

Morphometric Analysis of *Escobaria sneedii* var. *sneedii*, *E. sneedii* var. *lei*, and *E. guadalupensis* (Cactaceae)

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ABSTRACT. We used discriminant analysis to assess taxonomic status of three closely related, rare taxa within the cactus genus *Escobaria* (*E. guadalupensis*, *E. sneedii* var. *sneedii*, and *E. sneedii* var. *lei*). These three taxa consist of nine isolated populations; six of these populations consist of morphologically typical specimens (i.e., similar to the type specimen), while three populations are of questionable taxonomic status. We used the six morphologically typical populations (referred to as assigned populations) to derive predictive discriminant functions for each taxon. These discriminant functions were then applied to assigned populations to determine the status and taxonomic boundaries of each taxon, and to the three questionable populations (referred to as unassigned populations) to interpret their taxonomic status. Our model included four predictor variables: number of immature stems, mature stem diameter, number of radial spines, and length of the innermost central spines. Discriminant analysis correctly classified >93% of 186 individuals from the six assigned populations, suggesting a distinct status for each taxon. Applying the predictive discriminant functions to unassigned populations resulted in classifying a large percentage of individuals from each unassigned population into each of two taxa. This suggests that the unassigned populations consist of morphological intermediates, possibly as the result of hybridization. Meiotic chromosome numbers of $n = 11$ were determined for *E. guadalupensis*, *E. sneedii* var. *lei*, and the three unassigned populations.

Despite cacti being a dominant and conspicuous floral component in deserts of the Western Hemisphere, the taxonomy of most genera remains unstable because of complicating factors that include hybridization, disjunct distributions, polyploidy, and apogamy (Grant and Grant 1971; Pinkava and McGill 1979; Pinkava et al. 1985; Trushell 1985; Zimmerman 1985; Baker and Pinkava 1987; Pinkava et al. 1999). These complicating factors often result in complex taxonomic issues that are difficult to resolve using descriptive morphology and classical taxonomy, the approaches typically used for studies in the Cactaceae. In contrast, multivariate statistical analyses have proven valuable in assessing taxonomic status of many plant taxa (Pimentel 1979; Reyment et al. 1984; James and McCulloch 1990; Dibble et al. 1998; Hess and Stoyloff 1998), but have been used rarely for cacti (Trushell 1985; Baker and Pinkava 1987; Chamberland 1997).

For this study, we used discriminant analysis to examine phenetic relationships among three rare cacti in the genus *Escobaria* Britton & Rose: *E. guadalupensis* S. Brack & K. Heil, *E. sneedii* Britton & Rose var. *sneedii*, and *E. sneedii* var. *lei* (Rose ex Bödeker) D. Hunt. All three taxa are poorly defined

but each includes isolated populations that consist of morphologically typical individuals (i.e., similar to the type specimen). Several additional populations have a questionable taxonomic status as they have been considered intermediates between or combinations of the three study taxa. The two-fold purpose of this study is (1) to determine the appropriateness of the taxonomic status previously given to populations of morphologically typical individuals (hereafter, referred to as assigned populations), and (2) to determine the status of populations whose taxonomy is in question (hereafter, referred to as unassigned populations). Our approach uses assigned populations to derive predictive discriminant functions to predict group membership for each of the three taxa (Williams 1983). We then apply the discriminant functions to assigned populations to determine the status and taxonomic boundaries of each taxon, and to unassigned populations to interpret their taxonomic status.

The Species. The genus *Escobaria* [sometimes considered a subgenus of *Coryphantha* (Engelm.) Lem. (Benson 1982; Zimmerman 1985)] consists of about 35–40 small single- to multi-stemmed pin-cushion cacti. The genus is largely restricted to de-

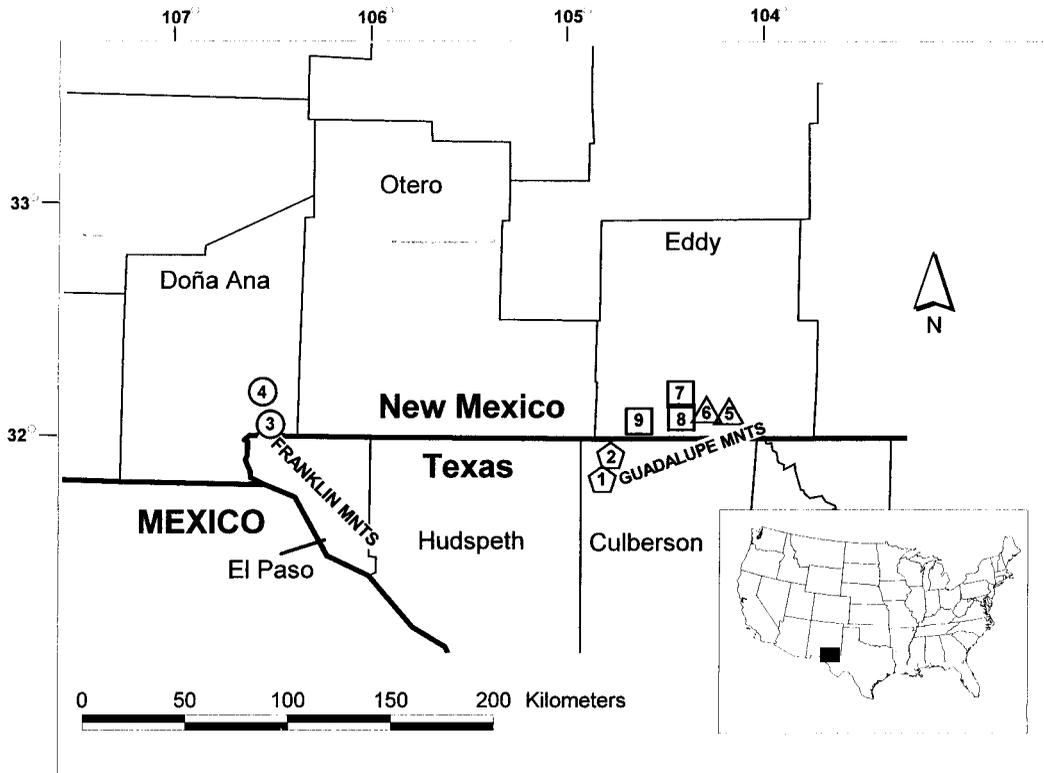


FIG. 1. Locations of study populations of *Escobaria* in the Franklin Mountains and Guadalupe Mountains, NM and TX: *E. guadalupensis* (pentagon); *E. sneedii* var. *sneedii* (circle); *E. sneedii* var. *leei* (triangle); unassigned populations, i.e., those with a questionable taxonomic status (square). The number within each symbol corresponds to those given under locale in Table 1. State boundaries and names are in bold font; county boundaries and names are in normal font.

sert and grassland habitats of the western and central United States and northern Mexico. In the broad sense, *E. sneedii* includes approximately nine varieties that are characterized by large druses, a pith with no medullary system, and central spines that radiate from the areole in a symmetrical and evenly spaced pattern (Zimmerman 1985). Based on these characters, *E. guadalupensis* is a closely related, possibly sister taxon, that differs from *E. sneedii* in lacking numerous immature stems (A. Zimmerman, pers. comm.).

The three taxa considered here, *E. guadalupensis*, *E. sneedii* var. *sneedii*, and *E. sneedii* var. *leei*, are restricted to areas in and adjacent to the Franklin and Guadalupe Mountains, Texas and New Mexico (Fig. 1). No other varieties of *E. sneedii* or closely related taxa are known to occur in this area. Overall, these three taxa consist of nine populations, all of which occur on limestone substrates (Benson 1982; Heil and Brack 1986). In all of these populations, individuals are scattered and occur at low densities.

Consequently, several of these populations are somewhat diffuse and include individuals from nearby areas. Each of the three taxa is currently known from two populations that are considered to be relatively well defined and similar to the type specimen (i.e., assigned populations). *Escobaria sneedii* var. *sneedii* occurs as two isolated populations in the vicinity of the Franklin Mountains at elevations < 1500 m; the nearest populations of closely related taxa occur about 200 km to the east in the Guadalupe Mountains (Fig. 1). Populations of the other two taxa, *E. guadalupensis* and *E. sneedii* var. *leei*, are restricted to the western and northeastern portions of the Guadalupe Mountains, respectively (Fig. 1). Populations of the two taxa are separated by 50–70 km. Populations of *E. guadalupensis* mostly occur at elevations above 1900 m, while those of *E. sneedii* var. *leei* mostly occur below 1400 m. Three additional populations of questionable taxonomic status (i.e., unassigned populations), occur in the Guadalupe Mountains. All three populations are located

TABLE 1. Location of study populations. Unassigned populations are those of questionable taxonomic status (see text). Under locale, GM = Guadalupe Mountains; FM = Franklin Mountains; numbers in parentheses correspond to those used to designate the study sites in Figs. 1 and 3. For collector, MAB = Marc A. Baker; ADZ = Allan D. Zimmerman; DAZ = Dale A. Zimmerman. N is the sample size for each population.

Taxon	Locale	N	Latitude, longitude	Elevation (m)	Collector & number
<i>E. guadalupensis</i>	Guadalupe Peak; Pine Spring Canyon; Bear Canyon; GM, TX (1)	33	31° 54'N, 104° 51'W	1900– 2650	MAB 13086, 13094, 13322
	Lost Peak; GM, TX (2)	30	31° 58'N, 104° 50'W	2350	MAB 13321
<i>E. sneedii</i> var. <i>sneedii</i>	Anthony Gap; FM, NM (3)	53	32° 00'N, 106° 30'W	1300	MAB 13102, 13323.2; DAZ 2810, 2105
	Bishop's Cap; FM, NM (4)	9	32° 11'N, 106° 35'W	1450	DAZ 2725
<i>E. sneedii</i> var. <i>lei</i>	Walnut Canyon (east); GM, NM (5)	31	32° 10'N, 104° 29'W	1350	MAB 13076
	Walnut Canyon (west); GM, NM (6)	30	32° 10'N, 104° 30'W	1400	MAB 13316
Unassigned populations	Rattlesnake Canyon; GM, NM (7)	45	32° 10'N, 104° 31'W	1400	MAB 13318, ADZ 1457
	Yucca Canyon; GM, NM (8)	46	32° 06'N, 104° 37'W	1800	MAB 13070, 13315.1
	Cottonwood Canyon; GM, NM (9)	38	32° 05'N, 104° 43'W	1950	MAB 13319, 13320, 13320.1

at sites intermediate in both elevation and geography to the populations of *E. guadalupensis* and *E. sneedii* var. *lei*. These three unassigned populations have been referred to as a combination of *E. sneedii* var. *sneedii* and *E. sneedii* var. *lei* (Heil and Brack 1985, 1986), and as intermediates between *E. guadalupensis* and *E. sneedii* var. *lei* (A. Zimmerman, pers. comm.).

Among the unassigned populations, Rattlesnake Canyon is problematical because this is the type locality for *E. sneedii* var. *lei*. The paradox of this site being the type locality as well as being designated as an unassigned population results from the high degree of morphological variability among individuals at Rattlesnake Canyon, with the type specimen representing an atypical individual in the population. In contrast, individuals from the two assigned populations of *E. sneedii* var. *lei* in Walnut Canyon are morphologically similar to the type specimen (A. Zimmerman, pers. comm.).

Chromosome number determinations in the *E. sneedii* complex have all been diploid ($n = 11$) (Weedin and Powell 1978; Pinkava et al. 1985; Zimmerman 1985; Weedin et al. 1989). Among our three study taxa, chromosome number has been determined only for *E. sneedii* var. *sneedii*.

MATERIALS AND METHODS

Study Populations. We examined morphometrics for all nine known populations (six assigned and three unassigned) of *E. sneedii* var. *sneedii*, *E. sneedii* var. *lei*, and *E. guadalupensis* (Fig. 1, Table 1). The six assigned populations included two populations for each of the three taxa. The three unassigned populations were located in Cottonwood, Yucca, and Rattlesnake Canyons, all in the Guadalupe Mountains; the latter population occurred within two km of the assigned population of *E. sneedii* var. *lei* at Walnut Canyon (Fig. 1). Within each population, individuals were sampled from an area of about 1–2 km². The only exception was Guadalupe Peak, where there were few individuals of *E. guadalupensis*. Consequently, individuals from two proximate sites, Bear Canyon and Pine Spring Canyon, were also included in this population.

Habitat for the two populations of *E. guadalupensis* and the unassigned population at Cottonwood Canyon consisted of Madrean evergreen woodland (Brown 1982a). Dominant plants included *Agave neomexicana* Woot. & Standl., *Cercocarpus montana* Raf., *Juniperus deppeana* Steud., *Nolina micrantha* I.M. Johnst., *Pinus edulis* Engelm., and *Quercus pauciloba* Rydb. All other sites were open Chihuahuan de-

TABLE 2. Taxonomic characters (Zimmerman 1985) that were assessed for their utility in conducting a morphometric analysis of *Escobaria*. The four characters in bold type were used in our analyses.

Taxonomic character
1. Number of immature stems
2. Number of mature stems
3. Mean diameter of mature stems
4. Mean length of innermost central spines
5. Number of radial spines
6. Maximum length of mature stem
7. Color of radial spines
8. Color of central spines
9. Color of spine tips
10. Distribution of dark spine tips
11. Spine pubescence
12. Radial spine appression
13. Central spine appression
14. Number of innermost central spines
15. Number of radiating central spines
16. Minimum length of radiating central spines
17. Maximum length of radiating central spines
18. Location of longest radial spine
19. Maximum length of radial spines
20. Total number of radial and central spines

serts scrub habitat (Brown 1982b), with dominant species including *Agave lechuguilla* Torr., *Berberis trifoliolata* Moric., *C. montanus*, *J. coahuilensis* (Martinez) Gaussen, and *Q. pauciloba*.

Morphological Characters. Field measurements are essential for morphometric studies of Cactaceae because few herbarium specimens are available and morphology is difficult to preserve on these specimens. Although field measurement of numerous characters for numerous individuals may be statistically ideal (James and McCulloch 1990), time constraints necessitated our choosing between sampling either numerous characters on few individuals or few characters on numerous individuals. We chose the latter route so as to maximize statistical power, with the goal being to select independent, quantitative characters that describe the morphology of both stems and spines. Characters were chosen from among those used in the most recent taxonomic revision of *Escobaria* (Zimmerman 1985) (Table 2). Character selection first involved omitting qualitative characters such as color because of difficulty in coding. Additionally, only one quantitative character was selected when two or more characters were likely correlated (e.g., minimum and maximum spine length, and number of mature and immature stems) or dependent (e.g., number of ra-

dial spines and total number of radial and central spines). The four remaining characters were number of immature stems, mature stem diameter, number of radial spines, and length of the innermost central spines. Consequently, we included one continuous and one discrete character for both stems and spines.

We tested the utility of these four characters for separating the three taxa using a multivariate analysis of variance (MANOVA). This preliminary analysis included 98 individuals sampled from five of the six assigned populations (N = 49 provided by A. Zimmerman and N = 49 collected by the authors during late 1998). The MANOVA demonstrated that all four characters varied significantly among the three taxa. For our final analysis, we collected data on these four characters from 224 additional individuals in June 1999 (N = 9–54 per population) (Table 1). Thus, our total sample size was 322 individuals. For the *E. sneedii* var. *sneedii* population at Bishop's Cap, we used only data provided by A. Zimmerman because additional individuals could not be located during field surveys. Consequently, the sample size for this population was low (N = 9).

Measurements were collected from mature individuals (i.e., those having stems with areolar grooves or evidence of previous reproduction). Although stem diameters of cacti vary with water content (Went 1982; Johnson et al. 1993), such variation is low within the *E. sneedii* complex (A. Zimmerman, pers. comm.). One mid-height diameter was recorded for all mature stems on each individual; the mean value was used in analyses. Immature stems were counted. Five mature areoles were removed from near the apex of each individual. On each areole, radial spines were counted and length of all innermost central spines was measured using an ocular micrometer at 10 under a binocular microscope. For both measures, we used the mean of the five areoles on each individual. Voucher specimens were deposited at Arizona State University and Guadalupe Mountains National Park (Table 1).

Data Analysis. The four dependent variables were tested using the MANOVA procedure in SPSS (SPSS 1990). Data were transformed, as necessary, to meet the assumptions of MANOVA. At least one variable did not meet homogeneity of variance assumptions after various transformations. Seven outlier observations were deleted to meet this assumption. The assumption of homogeneity of covariance matrices could not be met (Box's M test, $P = 0.002$).

Discriminant analysis was then performed on the

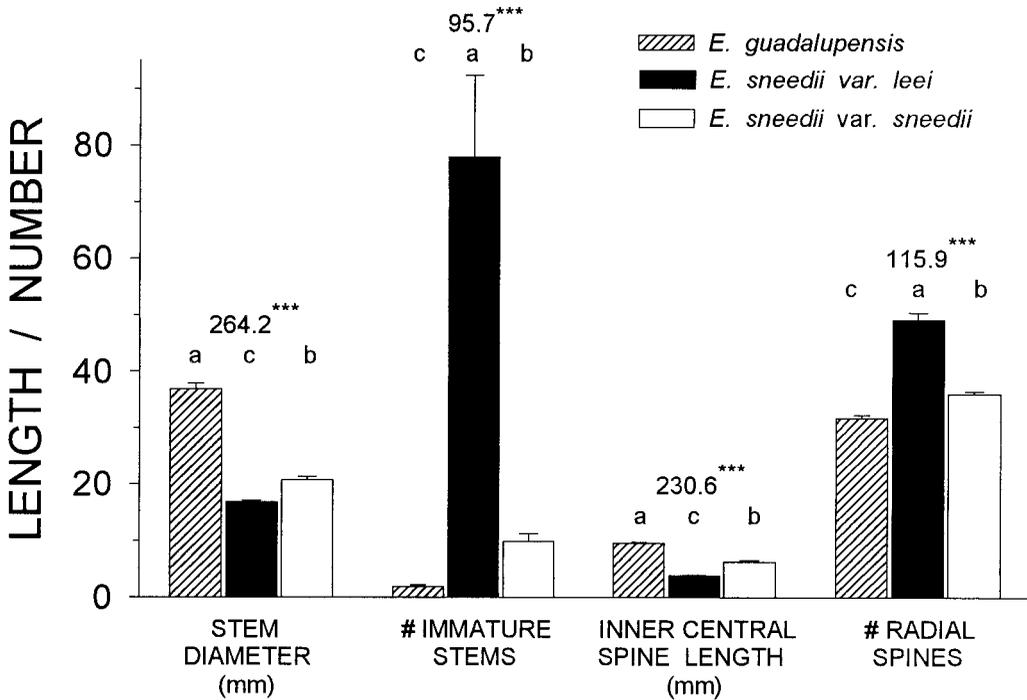


FIG. 2. Morphological variables (means ± 1 SE) used to analyze variation in *Escobaria guadalupensis*, *E. sneedii* var. *leei*, and *E. sneedii* var. *sneedii*. F values and significance levels above each variable were obtained from a MANOVA: *** = $P < 0.001$. Significant differences among taxa are based on an *a posteriori* Duncan's multiple range test ($P < 0.05$), and are given for each variable by the letters a, b, c: $a > b > c$.

same data set using *a priori* classification for assigned populations of the three taxa. This model assumes each population is discrete (i.e., all individuals at each locale comprise one taxon). The discriminant analysis (SPSS 1990) developed predictive discriminant functions for these taxa, which were applied to individuals in each assigned and unassigned population during the same execution. The four predictor variables were entered simultaneously using taxon as the grouping variable. The model used equal prior probabilities for groups when classifying individuals.

Chromosome Determinations. Flower buds were fixed in Carnoy's solution (3:1 mix of 95% ethanol: glacial acetic acid) and transferred to 70% ethanol after 24 h. Fixed anthers were squashed, stained in acetocarmine, mounted in Hoyer's medium, and counted (Pinkava and Baker 1985).

RESULTS

Morphometric Analyses. Multivariate analysis indicated that the three taxa differed significantly in respect to morphology (Wilks' lambda = 0.11; F

= 90.7; df = 8, 360; $P << 0.001$). All four variables differed significantly among the three taxa (Duncan's multiple range test, $P < 0.05$; Fig. 2). The discriminant functions correctly classified 93.5% of the individuals from assigned populations (Table 3; Fig. 3). Additionally, the mean probability of correct classification exceeded 90% for correctly classified individuals. As expected, correct classification was most effective for *E. guadalupensis* (100% of the individuals were correctly classified), while misclassifications were more common for the other taxa (Table 3; Fig. 3). The standardized coefficients of the canonical functions indicate the four predictor variables contributed similarly to discriminant function one. Mature stem diameter and length of the innermost central spines were the largest contributors to discriminant function two (Table 4).

The discriminant functions were then used to predict group membership for individuals from the three unassigned populations (Table 5). Two of these populations (Rattlesnake and Yucca Canyons) yielded similar results: over 60% of the individuals in both populations were classified as *E. sneedii* var.

TABLE 3. Summary classification of predicted group membership for assigned populations of *Escobaria sneedii* var. *sneedii*, *E. sneedii* var. *leei*, and *E. guadalupensis*, using discriminant analysis. Values are number (percent) of original grouped cases correctly classified. Seven outlier observations were omitted from this analysis in order to meet the assumption of homogeneity of variances. *Probability of correct classification for original grouped cases that were correctly classified.

Taxon	Predicted group membership			Total correct	Probability*
	<i>E. sneedii</i> var. <i>sneedii</i>	<i>E. sneedii</i> var. <i>leei</i>	<i>E. guadalupensis</i>		
<i>E. sneedii</i> var. <i>sneedii</i>	54 (87.1)	5 (8.1)	3 (4.8)	54/62 (87.1)	0.90
<i>E. sneedii</i> var. <i>leei</i>	4 (6.6)	57 (93.4)	0 (0.0)	57/61 (93.4)	0.93
<i>E. guadalupensis</i>	0 (0.0)	0 (0.0)	63 (100.0)	63/63 (100.0)	0.96
Total				174/186 (93.5)	

leei and the remaining individuals (with one exception from Yucca Canyon) were classified as *E. sneedii* var. *sneedii*. For Cottonwood Canyon, just over 70% of the individuals were classified as *E. sneedii* var. *sneedii* with the remainder classified as *E. guadalupensis*. The discriminant scores of individuals from Rattlesnake and Yucca Canyons overlapped with or were intermediate between *E. sneedii* var.

sneedii and *E. sneedii* var. *leei*, while most of those from Cottonwood Canyon were intermediate between *E. sneedii* var. *sneedii* and *E. guadalupensis* (Fig. 4).

Chromosome Determinations. Meiotic chromosome determinations of $n = 11$ were made for *E. guadalupensis* ($N = 1$ at Lost Peak), *E. sneedii* var. *leei* ($N = 1$ at each Walnut Canyon population), and

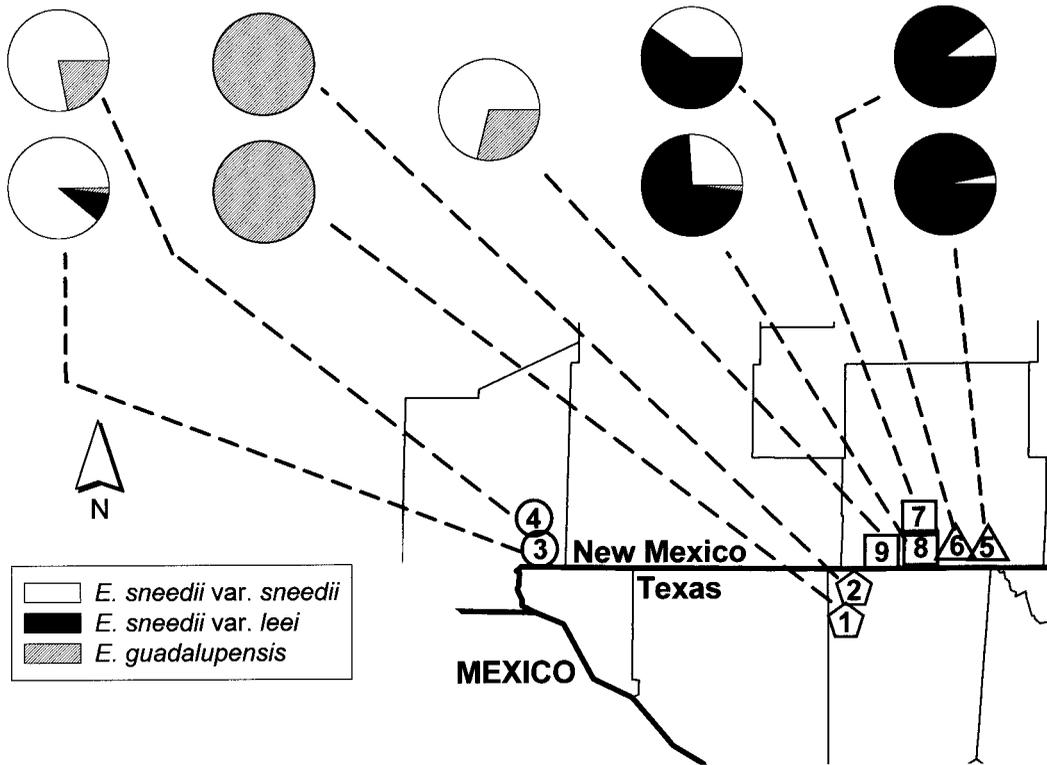


FIG. 3. Summary classification of predicted group membership for individuals in each of the nine populations of *Escobaria*. The pie charts illustrate the proportion of individuals placed into each of the three taxa. The number within each symbol corresponds to the location of each population as given in Fig. 1 and under locale in Table 1.

TABLE 4. Standardized coefficients for canonical discriminant functions for assigned populations of *Escobaria sneedii* var. *sneedii*, *E. sneedii* var. *lei*, and *E. guadalupensis*.

Predictor variable	Function 1	Function 2
Number of immature stems	-0.33	0.29
Mature stem diameter	0.53	0.99
Length of innermost central spines	0.40	-0.80
Number of radial spines	0.50	-0.09

in each of the three unassigned populations (N = 1 per site).

DISCUSSION

Classification of the Study Taxa. Discriminant analysis correctly predicted group membership for >93% of all individuals in the six assigned populations, thus providing the resolution necessary to classify individuals within the three unassigned populations. This resolution was achieved by using a sampling regime designed to minimize classification error, especially given the expectation of small group differences (Williams and Titus 1988; Williams et al. 1990). Consequently, a small number of variables was measured on numerous individuals of the three taxa, with an overall ratio of sample size to the number of variables of 46.5:1. In contrast to previous morphometric treatments within Cactaceae that included numerous characters (Trushell 1985; Zimmerman 1985; Baker and Pinkava 1987; Chamberland 1997), we achieved taxonomic separation using a few easily measured quantitative characters.

Predicted group membership from the discriminant analysis allows reassessing taxonomic status of these three *Escobaria* taxa. Correct classification for all individuals of *E. guadalupensis* indicates this taxon is morphologically distinct from the other two, suggesting it should be retained at the species level. The two varieties of *E. sneedii* were distinct, but the percentage of misclassified individuals (7–13%; Table 3; Fig. 3) suggests a closer taxonomic relationship. We thus retain their varietal status.

Applying the discriminant functions derived from the assigned populations to unassigned populations resulted in placing a large percentage of individuals from each unassigned population into each of two taxa (Fig. 3). Such classification, relative to that for assigned populations of the three taxa, suggests that unassigned populations consist of

TABLE 5. Summary classification of predicted group membership for individuals in three unassigned populations of *Escobaria*, i.e., those with a questionable taxonomic status. Group membership is predicted from the canonical discriminant functions derived from assigned populations of *E. sneedii* var. *sneedii*, *E. sneedii* var. *lei*, and *E. guadalupensis*, using discriminant analysis. Values are number (percent) of individuals.

Location	Predicted group membership			Total
	<i>E. sneedii</i> var. <i>sneedii</i>	<i>E. sneedii</i> var. <i>lei</i>	<i>E. guadalupensis</i>	
Cottonwood Canyon	27 (71.1%)	0 (0.0%)	11 (28.9%)	38
Yucca Canyon	12 (26.1%)	33 (71.7%)	1 (2.2%)	46
Rattlesnake Canyon	18 (40.0%)	27 (60.0%)	0 (0.0%)	45
Total	57 (44.2%)	60 (46.5%)	12 (9.3%)	129

morphological intermediates, possibly as the result of hybridization. Hybridization is common among homoploid cactus species (Grant and Grant 1971; Pinkava and McGill 1979; Trushell 1985; Baker and Pinkava 1987; Pinkava et al. 1999) and seems likely among these taxa given the apparent absence of reproductive barriers; flower morphology, color, and phenology are similar, and all individuals examined thus far have been diploid. Based on our findings, the unassigned population in Cottonwood Canyon appears intermediate between *E. guadalupensis* and *E. sneedii* var. *sneedii*, and the unassigned populations at Rattlesnake and the Yucca Canyons appear to be intermediate between *E. sneedii* var. *lei* and *E. sneedii* var. *sneedii*. These conclusions differ from those of previous authors, who identified plants in the Cottonwood Canyon population as *E. sneedii* var. *sneedii* (Heil and Brack 1986) or as intermediate between *E. guadalupensis* and *E. sneedii* var. *lei* (A. Zimmerman, pers. comm.). Plants within Rattlesnake and Yucca Canyons were previously identified as *E. sneedii* var. *sneedii* (Heil and Brack 1985), and as *E. sneedii* var. *lei* (Zimmerman 1985).

One potential problem with our analysis is that predictive discriminant analysis forces membership of unassigned populations into one of the three assigned taxa. Because this technique forces group membership, it typically is used to classify individuals according to sex or some similar variable where all possible groups of membership are known *a priori*. For this study, we believe that all potential groups of membership (taxa) are included for two reasons. First, no other varieties of *E. sneedii* or closely related taxa occur in or near our study

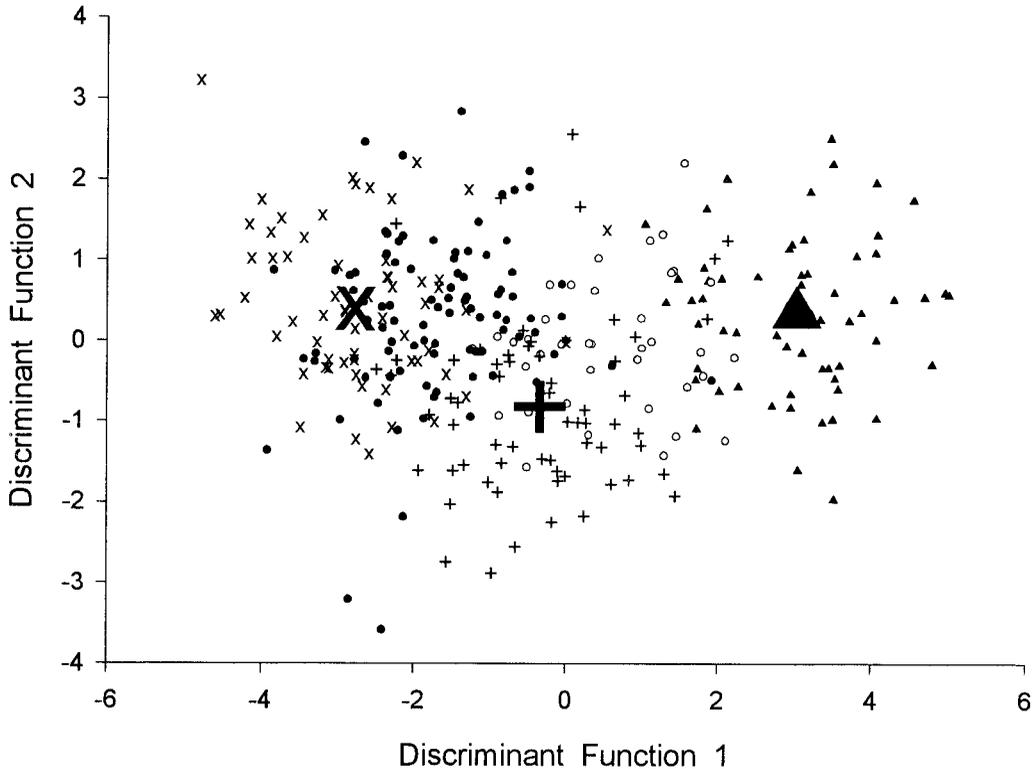


FIG. 4. Discriminant scores for individuals of *Escobaria guadalupensis* (▲), *E. sneedii* var. *sneedii* (+), and *E. sneedii* var. *lei* (×) and unassigned populations at Rattlesnake and Yucca Canyons (pooled)(●) and Cottonwood Canyon (○). The scores of all individuals are projected onto the two-dimensional space defined by discriminant functions one and two. The larger symbols are the unstandardized canonical discriminant functions evaluated at the group means (centroids).

populations, and second, all unassigned populations had previously been referred to as some combination of the assigned taxa (see above).

Biogeography and History. A biogeographical feature that is common to many cacti of the Chihuahuan Desert, including the three *Escobaria* in this study, is the occurrence of disjunct populations and narrow endemics (Hernandez and Barcenas 1995). Such geographically isolated populations result from (1) long-distance dispersal to isolated suitable habitats (suggesting that much of the intervening habitat is unsuitable) or (2) range contraction in species that were previously more geographically widespread, but have since gone extinct in portions of their range (Gibson and Nobel 1986; Brown and Lomolino 1998). Long-distance dispersal, especially via birds or bats, occurs in other cacti (Steenbergh and Lowe 1977), but its role in these three *Escobaria* is unclear. The isolated low-density populations along with the fact that the fruits mature in early summer and are largely gone by late

summer, suggest a minor role for long-distance dispersal because the fruits would be largely unavailable to fall migrating birds. In regard to geographic ranges, recent analysis of cacti in the Chihuahuan Desert demonstrates that (1) species richness is much higher at moderate elevations than in hot, dry desert areas, and (2) many rare cacti (including the three *Escobaria* in this study) are now restricted to these more moderate mid-elevation habitats (Hernandez and Barcenas 1995). Historically, these more moderate habitats were much more widespread in the Chihuahuan Desert, but are now localized as a result of increasing aridity over the last 10,000–20,000 years (Axelrod 1979; Van Devender 1990). This increasing aridity would also adversely affect cactus because the local geographic distribution of many species is limited by low precipitation (Jordan and Nobel 1981, 1982). Consequently, we favor the hypothesis that these three *Escobaria* consist of relict populations that are remnants of more widespread geographic ranges. This hypothesis could be

tested by assessing the role of various abiotic factors in limiting distribution of these three *Escobaria*. For example, a two-factor experiment (moisture level x soil type) could compare germination and survival across several moisture regimes that include a range of soils on which a species does and does not occur.

If populations of these taxa were much more widespread historically, then an alternative taxonomic scenario might be that *E. sneedii* var. *leei*, *E. sneedii* var. *sneedii*, and the unassigned populations classified as a combination of these two taxa represent a geographic cline of one morphologically variable taxon. With many populations in the cline now extinct, the extant populations would be morphologically distinct. The large percentage of individuals classified as *E. sneedii* var. *sneedii* at Cottonwood Canyon, which is more proximate to populations of both *E. guadalupensis* and *E. sneedii* var. *leei*, would argue against this hypothesis, thus favoring the idea that these two varieties are morphologically distinct. The large influence of *E. sneedii* var. *sneedii* in this population also supports the argument that this taxon was more widespread historically.

An alternative evolutionary scenario is that *E. sneedii* var. *sneedii* results from hybridization between *E. sneedii* var. *leei* and *E. guadalupensis*. Our morphological data support this hypothesis as the discriminant scores clearly separate the three taxa, with *E. sneedii* var. *sneedii* occupying an intermediate position (Fig. 4). Furthermore, values for all four morphological variables for *E. sneedii* var. *sneedii* are intermediate to those of the other two taxa (Fig. 2). From a biogeographic perspective, however, the hybrid origin of *E. sneedii* var. *sneedii* could only have occurred if the two parental taxa were previously more widespread and sympatric. Assuming this was the case, then the present geographic separation of *E. sneedii* var. *sneedii* from the other two taxa could have resulted from (1) geographic isolation as the populations of all three taxa retreated or (2) that changing climatic conditions effected differential survival of the taxa across a longitudinal gradient. Overall, the morphological evidence supports the hypothesis that *E. sneedii* var. *sneedii* results from hybridization between *E. sneedii* var. *leei* and *E. guadalupensis*, while the biogeographic data are less convincing. Determining the phylogenetic relationships of these three taxa would probably be best resolved using DNA sequence data that includes all closely related taxa and at least one out-group taxon.

At present, *E. guadalupensis* appears to be isolated from the other two taxa by its occurring at higher elevations (Table 1). Interestingly, the unassigned populations at Yucca Canyon and especially Cottonwood Canyon are more proximate to and occur at elevations similar to those occupied by *E. guadalupensis* (> 1850 m). Yet, most individuals in both populations were classified as *E. sneedii* var. *sneedii*, and relatively few individuals were classified as *E. guadalupensis*. The cause for the low influence of *E. guadalupensis* in these populations is unclear. One potential explanation is that the more distant taxonomic relationship between *E. guadalupensis* and *E. sneedii* than between the two varieties of *E. sneedii* results in lower viability between crosses of the former pair of taxa. In contrast, the unassigned population at Rattlesnake Canyon occurred at elevations similar to those occupied by *E. sneedii* var. *sneedii* and *E. sneedii* var. *leei* (< 1400 m), and showed no influence of *E. guadalupensis*.

Overall, discriminant analysis provided a powerful tool for assessing the phenetic relationships among closely related and morphologically similar taxa. Such analyses should be expanded to the entire *E. sneedii* complex or applied to other groups of cacti in which hybridization and morphological similarity result in questionable taxonomic status. This method should also be useful for evaluating the status of as yet unknown populations of these three *Escobaria* taxa.

TAXONOMY

Based on our analyses, the following key will identify populations of these three *Escobaria*. Note, however, additional populations may be located, and these are likely to display a high degree of morphological variability among individuals or consist of individuals with morphological characters that are intermediate to some combination of these three taxa. Consequently, at least several individuals should be used to identify these populations.

- A- Mature individuals mostly with more immature stems than mature stems; average length of innermost central spines < 8 mm; average mature stem diameter < 30 mm B
- AA- Mature individuals rarely with more immature stems than mature stems; average length of innermost central spines > 9 mm; average mature stem diameter > 35 mm *E. guadalupensis*
- B- Average length of innermost central spines <

- 5 mm; number of radial spines > 40
 *E. sneedii* var. *leei*
 BB- Average length of innermost central spines >
 5 mm; number of radial spines < 40
 *E. sneedii* var. *sneedii*

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