Further Elucidation of the Taxonomic Relationships and Geographic Distribution of *Escobaria sneedii* var. *sneedii*, *E. sneedii* var. *leei*, and *E. guadalupensis* (Cactaceae)

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ABSTRACT. Individuals of *E. sneedii* var. *sneedii* were found to occur in greater abundance within the Guadalupe Mountains than was previously recorded. No additional populations morphologically intermediate between *E. guadalupensis* and *E. sneedii* were found. Taxonomic affiliation and geographic distribution among three *Escobaria* taxa were readdressed with phenetic analyses. Principle components analysis (PCA) showed moderate resolution between individuals representing *E. guadalupensis* and *E. sneedii*. Resolution was poor between those of *E. sneedii* var. *sneedii* and *E. sneedii* var. *leei*. Results from discriminant analysis (DA) correctly classified individuals within populations of *E. guadalupensis*, *E. sneedii* var. *sneedii* and *E. sneedii* var. *leei* 100, 79.6, and 86.4 percent, respectively. The taxonomic recognition of *E. sneedii* var. *leei*, as separate from *E. sneedii* var. *sneedii* is tenuous.

INTRODUCTION

Escobaria sneedii Britton & Rose and its relatives are endemic to various isolated mountain ranges of the Chihuahuan Desert. They are popular in horticulture because their diminutive size and cold-tolerance. Two taxa, *E. sneedii* var. *sneedii* and *E. sneedii* var. *leei* (Rose *ex* Bödecker) D. R. Hunt are given special status legal protection by the United States Government. *Escobaria sneedii* var. *sneedii* is listed as Endangered and *E. sneedii* var. *leei* is listed as Threatened (U. S. Fish & Wildlife Service 1993).

According to Benson (1982), *Escobaria sneedii* includes two varieties, *E. sneedii* var. *sneedii* and *E. sneedii* var. *leei*. Benson's classification is monothetic in nature and his segregation of *E. sneedii* from other species is based on a single unique character: profuse branching of immature stems. Because of the danger in monothetic groups being artificial, especially those relying on a single character (Sneath & Sokal 1973), Zimmerman's (1985) treatment of the *E. sneedii* complex represents a more natural grouping. Using a more polythetic approach, Zimmerman expands this circumscription of *E. sneedii* to include all *Escobaria* with evenly radiating central spines in conjunction with small, cespitose stems that lack a medullary system. In his broader view, he recognizes a total of nine varieties. His classification is based on a number of shared character states and it is unnecessary for any one taxonomic variety to possess any single state. In addition, the classification of any one population may depend on the mean value for some or all character states and some taxa may only be differentiated using a combination of such means. Thus, identification at the varietal level based on a single individual within *E. sneedii* may not always be possible.

Soon after the completion of Zimmerman's monograph, a closely related taxon, *Escobaria guadalupensis* Brack & Heil, was described by Heil & Brack (1986). Heil & Brack (1986) separate *E. guadalupensis* from *E. sneedii* based on its lack of dimorphic, profusely branching stems. In the broad sense of *E. sneedii* (Zimmerman 1985), *E. guadalupensis*, therefore, would not be excluded.

According to Zimmerman (1985, 1993), known populations of *E. sneedii* var. *sneedii* are restricted to the Franklin Mountains area of Texas and New Mexico between El Paso and Las Cruces. All known populations of *E. guadalupensis* occur within a narrow geographical range, mostly at higher elevations, in the Guadalupe Mountains of Texas within the Guadalupe Mountains National Park. All known populations of *E. sneedii* var. *leei* occur at low elevations in the vicinity of Carlsbad Caverns National Park (CCNP), New Mexico. In contrast, Heil and Brack (1985) define the distribution of *E. sneedii* var. *leei* as confined to areas within the eastern half of CCNP and define all related populations within the western half as *E. sneedii* var. *sneedii*. Although they report a small degree of sympatry between the two varieties, they find no evidence for hybridization between the two taxa. They separate the two taxa based on spine orientation, *E. sneedii* var. *leei* having deflexed spines and *E. sneedii* var. *sneedii* having spreading spines. An alternate view suggests (Zimmerman 1993) that differences in morphology among populations of *E. sneedii* within CCNP may due to introgression stemming from hybridization between *E. sneedii* var. *leei* and *Escobaria guadalupensis*, or that these intermediate forms represent ancestral populations from which both *E. sneedii* and *E. guadalupensis* have radiated. The smaller stems and tightly compacted appressed-spines of *E. sneedii* var. *leei*, for instance, could be adaptations to arid conditions at lower elevations and the larger stems, and longer, spreading spines of *E. guadalupensis* may be adaptations to more mesic conditions and differences in herbivore strategy at higher elevations.

Chromosome number determinations have all been diploid (*n*= 11) within the *E. sneedii* complex (Pinkava et al. 1985, Weedin & Powell 1978, Weedin et al. 1989, Zimmerman 1985, Baker & Johnson 2000) and, therefore, polyploidy does not appear to be a genetic barrier.

In light of controversy over the circumscriptions of these taxa, Baker and Johnson (2000) undertook phenetic analyses to elucidate diagnostic characters and to determine the taxonomic status of individuals within three unplaced populations. Discriminant analysis (DA) correctly classified individuals of *E. guadalupensis* 100 percent, while there were more misclassifications for the two varieties of *E. sneedii*. In two of the Guadalupe Mountains populations, about one-third of the individuals were classified as *E. sneedii* var. *sneedii* and about two-thirds as *E. sneedii* var. *leei*. For Cottonwood Canyon West, about 70 percent of the individuals were classified as *E. sneedii* var. *sneedii* and about 30 percent as *E. guadalupensis*. In part, the results of Baker and Johnson (2000) supported Zimmerman's hypothesis that the unidentified populations of *E. sneedii*-related individuals within the Guadalupe Mountains of New Mexico represented intermediates between *E. guadalupensis* and *E. sneedii.*

Individuals of these same populations, however, were morphologically indistinguishable from those 200 km distant and near the type locality of *E. sneedii* var. *sneedii*. Although this scenario may initially seem contradictory to the concept of genetic drift, the lack of morphologic and taxonomic separation owing to geographic isolation is not an unusual phenomenon in evolution. Populations may be geographically isolated for long periods of time without diverging. enough to be recognized taxonomically (Stebbins 1950). Recently, Thompson (1997) refuted her initial hypothesis that geographically proximate populations of *Lobelia* would cluster in terms of phenetic structure. In fact, it has long been accepted by systematists that adaptive radiation through climatic and edaphic conditions is a more powerful process of differentiation than is genetic drift from spacial isolation (Stebbins 1950). In this sense, it would not be unusual for populations of *E. guadalupensis* and *E. sneedii* var. *leei*, which occur within areas of climatic and edaphic extremes, to have evolved more rapidly from ancestral populations within the Guadalupe Mountains than have the geographically isolated populations of *E. sneedii*. Also, it is more parsimonious for two extreme morphotypes to radiate by peripheral and ecological isolation, than for the two extremes to hybridize and give rise to a wide-ranging intermediate (Barlow-Irick 1995). Zones of intergradation, such as those represented by some of the Guadalupe Mountains populations of *E. sneedii*, are common occurrence during the divergence of population systems (Grant 1971).

The main objective of this study was to survey within the Guadalupe Mountains for populations of the *Escobaria sneedii/E. guadalupensis* complex occurring geographically intermediate to the western and eastern clusters of known populations, and to further assess taxonomic relationships using the morphological criteria established by Baker and Johnson (2000).

METHODS

Surveys were conducted within the Guadalupe Mountains during June 2001 between latitude 32° 04' and 32° 10'N and longitude 104° 33' and 104° 42'W (Fig. 1).

A total of 95 individuals were measured for the four characters diagnostic within the taxonomic group (Baker & Johnson 2000). The new data were incorporated into the Baker and Johnson (2000) data set and analyzed using algorithms within the SYSTAT7 statistical package of SPSS7 and SPSS7 version 10.0. Data were transformed as necessary in an attempt to meet assumptions of homogeneity of variance.

Apriori analyses (individuals ungrouped) were performed using principal components analysis. The original Bishop's Cap population was excluded from the PCA analysis. Posterior analyses (individuals pre-grouped) were performed using discriminant functions.

RESULTS

Of the five areas searched, five populations were found, filling in geographical gaps among previously known populations (Table 1, Fig. 1). The primary plant associates for each population are given in Appendix 1. Populations of *E. sneedii* ranged between 4,200 ft (1280 m) and 6,500 ft (1980 m) elevation and were fairly evenly distributed over at least 80 mi² (207 km²) of habitat within the Guadalupe Mountains, between upper Cottonwood Canyon, where *E. guadalupensis* forms occur, and Walnut Canyon, where *E. sneedii* var. *leei* forms occur. Roughly extrapolating from population densities, it is estimated that there are an average of at least 1,000 individuals per square mile (2.59 km) or a total of ca. 80,000 individuals in this area of the Guadalupe Mountains.

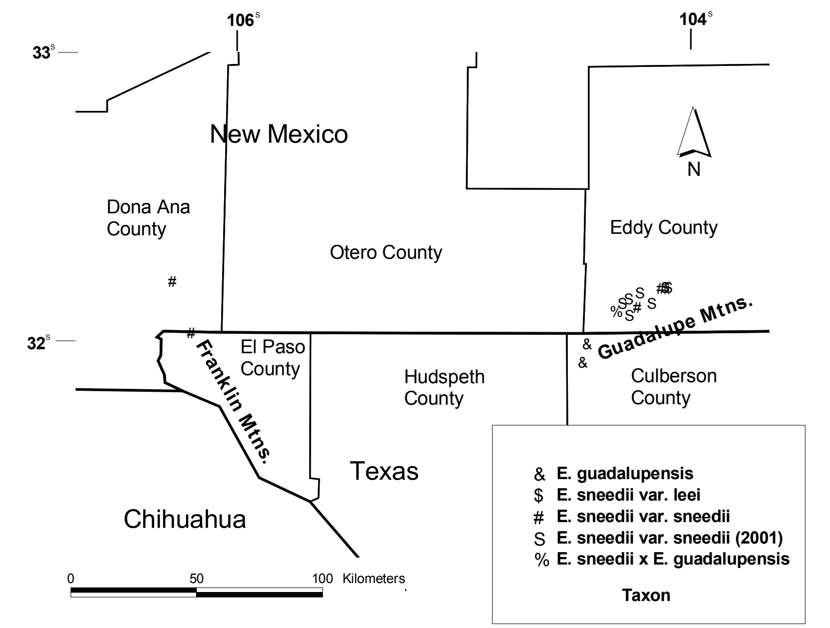

FIGURE 1. Locations of study populations of *Escobaria* in the Franklin and Guadalupe Mountains, NM and TX.

The first factor of the PCA accounted for 55.7percent of the total variation and the second factor for only 19.7 percent (Table 2). Figure 2 represents a scatterplot of factor 1 vs. factor 2. Although individuals are well-grouped

Table 1. Locations of 2001 populations for *Escobaria sneedii*.

Site	Elevation	Longitude / Latitude	N	Habitat	Voucher Number
Bear Canyon	1815m	32º 09'N 104º 36'W	20	limestone shelves in transition scrub, steep NW-facing hillside	*MB14106*
Putman Canyon	1890-1950m	32º 07'N 104º 39'W	25	limestone shelves in transition scrub, SE-NE-facing hillsides	*MB14107*
Cottonwood Canyon East	1980m	32º 06'N 104º 41'W	15	limestone shelves in transition scrub, NW-facing hillside	*MB14111*
Slaughter Canyon	1280-1465m	32º 06'N 104º 33'W	50	south to SW-facing limestone hillside of mostly rounded bedrock, desert scrub	*MB14115*
Double Canyon	1495-1675m	32º 04'N 104º39'W	50	east-facing hillside of mostly exposed rounded and weathered limestone, desert scrub	*MB14119*

within taxa, the three groups were not separate from one another. Individuals of *E. sneedii* var. *sneedii* and *E. sneedii* var. *leei* showed considerable overlap. As expected, individuals of the Cottonwood West population were plotted among those of both of *E.* sneedii var. sneedii and *E.* guadalupensis.

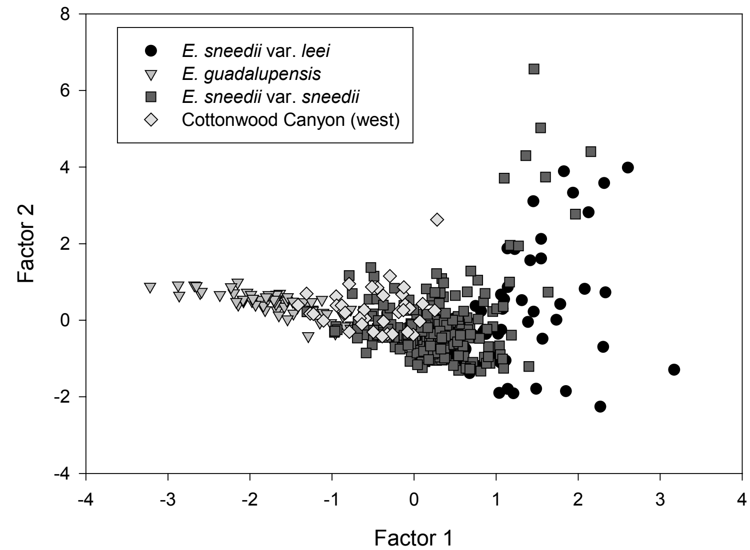

FIGURE 2. Scatterplot of PCA factor one vs. factor two, by taxon. Individuals of Cottonwood Canyon West population plotted separately

Results similar to those of the PCA were obtained from Discriminant analysis. Table 4 presents predicted group membership among the three taxa, which excluded the Bishop's Cap and the Cottonwood Canyon West populations. As with the Baker and Johnson (2000) study, individuals within the *E. guadalupensis* populations were classified correctly 100 percent. Individuals within the *E. sneedii* var. *sneedii* and *E. sneedii* var. *leei* populations were correctly classified 79.6 percent and 86.4 percent, respectively. Since individuals of the Bishops cap and Cottonwood Canyon West populations were left ungrouped, the DA grouped these individuals according to one of the three defined taxa. For the Cottonwood Canyon West population, 41.2 percent were classified as *E. guadalupensis* and 51.8 percent of the individuals were classified as *E. sneedii* var. *sneedii*. Within the Bishop's Cap population 30 percent were classified as *E. guadalupensis* and 70 percent of the individuals were classified as *E. sneedii* var. *sneedii*.

TABLE 2. PCA component loadings for each character, by factor.

Character	Factor 1	Factor 2
Inner central spine length	-0.9	0.2
Maximum stem diameter	-0.8	0.0
Number of radial spines per areole	0.7	-0.4
Number of immature stems	0.6	0.8
Percent of total variance explained	55.7	19.7

DISCUSSION AND CONCLUSIONS

The range of *E. sneedii* within the Guadalupe Mountains was found to be much more extensive than was previously recorded. Morphology, as based on the characters used in this study, of most *E. sneedii* individuals within the Guadalupe Mountains was indistinguishable from those in the Franklins Mountains (type locality). The exceptions being the Cottonwood Canyon West and the two Walnut Canyon Populations.

TABLE 3. Classification Results from discriminant analysis. Cottonwood Canyon West and Bishops Cap individuals grouped according to one of the three defined taxa.

	Predicted Group Membership			
Taxon	*E. guadalupensis*	*E. sneedii* var. *sneedii*	*E. sneedii* var. *leei*	Total
	By number of individuals			
E. guadalupensis	32	0	0	32
E. sneedii var. *sneedii*	9	187	39	235
E. sneedii var. *leei*	0	8	51	59
Cottonwood Canyon West	14	20	0	34
Bishops Cap	7	3	0	10
	By percent of individuals			
E. guadalupensis	**100**	0	0	100.0
E. sneedii var. *sneedii*	3.8	**79.6**	16.6	100.0
E. sneedii var. *leei*	0	13.6	**86.4**	100.0
Cottonwood Canyon West	41.2	58.8	0	100.0
Bishops Cap	70	30	0	100.0
81.0% of original grouped cases correctly classified. Box's M = 458.4, Approx. F = 22.4				

Analyses herein did not indicate that populations within each taxon were morphologically distinct from those of the other taxa. However, when populations of intermediate morphology were excluded from the analysis, DA classified correctly nearly all individuals of *E. guadalupensis* from those of *E. sneedii*. As with the Baker and Johnson (2000) data, the Cottonwood Canyon West population appeared to be taxonomically intermediate between *E. guadalupensis* and *E. sneedii*. The Bishop's Cap population was somewhat more problematical. It was excluded in the present PCA and left ungrouped in the DA because the sample size was low (N = 10) and because a recent visit to the site recorded individuals morphologically intermediate between those of typical *E. sneedii* and *E. tuberculosa* (Engelm.) Britton & Rose (personal observation). Thus, the large stems and long spines of the Bishop's Cap *E. sneedii* individuals (Baker & Johnson 2000) may be a product of hybridization with a taxon outside the scope of the present study.

The taxonomic recognition of *E. sneedii* var. *leei,* as separate from that of *E. sneedii* var. *sneedii,* was shown to be tenuous. Within populations classified as *E. sneedii* var. *sneedii*, 16.6 percent of the individuals were misclassified as those belonging to *E. sneedii* var. *leei*, and within populations of *E. sneedii* var. *leei*, 13.6 percent of the individuals were misclassified as those belonging to *E. sneedii* var. *sneedii*. Populations of *E. sneedii* var. *leei* were restricted to a single, small canyon that is not geographically distant from populations currently classified as *E. sneedii* var. *sneedii*.

With respect to the taxonomic status of *E. guadalupensis*, the data herein added little to that of the Baker and Johnson (2000) study. Further work is needed to assess the geographic extent of morphological intermediacy between *E. guadalupensis* and *E. sneedii*.

Of the three taxa, individuals of *E. sneedii* var. *sneedii* were the most abundant, geographically widespread, and morphological variable and intermediate. For these reasons, *E. sneedii* probably represents the ancestral form that gave rise to *E. guadalupensis* to the west and *E. sneedii* var. *leei* to the east. The Franklin Mountains' *E.*

sneedii may represent an incipient population that dispersed from the Guadalupe Mountains or residual populations of a once much larger distribution.

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APPENDIX 1

Plant associates within 2001 populations for *Escobaria sneedii*.

Site	Associates
Bear Canyon	*Agave lechuguilla, Cercocarpus montanus, Chrysactinia mexicana, Dalea formosa, Dasylirion leiophyllum, Echinocereus triglochidiatus* var. *gurneyi, Heterotheca villosa, Juniperus deppeana, Muhlenbergia pauciflora, Nolina micrantha, Opuntia engelmannii, Parthenium incanum, Petrophyton caespitosum, Quercus pungens, Rhus trilobata,* and *Yucca baccata*.
Putman Canyon	*Acacia greggii, Agave lechuguilla, Cercocarpus montanus, Chrysactinia mexicana, Dasylirion leiophyllum, Echinocereus triglochidiatus* var. *gurneyi, Eriogonum jamesii, Evolvulus nuttallianus, Fendlera rupicola, Garrya wrightii, Hesperostipa neomexicana, Hedyotis nigricans, Juniperus scopulorum, Muhlenbergia emersleyi, M. pauciflora, Opuntia engelmannii, Pinus ponderosa, Quercus pungens, Rhus microphylla*, and *Yucca baccata*
Cottonwood Canyon East	*Arbutus xalapensis, Agave lechuguilla, A. parryi, Chrysactinia mexicana, Cercocarpus montanus, Dasylirion leiophyllum, Echinocereus triglochidiatus* var. *gurneyi, Fendlerella utahensis, Garrya wrightii, Hedeoma plicata, Hesperostipa neomexicana, Juniperus deppeana, Muhlenbergia pauciflora, Nolina micrantha, Opuntia engelmannii, Petrophyton caespitosum, Pinus edulis, P. ponderosa, Quercus pungens, Talinum pulchellum, Vitis arizonica* and *Yucca baccata*
Slaughter Canyon	*Acacia roemeriana, Agave lechuguilla, Aloysia wrightii, Aristida purpurea, Berberis trifoliata, Bernardia obovata, Bouteloua eriopoda, Condalia ericoides, Dalea formosa, Dasylirion leiophyllum, Echinocereus stramineus, E. triglochidiatus* var. *gurneyi, Escobaria strobiliformis, Fouquieria splendens, Juniperus pinchotti, Krameria grayi, Muhlenbergia pauciflora, Opuntia engelmannii, O. macrocentra, Quercus pungens, Rhus microphylla, Thelocactus bicolor, Tridens muticus,* and *Yucca faxoniana*
Double Canyon	*Acacia roemeriana, Agave lechuguilla, Aristida purpurea, Artemisia ludoviciana, Dalea bicolor, Dalea formosa, Dasylirion leiophyllum, Echinocereus triglochidiatus, Eriogonum hieracifolium, Escobaria strobiliformis, Fouquieria splendens, Juniperus pinchotti, Muhlenbergia pauciflora, Parthenium incanum, Quercus pungens,* and *Rhus microphylla*