above the base of the thickest central spine.
Central spine thickness (horizontal)	The horizontal (lateral) thickness just above the base of the thickest central spine.
Width of curvature	The distance as measured perpendicular from the axis of the spine to its apex
Tubercle height	The distance from the base to the tip of a tubercle.
Upper tubercle Width	The width of the base of the tubercle.
The following character was measured on the row of fully turgid tubercles closest to the base of the plant.	
Lower tubercle Width	The width of the base of the tubercle.

Data for each individual (OTU) were entered into an Excel 2000® spreadsheet. For those characters measured thrice per individual, the average was entered. Rows were defined as OTU's and columns as characters. Data were then imported into Systat® 10 (SPSS Inc 2000) for analyses.

Results

Descriptive Statistics are presented in Table 3. Certain characteristics among the taxa are apparent from the mean values. Number of immature stems and central spine thickness is greatest in *C. robustispina* ssp. *robustispina* than, total number of spines and tubercle height is greatest in *C. robustispina* ssp. *uncinata,* total number of spines was fewest in of *C. robustispina* ssp. *scheeri,* and tubercles were shortest in *C. poselgeriana*.

Manova

Dependent variables were tested using the MANOVA procedure of SPSS® version 10.0. Data were transformed, as necessary to meet the assumptions of MANOVA. Some characters did not meet homogeneity of variance assumptions after various attempts at transformation (Table 4). For this reason, Central spine number, radial spine number and central spine length were left untransformed for the DA. Tukey HSD post hoc test showed that most characters were significantly different at <.001 among the four taxa. Tubercle height and lower tubercle width between *C. robustispina* spp. *robustispina* and *C. robustispina* spp. *uncinata*, were significant at <.01. The following comparisons were not significant: radial spine number between *C. robustispina* spp. *robustispina* and *C. poselgeriana* or between *C. robustispina* spp. *uncinata* and *C. robustispina* spp. *scheeri*, radial spine length between *C. robustispina* spp. *robustispina* and *C. robustispina* spp. *uncinata*, and central spine curvature between *C. robustispina* spp. *robustispina* and *C. robustispina* spp. *uncinata* or between *C. robustispina* spp. *scheeri* and *C. poselgeriana*.

Table 3. Descriptive statistics, by taxon.

Statistic	Ht. Stem	Dia. Stem	No. Mature Stems	No. Immat. Stems	C. Spine No.	Radial Spine No.	C. Spine Len.	Radial Spine Len.	C. Spine W.	C. Spine Thickn.	C. Spine Curv.	Tub. Ht.	Upp. Tub. W.	Low. Tub. W.
						C. robustispina spp. *uncinata*								
N of cases	100	100	100	100	100	100	100	100	100	100	100	100	100	100
Minimum	23	56	1.0	0.0	1.0	7.7	18.0	14.3	0.8	0.6	0.0	14.7	8.3	12.0
Maximum	165	153	7.0	15.0	4.3	16.3	45.3	37.0	1.8	1.5	10.0	36.3	20.0	37.0
Mean	**78**	**95**	**1.2**	**0.6**	**2.8**	**11.1**	**33.0**	**24.8**	**1.3**	**1.1**	**2.9**	**26.0**	**12.9**	**22.9**
Standard Dev	31	20	0.7	1.8	0.7	1.7	6.1	4.5	0.2	0.2	2.2	4.8	1.8	4.7
Kurtosis	-02	-05	41.0	39.5	-0.1	0.3	-0.3	0.2	-0.1	0.3	1.0	-0.5	2.0	0.1
						C. robustispina ssp. *robustispina*								
N of cases	104	104	104	104	104	104	104	104	104	62	104	104	62	104
Minimum	29	66	1.0	0.0	1.0	7.3	16.0	14.3	1.2	1.1	0.0	12.2	10.6	13.0
Maximum	210	142	7.0	11.0	4.0	12.3	40.7	40.0	2.8	2.0	9.7	33.3	21.3	36.3
Mean	**108**	**102**	**1.5**	**2.3**	**2.1**	**9.5**	**29.1**	**25.0**	**1.7**	**1.5**	**3.1**	**22.8**	**13.9**	**23.2**
Standard Dev	42	19	1.2	2.7	0.8	1.0	4.5	3.9	0.3	0.2	1.7	4.1	2.1	5.3
Kurtosis	-05	-06	9.5	0.9	-0.5	0.1	0.3	1.4	1.5	0.0	1.4	-0.2	2.1	-0.6

Table 3. Descriptive statistics, by taxon.

Statistic	Ht. Stem	Dia. Stem	No. Mature Stems	No. Immat. Stems	C. Spine No.	Radial Spine No.	C. Spine Len.	Radial Spine Len.	C. Spine W.	C. Spine Thickn.	C. Spine Curv.	Tub. Ht.	Upp. Tub. W.	Low. Tub. W.
						C. robustispina ssp. *scheeri*								
N of cases	96	96	96	96	96	96	96	96	96	96	96	96	96	96
Minimum	27	43	1.0	0.0	0.3	6.0	12.7	10.7	0.4	0.4	0.0	8.0	5.0	10.7
Maximum	223	113	4.0	2.0	2.3	12.3	33.0	29.0	1.3	1.2	3.3	26.3	16.3	23.7
Mean	**63**	**75**	**1.2**	**0.1**	**1.0**	**8.6**	**23.0**	**18.0**	**0.8**	**0.7**	**0.5**	**16.4**	**9.1**	**16.5**
Standard Dev	34	15	0.5	0.3	0.2	1.2	4.0	3.3	0.2	0.2	0.8	3.4	2.2	3.2
Kurtosis	57	-08	10.4	26.8	21.3	-0.1	-0.1	0.6	0.2	-0.1	3.7	0.5	0.4	-0.7
						C. poselgeriana								
N of cases	96	96	96	96	96	96	96	96	96	96	96	96	96	96
Minimum	30.0	66.0	1.0	0.0	1.0	8.0	27.7	21.3	1.1	1.0	0.0	06	09	21
Maximum	161.0	121.0	2.0	0.0	1.0	15.3	49.7	39.7	1.9	1.9	1.7	18	25	49
Mean	**70.1**	**90.1**	**1.0**	**0.0**	**1.0**	**11.5**	**36.5**	**29.9**	**1.4**	**1.4**	**0.4**	**12**	**16**	**35**
Standard Dev	26.1	11.4	0.1	0.0	0.0	1.7	4.5	4.2	0.2	0.2	0.4	02	03	06
Kurtosis	0.4	0.1	96.0			-0.6	-0.1	-0.5	-0.3	-0.4	0.4	-04	07	-02

Table 4. Levene's Test of Equality of Error Variances.

Character	F	df1	df2	Sig.
Stem diameter	11.644	3	350	.000
Stem diameter, SQR	9.976	3	350	.000
Central spine number	100.380	3	350	.000
Central spine number, SQR	93.306	3	350	.000
Central spine number, (SQR) SQR	85.980	3	350	.000
Radial spine number	10.578	3	350	.000
Radial spine number, SQR	6.638	3	350	.000
Radial spine number, (SQR) SQR	5.183	3	350	.002
Central spine length	6.510	3	350	.000
Central spine length, log	6.005	3	350	.001
rad sp len	3.496	3	350	.016
Radial spine length, log	2.013	3	350	.112
Central spine width	2.032	3	350	.109
Central spine thickness, vertical	1.479	3	350	.220
Curvature of central spine	59.426	3	350	.000
Tubercle height	59.170	3	350	.000
Tubercle height, log	1.031	3	350	.379
Lower tubercle width	54.771	3	350	.000
Lower tubercle width, log	2.206	3	350	.087

Principal Components Analysis

The first three PCA factors explained 72.9% of the total variance (Table 5). Factor one, which was important in grouping individuals of both *C. poselgeriana* and *C. robustispina* ssp. *scheeri*, had greatest component loadings for central spine length, radial spine length, number of radial spines, central spine thickness, and width of lower tubercle (Figure 3). Factor two, which was most important for grouping *C. poselgeriana,* had greatest component loadings for width of lower tubercle, central spine number, tubercle height, and central spine curvature (Figures 3 and 4). Factor three, which explained the least amount of total variance and was the only factor that was important for grouping individuals of *C. robustispina* ssp. *robustispina* from those of *C. robustispina* ssp. *uncinata*, had greatest component loadings for number of radial spines, central spine thickness, and number of immature stems (Figure 4). Individuals of *C. robustispina* ssp. *uncinata* that are geographically closer to those of *C. robustispina* ssp. *robustispina* are plotted farthest from those of *C. robustispina* ssp. *robustispina* (Figure 5).

Table 5. Component loadings of first three PCA factors.

	Factor 1	Factor 2	Factor 3
Central spine length	**0.9**	-0.3	-0.1
Radial spine length	**0.9**	-0.3	0.1
Number of radial spines	**0.7**	-0.2	**-0.4**
Central spine thickness (vertical)	**0.6**	0.1	**0.6**
Width of lower tubercle	**0.6**	**-0.5**	0.2
Central spine number	0.5	**0.6**	**-0.4**
Tubercle height	0.4	**0.7**	-0.2
Central spine curvature	0.3	**0.7**	0.2
Number of immature stems	0.2	0.4	**0.6**
Percent of total variance explained	35.4	22.9	14.6

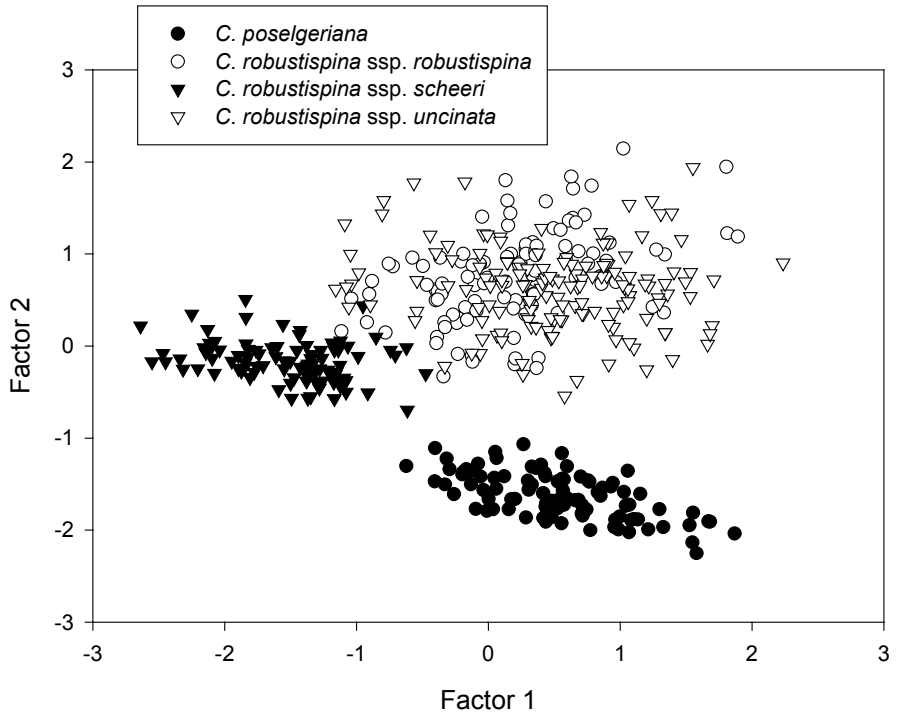

Figure 3. Scatterplot of PCA factor 1 vs factor 2, individuals identified by *a priori* taxon.

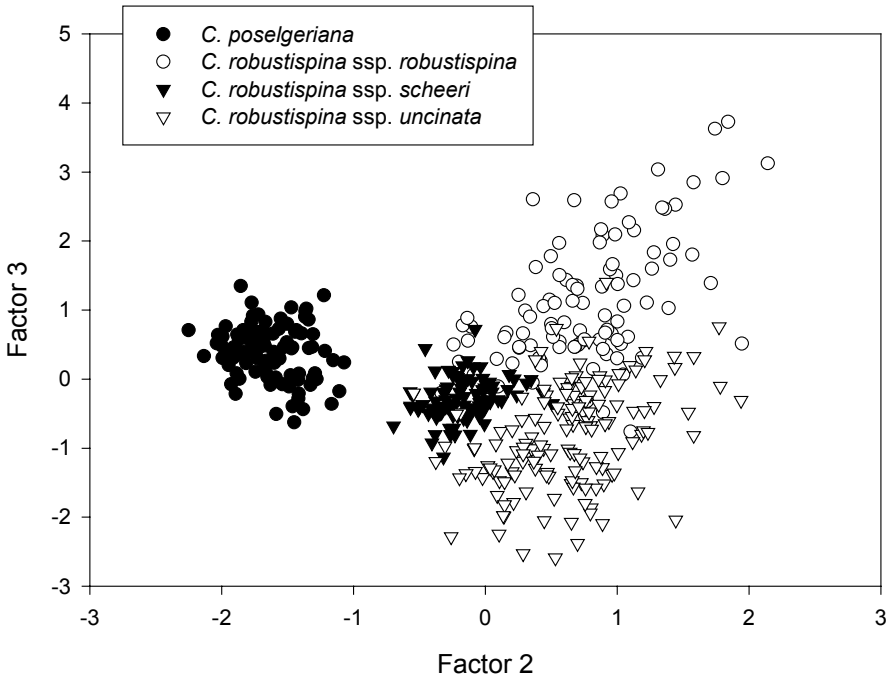

Figure 4. Scatterplot of PCA factor 2 vs factor 3, individuals identified by *a priori*i taxon.

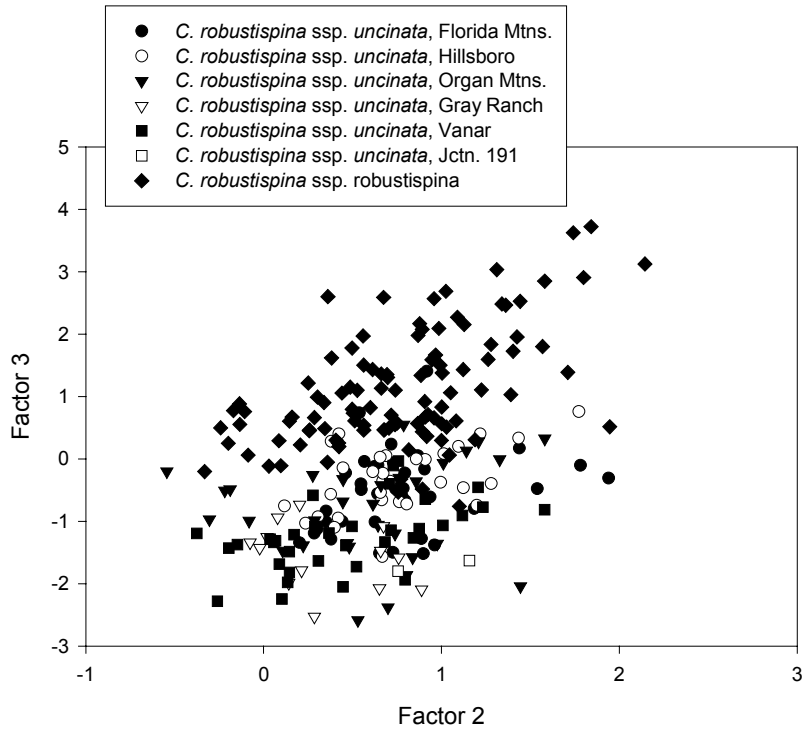

Figure 5. Scatterplot of PCA factor 2 vs factor 3, individuals of *C. robustispina* ssp. *robustispina* and *C. robustispina* ssp. *uncinata* only with those of *C. robustispina* ssp. *uncinata* identified according to population.

Discriminant analysis

Predicted group membership for individuals among the four taxa are given in Table 6. Individuals occurring in populations of *Coryphantha robustispina* ssp. *scheeri* and *C. poselgeriana* were classified correctly 100 percent. Of the 149 individuals of *C. robustispina* ssp. *uncinata*, 5 (3.4%) were misclassified as *C. robustispina* ssp. *robustispina* and 4 (2.7%) were misclassified as *C. robustispina* ssp. *scheeri*. Of the 104 individuals of *C. robustispina* ssp. *robustispina*, 5 (4.8%) were misclassified as *C. robustispina* ssp. *uncinata* and 3 (2.9%) were misclassified as *C. robustispina* ssp. *scheeri.* When individuals of the three supplementary sites (those of intermediate geography between *C. robustispina* ssp. *uncinata* and *C. robustispina* ssp. *robustispina*, were left ungrouped, 49 (98%) of the individuals are classified as *C. robustispina* ssp. *uncinata* and 1 (2%) was classified as *C. robustispina* ssp. *scheeri.* In other words, none of the individuals of *C. robustispina* ssp. *uncinata* within populations closest to those of *C. robustispina* ssp. *robustispina* were classified as *C. robustispina* ssp. *robustispina*.

Table 6. Classification Results of DA: Predicted Group Membership. Wilks' lambda = 0.01, Approx. F = 162.3

TAXON	*C. robustispina* ssp. *uncinata*	*C. robustispina* ssp. *robustispina*	*C. robustispina* ssp. *scheeri*	*C. poselgeriana*
C. robustispina ssp. *uncinata*	140	5	4	0
C. robustispina ssp. *robustispina*	5	96	3	0
C. robustispina ssp. *scheeri*	0	0	96	0
C. poselgeriana	0	0	0	96
C. robustispina ssp. *uncinata*	94.0%	3.4%	2.7%	0%
C. robustispina ssp. *robustispina*	4.8%	92.3%	2.9%	0%
C. robustispina ssp. *scheeri*	0%	0%	100.0%	0%
C. poselgeriana	0%	0%	0%	100.0%

Discussion and Conclusions

Results indicate that among the various classifications of Section Robustispina, Taylor's treatment best reflects the degree of morphological variation between populations as compared to that among populations. All four taxa, as far as we know, are allopatric with good to excellent morphological separation among them. DA correctly classified individuals 97 percent, ranging from 92.3 percent to 100 percent.

Individuals defined *a priori*i as *C. poselgeriana* formed a morphologically discrete group. The second factor of the PCA, which accounted for a large portion of the total variation (22.9%), was almost wholly dedicated to differences between individuals of *C. poselgeriana* and those of the other three taxa. Furthermore, all of the individuals within populations identified *a priori*i as *C. poselgeriana* were correctly classified and none of the individuals from other taxa were misclassified as *C. poselgeriana*. Except for radial spine number, which was not significant from that of *C. robustispina* spp. *robustispina* and central spine curvature, which was not significantly different from that of *C. robustispina* spp. *scheeri*, overall values of all characters for *C. poselgeriana* were significantly different from those of the other taxa. These data indicate that *C. poselgeriana* belongs as a species separate from the remaining taxa.

Individuals of *C. robustispina* spp. *scheeri* formed a morphologically coherent group. The first factor of the PCA indicated that 35.5 percent of the total variation among all of the individuals measured was best explained by differences between individuals of *C. robustispina* spp. *scheeri* and those of the other two subspecies. Individuals within *a priori*i populations of *C. robustispina* spp. *scheeri* were classified correctly 100 percent and individuals within populations of the other two subspecies were misclassified as *C. robustispina* spp. *scheeri* less than 3 percent. The only character not significantly different between *C. robustispina* spp. *scheeri* and its geographically closest relative, *C. robustispina* spp. *uncinata*, was number of radial spines. These data, combined with geographic data, indicate that *C. robustispina* spp. *scheeri* deserves taxonomic recognition and may be worthy of specific status.

The two groups of individuals defined *a priori* as *C. robustispina* ssp. *uncinata* and *C. robustispina* ssp. *robustispina* were the least separate morphologically, especially with respect to one another. Some of the statistical fuzziness can be attributed to the much greater morphological variation among individuals of these two taxa. The two groups each possessed the highest standard deviations for five characters, *C. poselgeriana* possessed the highest for three, and *C. robustispina* spp. *scheeri* for none. Although PCA did not indicate that all individuals between the two taxa were morphologically discrete, there was an indication that individuals closest geographically were. Although, this does not necessarily evidence characters displacement, it does weaken the assumption that the two groups form a morphological/geographical cline. DA misclassified individuals between *C. robustispina* ssp. *uncinata* and *C. robustispina* ssp. *robustispina* only 0.4 percent, which is low by standards for subspecific taxa within the Cactaceae (Baker & Johnson 2000). At present, the two taxa can be separated taxonomically by geographic range and by all

non-age-dependent characters except for central spine curvature and radial spine length.

The preliminary results herein indicate that all of four of the groups are taxonomically valid. Once morphological differences are discovered, they cannot be taken away, unless additional individuals, most likely from additional populations, are measured and found to be morphologically intermediate. With further study, it is likely that populations of *C. robustispina* spp. *scheeri* will be re-elevated to species rank. Putative morphological intermediates between *C. robustispina* spp. *scheeri* and *C. robustispina* spp. *uncinata* (A. Zimmerman, pers. comm. 2004) should be investigated with respect to their occurrence, geographical extent and population densities. The taxonomic relationship between *C. robustispina* spp. *robustispina* and *C. robustispina* spp. *uncinata* is complicated by the large amount of morphological variation within each group. Although no populations are known that are both geographically and morphologically intermediate between the two taxa, more consistently diagnostic characters will need to be discovered before elevating the two groups taxonomically.

The use of only stem characters for this study does not weaken the taxonomic findings herein. The measurement of additional characters, however; such as those associated with other stem characters, including extra-floral nectaries; flowers; fruits; and genetic markers; may strengthen the taxonomic validity of the taxa considered.

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