REASSESSMENT OF SUBSPECIFIC TAXA WITHIN *PEDIOCACTUS PEEBLESIANUS* (CACTACEAE) BY MULTIVARIATE ANALYSIS OF MORPHOLOGICAL CHARACTERS

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ABSTRACT

A study was undertaken to determine whether there are groups of populations within *Pediocactus peeblesianus* that when considered collectively possess combinations of morphological character values that are significantly different between or among other groups and whether any such groupings correlate with geography. A total of 323 individuals were measured for 17 stem characters in 11 populations, including three populations of the outgroup, *Pediocactus sileri*. The morphological data suggested no practical geographic manner in which to segregate taxonomic groups of populations within *P. peeblesianus*. A weak morphological cline occurred from west to east, in which central spines increased in number and length, and radial spines decreased in thickness. Values for four characters correlated significantly with stem diameter, indicating that a significant amount of the morphological variation within *P. peeblesianus* can be explained by plant size. Historically, the taxon *P. peeblesianus* var. *peeblesianus* was evidently based on neotenous individuals occurring on very shallow soils, while *P. peeblesianus* var. *fickeiseniorum* was based on individuals occurring on deeper soils farther west along the cline. In light of our findings, we see no reason to recognize infraspecific taxa within *P. peeblesianus*.

RESUMEN

Se llevó a cabo un estudio para determinar si hay grupos de poblaciones dentro de *Pediocactus peeblesianus* que, cuando se consideran colectivamente, poseen combinaciones de valores de caracteres morfológicos que son significativamente diferentes entre grupos y si tales agrupaciones se correlacionan con la geografía. Se midieron 17 caracteres del tallo en un total de 323 individuos de 11 poblaciones, incluidas tres del grupo externo, *Pediocactus sileri*. Los datos morfológicos no sugirieron ninguna forma geográfica práctica para segregar grupos taxonómicos de poblaciones dentro de *P. peeblesianus*. Se produjo una débil línea morfológica de oeste a este, en la que las espinas centrales aumentaron en número y longitud, y las espinas radiales disminuyeron en grosor. Los valores de cuatro caracteres se correlacionaron significativamente con el diámetro del tallo, lo que indica que una cantidad significativa de la variación morfológica dentro de *P. peeblesianus* puede explicarse por el tamaño de la planta. Históricamente, el taxón *P. peeblesianus* var. *peeblesianus* evidentemente se basó en individuos neoténicos que se encontraban en suelos muy poco profundos, mientras que *P. peeblesianus* var. *fickeiseniorum* se basó en individuos que se encontraban en suelos más profundos más al oeste a lo largo del cline.

INTRODUCTION

The primary goal of this study was to assess the justification for infraspecific taxa within *Pediocactus peeblesianus* (Croizat) L.D. Benson, in determining whether there are groups of populations within that possess combinations of morphological character values that are significantly different between or among groups and whether any such groupings correlate with geography. Because morphology is the most pragmatic means of circumscribing specific and subspecific taxa, results from large-sample morphological studies are crucial for the assessment of the nature of morphological variation, geographic distribution, and taxonomic validity of subspecific taxa, especially for those that lack qualitative characteristics. In addition, our morphological sampling was non-destructive, which is especially important given the rarity of the taxa studied. Presently, circumscriptions of subspecific taxa within *P. peeblesianus* are tenuous, based primarily on spine and stem characters with overlapping character values.

To test the hypothesis that certain population groups of *Pediocactus peeblesianus* possess character means that are significantly different from other groups, we performed a multivariate study to compare the degree of morphological variation of stem characters within populations to that of variations among populations throughout the range of the species. Three populations of *P. sileri* (Engelm. ex J.M. Coult.) L.D. Benson

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were also sampled as a statistical outgroup. The assumption was made that all individuals within a population were freely interbreeding and of the same taxon.

Peebles (1941) was the first to bring individuals of what is here referred to as *Pediocactus peeblesianus* to the attention of the public, with the photograph of a grafted specimen captioned "Undescribed Arizona cactus in Echinocactanae. Spines very densely hairy and superficially resembling a spike of the cat-tail (*Typha*). to 3 cm. in [stem] diameter." The following year Kearney and Peebles (1942, pp. 1035–1036) included a reference to *P. peeblesianus* in their treatment of the Arizona flora:

> *Echinocactus*. A species of *Echinocactus* was discovered in 1939 in the vicinity of Holbrook, Navajo County. Reference to this discovery is omitted from the text (see pp. 599–603) for the reason that the new species has not been described. Plants short-cylindric, about 2.5 cm. high, 2 cm. in diameter, strongly tuberculate. not ribbed; spines small in diameter, unique in having a thick dense coat of hair, in this respect resembling the flowering spikes of the cattail (*Typha*); flowers 16 mm. long, campanulate, the outer perianth segments broadly oblong, rounded-obtuse, maroon, the inner segments narrower, subacute, apiculate, whitish with a faint pink median strip.

Croizat (1943) formally described Peeble's unique cactus as *Navajoa peeblesiana*. Croizat listed the holotype as "Arizona, Navajo Co.: vicinity of Holbrook, apparently found by Mr. Whittaker of the Arizona Highway Department", as stated on a label on the type-sheet, in the herbarium of the U. S. Field Station, Sacaton, Arizona. By 1957 and prior to its closing, herbarium specimens of the U. S. Field Station, Sacaton were moved to ARIZ (Ferguson 2014). Benson (1982) reported that the type was deposited at ARIZ (accession number 137135, University of Arizona, Tucson), with isotypes at GH (Harvard University, Cambridge, Massachusetts) and DES (DES00008520, DES00001888, Desert Botanical Garden, Phoenix, Arizona). However, there are two sheets at DES, one collected in 1953, and the other in 1956, which could not have been seen by Croizat for his original description, therefore neither sheet can represent a type. The sheet at GH (01677569) is labelled as *Navajoa peeblesiana* Croiz. and is dated October 1943. Some of the handwriting is illegible, but the label certainly does not refer to Mr. Whittaker. Also, Croizat published his description in June of 1943, so this sheet also could not have been seen by him prior to his publication. Therefore, only one type is known, which is the holotype at ARIZ.

Benson (1962) placed *Navajoa peeblesiana* within the genus *Pediocactus* with little explanation. He retained the name *Navajoa* as a section within *Pediocactus* based on the surface of the spines and the tissues beneath them being spongy-fibrous.

The epithet *fickeisenii* was first used by Backeberg (1960), as *Navajoa fickeisenii*, to describe populations of what we now recognize as *Pediocactus peeblesianus* 300 miles west of the type locality of *Navajoa peeblesiana*. Backeberg based his new species on its longer spines and yellow flowers. Unfortunately, the name was invalid because Backeberg did not designate a type. Benson (1962) reported that this population was originally discovered by Mr. and Mrs. Denis Cowper of Belen, New Mexico in May 1956, but photographs of the plants were sent to Backeberg by Mrs. Fickeisen. Benson placed *N. fickeiseniorum* under *Pediocactus* as *P. peeblesianum* var. *fickeisenii,* but, being based on an illegitimate basionym, this name was also not valid. In 1961, Backeberg validated the name with an unspecified type from his collection, but this type specimen has not been found. Because he named the species after Mr. and Mrs. Fickeisen, the spelling *N. fickeiseniorum* is correct. Reveal (2012) explains this nomenclatural conundrum in length and lectotypifies *N. fickeiseniorum* Backeb. as Fig. 2702, page 2876, from Backeberg (1961). Taxonomically, Reveal (2012) recognizes the taxon as *Pediocactus peeblesianus* subsp. *fickeiseniorum* Lüthy.

Porter (2010) explored DNA sequences from the chloroplast *trnL-F* region in order to assess genetic relationships among the species of *Pediocactus*. He found significant statistical support from *trnL-F* sequences for the inclusion of nine species in the genus *Pediocactus*. However, his data did not justify the segregation of the genera *Navajoa*, *Pilocanthus*, *Puebloa*, and *Utahia*. With respect to populations of *P. peeblesianus*, Porter reported a unique chloroplast type in *trnL-F* sequences within all of the individuals near Joseph City, which have traditionally been referred to as *P. peeblesianus* var. *peeblesianus*. Samples from populations defined as *P. peeblesianus* var. *fickeiseniae* all possessed slightly different chloroplast types that were more similar to each other than to those of the typical variety. Therefore, his data supported the recognition of two genetic races of *P. peeblesianus*. However, Porter recognized that his results were potentially biased due to sampling. He sampled 18 individuals of *P. peeblesianus* var. *peeblesianus* but only three of *P. peeblesianus* var. *fickeiseniae*. Porter (2014, pers. comm.) suggests that, even for DNA studies, a minimum sample size of 30 individuals per population is necessary to properly assess genetics at the population level. Porter (2010) also recognized that the Joseph City individuals varied considerably in their morphology, with some approaching typical *P. peeblesianus* var. *fickeiseniae*.

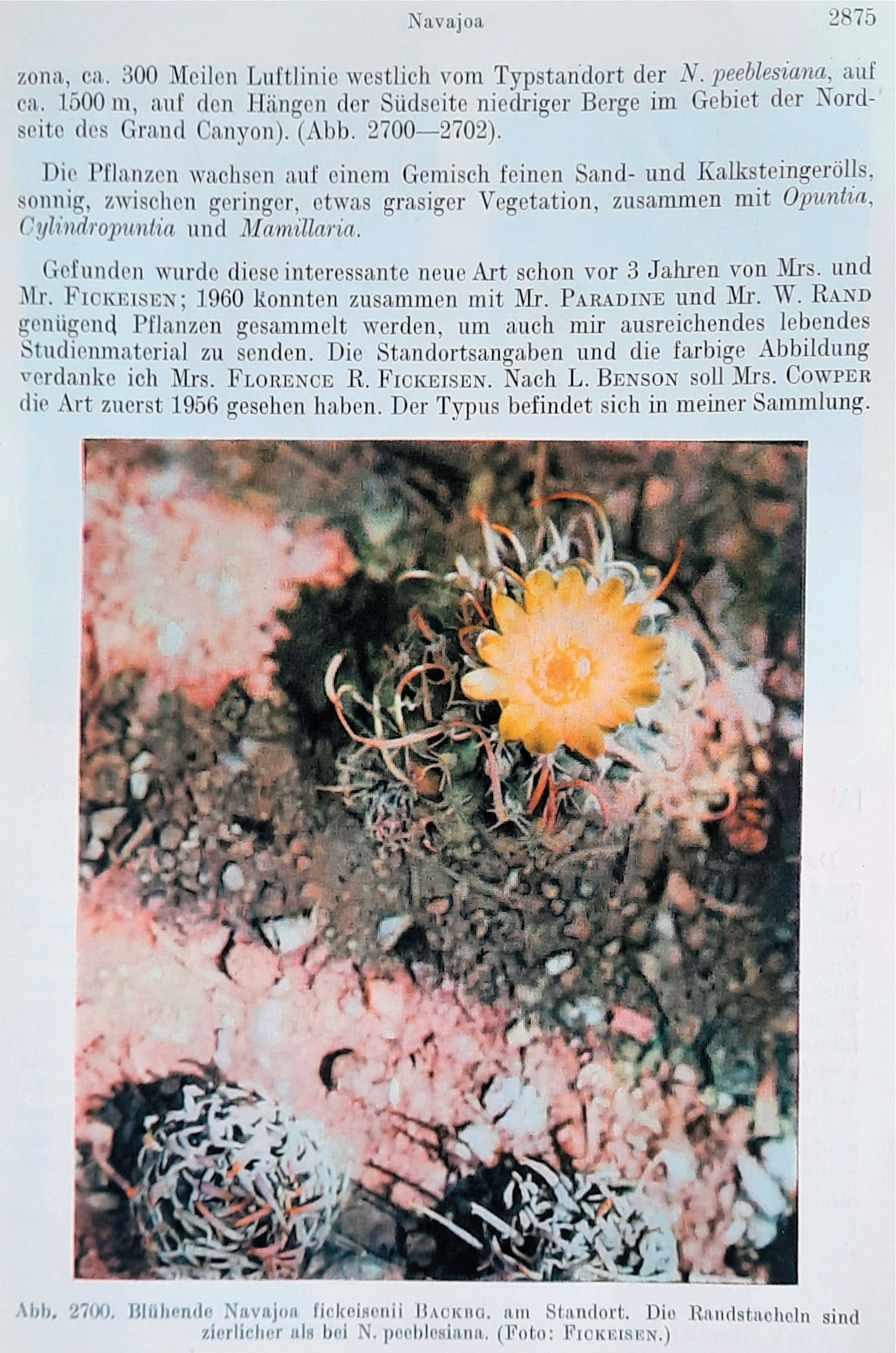
Hochstätter (2007) recently self-published a treatment of *Pediocactus* and its relatives in which he placed *P. peeblesianus* back within the genus *Navajoa* (Fig. 1). His argument for the separation of the two genera was based on Konnert's (2007) isoenzyme analysis of *Pediocactus*, *Navajoa*, *Toumeya*, and *Sclerocactus* and on Hentzshel's (1989) and Frank's (2007) scanning electron micrographs of *Pediocactus* and related genera. Konnert's small sample size (*n*=9) and the resulting ambiguous differentiation among samples of Hochstätter's *Pediocactus* and *Navajoa* (*n*=1) do not appear to support the recognition of *Navajoa* as a separate genus from *Pediocactus*. The results for Hentzshel's and Frank's studies were similarly ambiguous for differentiation of *Pediocactus* and *Navajoa,* with the seed morphology of *Navajoa* clearly within the range of *Pediocactus*. Within *N. peeblesiana*, Hochstätter (2007) listed three subspecies: *N. peeblesiana* subsp. *peeblesiana*, *N. peeblesiana* subsp. *fickeiseniae,* (roughly equivalent to Benson's *P. peeblesianus* var. *fickeisenii*); and *N. peeblesiana* subsp. *menzelii*. According to Hochstätter, *Navajoa peeblesiana* subsp. *menzelii* is defined by its brownish flower, versus its generally yellowish flower in the other subspecies, and its more robust habit. The type, which was stated to be deposited at the herbarium of Boise State University (SRP), was never accessioned (James Smith, pers. comm. 2014).

Pediocactus peeblesianus (Croizat) L.D. Benson var. *maianus* L.D. Benson (Fig. 2), which was published by Benson in 1969, is a name of dubious taxonomic validity. The type was collected by J.W. Toumey, April 23, 1897, near Prescott, Yavapai Co , Arizona (US535244). According to Benson (1982) it is represented only by the type specimen and may be a juvenile plant of *Echinocereus fendleri*. David Keil collected a specimen of *E. fendleri* at Lynx Creek, Yavapai County (ASU250226), which is only 10 km east of Prescott. No collections of *Pediocactus* are known from Yavapai County. The first author reviewed the type at the United States National Herbarium (US) in July 2014 and concluded that the specimen belongs within *E. fendleri* (Fig. 3).

Pediocactus peeblesianus has also been placed within the genera *Echinocactus* (Benson 1950), *Neonavajoa* (Doweld 1999), *Utahia* (Kladiwa 1969), and *Toumeya* (Marshall 1947). *Neonavajoa* was proposed by Doweld (1999) because he felt that the previously published name *Navajoia* G. R. Wieland, which referred to a fossil cycad, constituted an earlier homonym. According to Reveal however, the name *Navajoia* was not validly published (J. Reveal, pers. comm. 2014). Furthermore, the Committee for Spermatophyta voted that the two names not be treated as homonyms (Brummitt 2001).

MATERIALS AND METHODS

Fieldwork was conducted between 7 April and 5 May 2014. Site descriptions are presented in Table 1. Fig. 4 presents an overview of the study sites. Because these taxa are listed as federally endangered, no physical specimens were collected during this study. For most sites, specimen vouchers from previous collections were available at various institutions, and photo vouchers were made for the remaining sites. Sample sizes of the populations were unequal, ranging from 29 to 32, except for population eight, where only 20 individuals could be located. The target sample size was 30 individuals for each population and three populations for each taxon, recommended as a minimum sample size by Baker & Butterworth (2013). For *Pediocactus peeblesianus* var. *peeblesianus,* only two sites were available, as permission to access a third site was refused by the landowner. Although the two sites sampled for *P. peeblesianus* var. *peeblesianus* were only 2.4 km apart, individuals of the eastern site (8) occurred on very shallow soils near the edges of cliffs, while those of the western site (7) occurred on deeper soils on slopes and the tops of low hills. Six populations were sampled for what were considered to be *P. peeblesianus* var. *fickeisenii*, the additional sampling was done in order to test the possibility



Navajoa 2875

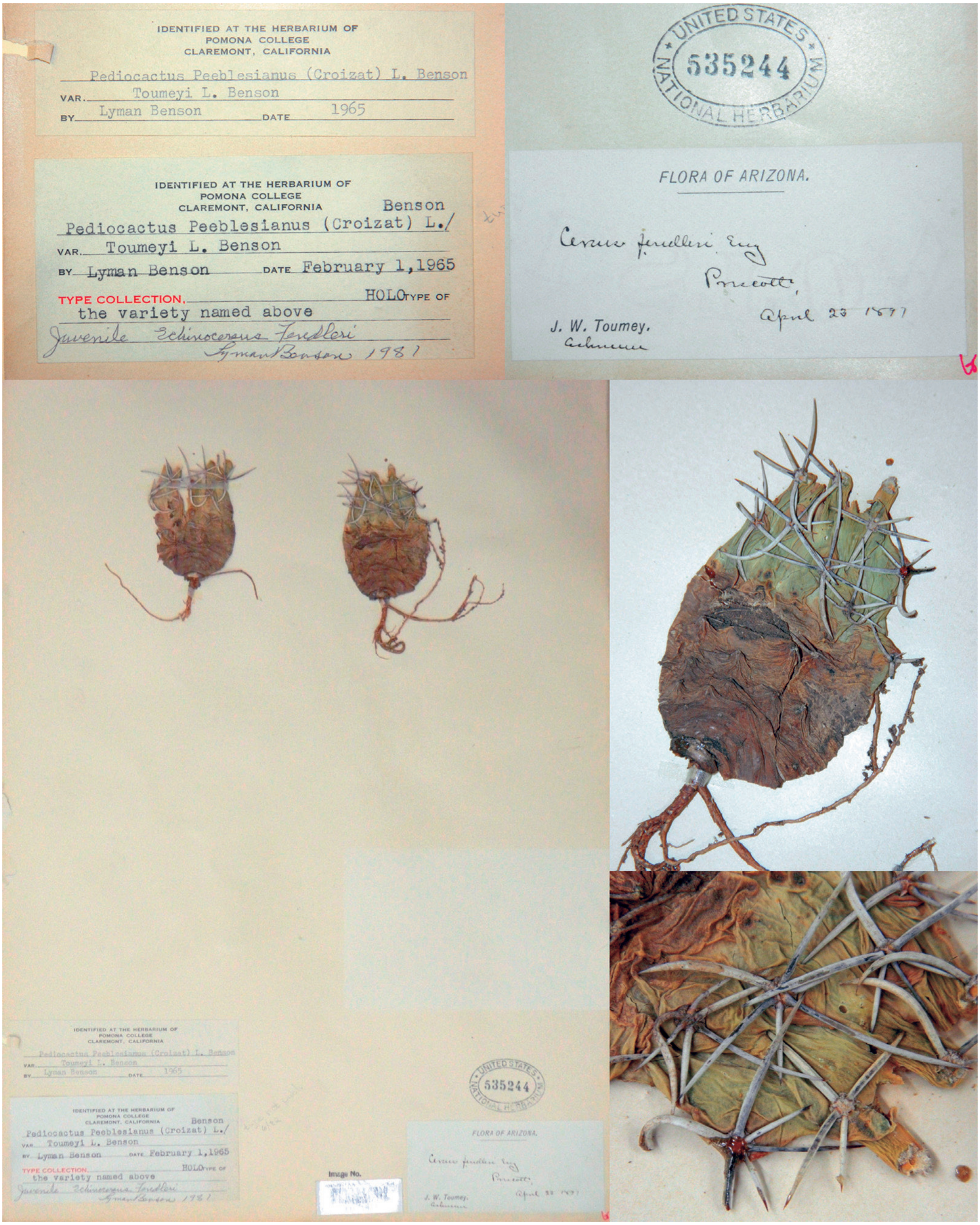
zona, ca. 300 Meilen Luftlinie westlich vom Typstandort der *N. peeblesiana*, auf ca. 1500 m, auf den Hängen der Südseite niedriger Berge im Gebiet der Nordseite des Grand Canyon). (Abb. 2700—2702).

Die Pflanzen wachsen auf einem Gemisch feinen Sand- und Kalksteingerölls, sonnig, zwischen geringer, etwas grasiger Vegetation, zusammen mit *Opuntia*, *Cylindropuntia* und *Mamillaria*.

Gefunden wurde diese interessante neue Art schon vor 3 Jahren von Mrs. und Mr. Fickeisen; 1960 konnten zusammen mit Mr. Paradine und Mr. W. Rand genügend Pflanzen gesammelt werden, um auch mir ausreichendes lebendes Studienmaterial zu senden. Die Standortsangaben und die farbige Abbildung verdanke ich Mrs. Florence R. Fickeisen. Nach L. Benson soll Mrs. Cowper die Art zuerst 1956 gesehen haben. Der Typus befindet sich in meiner Sammlung.

Abb. 2700. Blühende Navajoa fickeisenii Backbg. am Standort. Die Randstacheln sind zierlicher als bei N. peeblesiana. (Foto: Fickeisen.)

Fig. 1. Holotype according to Hochstätter (2007) for *Navajoa fickiesenii* Backeb., in Backeberg (1961). (Fig. 2700, p. 2875)



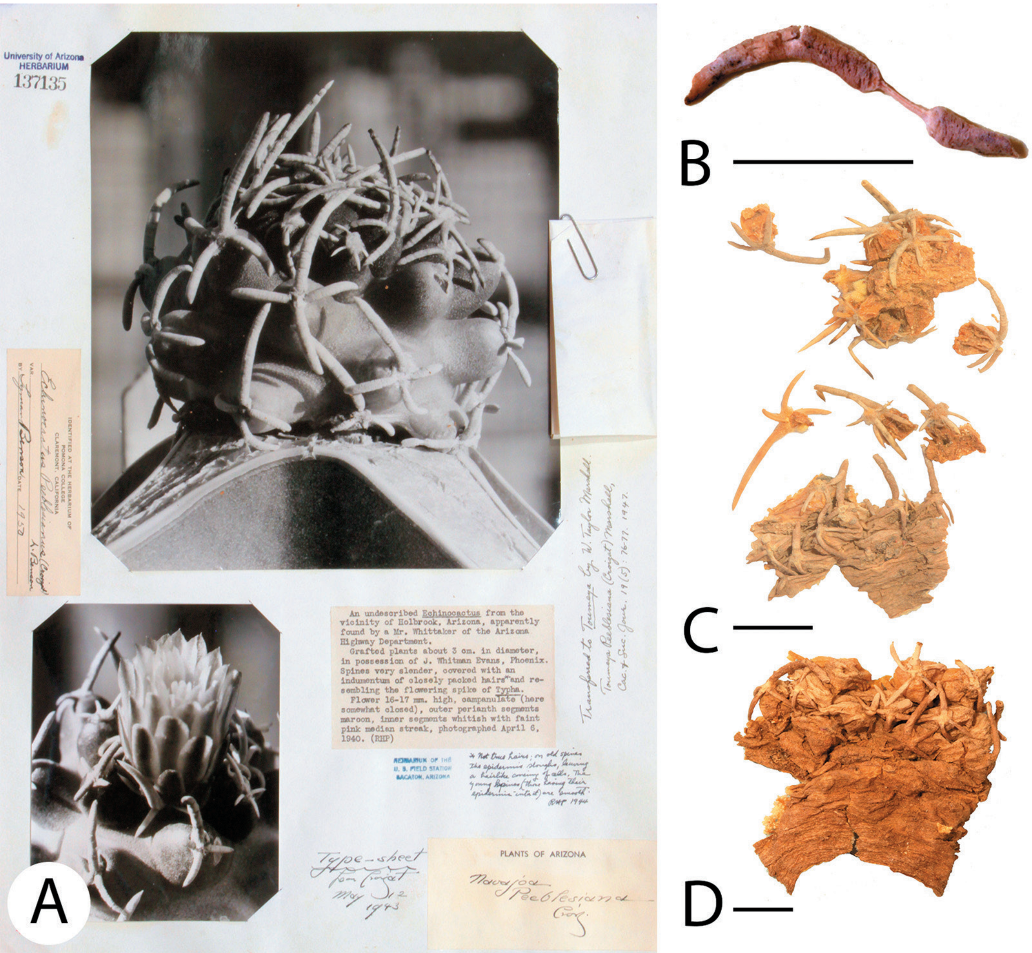
IDENTIFIED AT THE HERBARIUM OF
POMONA COLLEGE
CLAREMONT, CALIFORNIA
Pediocactus Peeblesianus (Croizat) L. Benson
VAR. Toumeyi L. Benson
BY Lyman Benson DATE 1965

IDENTIFIED AT THE HERBARIUM OF
POMONA COLLEGE
CLAREMONT, CALIFORNIA
Pediocactus Peeblesianus (Croizat) L./Benson
VAR. Toumeyi L. Benson
BY Lyman Benson DATE February 1,1965
TYPE COLLECTION, HOLOTYPE OF
the variety named above
Juvenile Echinocereus Fendleri
Lyman Benson 1981

UNITED STATES NATIONAL HERBARIUM
535244

FLORA OF ARIZONA.
Cereus fendleri Eng
Prescott,
April 23 1877
J. W. Toumey.
Collector

Fig. 2. Holotype for *Pediocactus peeblesianus* (Croizat) L.D. Benson var. *maianus* L.D. Benson. Note that Benson annotated this specimen in 1965 as the holotype for *P. peeblesianus* var. *toumeyi* L.D. Benson but apparently decided to change the name before his publication in 1969.



An undescribed Echinocactus from the vicinity of Holbrook, Arizona, apparently found by a Mr. Whittaker of the Arizona Highway Department.

Grafted plants about 3 cm. in diameter, in possession of J. Whitman Evans, Phoenix. Spines very slender, covered with an indumentum of closely packed hairs* and resembling the flowering spike of Typha.

Flower 16-17 mm. high, campanulate (here somewhat closed), outer perianth segments maroon, inner segments whitish with faint pink median streak, photographed April 6, 1940. (RHP)

* Not true hairs; on old spines the epidermis sloughs, leaving a hairlike covering of cells. The young spines (those having their epidermis intact) are smooth. RHP 1944

Fig. 3. Holotype for *Navajoa peeblesianus* Croizat, ARIZ 137135. A. **Entire herbarium sheet; B.** **spine cut away by Peebles to show inner core; C.** **stem fragments from packet; D.** **largest stem fragment from packet.**

that populations north of the Colorado River on the Arizona Strip represented a separate taxon from those south and east of the Colorado River. The southeasternmost population of *P. peeblesianus* var. *fickeisenii* was near the type locality of *Navajoa peeblesiana* var. *menzelii*. Hochstätter (2007) reported only a single population for this taxon.

A total of 323 individuals were measured in 11 populations, including three populations of the outgroup, *Pediocactus sileri*. Porter (2010) indicated that either *P. sileri* or *P. bradyi* L.D. Benson would be the best choices for an outgroup, however, only a single population is known for *P. bradyi* and therefore not statistically robust. Only reproductively mature individuals or individuals with stem diameters greater than or equal to the smallest reproductively mature individuals in the population were measured. The 17 stem characters measured are presented in Table 2. Two characters, stem diameter and stem number, were not used in the multivariate analyses because of their obvious correlation with age. However, stem diameter was used in the linear regression analyses. The two measurements of radial spine thickness were omitted from the multivariate analyses but were used to generate radial spine sponginess, which was included in the analysis. Reproductive data were also recorded, including numbers of buds, flowers, and fruits, in order to assess the minimum stem size for reproductively mature individuals and to aid in conservation efforts.

Table 1. Locations of study populations sampled in the morphological analysis.

Population name and number	Species	Historical nomenclature/Representative voucher	Locality
Cataract Canyon; 1	*P. peeblesianus*	Type locality for *Navajoa peeblesiana* subsp. *menzelii*; *Goodwin 1534, 1535* (ASC)	E of Cataract Canyon, 69 km N of Williams, Coconino Co., Kaibab Limestone shelves and ridgetops
Gray Mountain; 2	*P. peeblesianus*	*P. peeblesianus* var. *fickeiseniae*; *Cloud-Hughes 0141* (NAVA, photo voucher)	Tappan Wash, SE of Gray Mountain, 66 km N of Flagstaff, Coconino Co., Kaibab Limestone shelves, gravelly slopes, and ridgetops
Little Colorado River Gorge; 3	*P. peeblesianus*	*P. peeblesianus* var. *fickeiseniae* type locality; photo in Backeberg, *Benson 15745* (POM 285856)	S side of the Little Colorado River Gorge, WNW of Cameron, 81 km N of Flagstaff, Coconino Co., Kaibab Limestone shelves and gravelly slopes
North Canyon; 4	*P. peeblesianus*	*P. peeblesianus* var. *fickeiseniae*; *R. Gierisch 4957* (ASU 152139, ARIZ 270864)	House Rock Valley, N side of North Canyon Wash, S of the SW end of Vermillion Cliffs, 72 km SE of Fredonia, Coconino Co., gravelly slopes
Antelope Valley; 5	*P. peeblesianus*	*P. peeblesianus* var. *fickeiseniae*; *G. K. Brown 663* (ASU 99586)	Antelope Valley, lower W slope at the N end of Sunshine Ridge, 40 km SW of Fredonia, Mohave Co.; gravels and fine silt
Hurricane Valley; 6	*P. peeblesianus*	*P. peeblesianus* var. *fickeiseniae*; *Cloud-Hughes 0142* (ASU, photo voucher)	Hurricane Valley, NNW of the mouth of Sunshine Draw, NNE of Diamond Butte, 55 km SSE of St. George, UT, Mohave Co., gravels and fine silt
Joseph City 01; 7	*P. peeblesianus*	*P. peeblesianus* var. *peeblesianus*; *Susie Smith s.n.* 1992 (ASU 186503)	East of Joseph City, NE of the confluence of Tanner Wash and the Little Colorado River, Navajo Co., gravelly slopes and tops of low hills
Joseph City 02; 8	*P. peeblesianus*	*P. peeblesianus* var. *peeblesianus*; *Whittaker s.n.* (ARIZ 137135)	ESE of Joseph City, ENE of the confluence of Tanner Wash and the Little Colorado River, Navajo Co., shallow soils with gravel and rock near the edges of breaks
Upper Clayhole Valley; 9	*P. sileri*	*P. sileri*; *Cloud-Hughes 0142* (ASU, photo voucher)	Above and east of Upper Clayhole Valley, 6.2 km WSW of Yellowstone Spring, 65 km SE of St. George, Utah, Mohave Co., Arizona
Lost Spring Mountain; 10	*P. sileri*	*P. sileri*; *Cloud-Hughes 0143* (ASU, photo voucher)	2.7 km S of the S edge of Lost Spring Mountain, 3.1 km E of Lytle Spring, 42 km ESE of St. George, Utah, Mohave Co., Arizona
Warner Ridge 11	*P. sileri*	*P. sileri; Neese 1902* (NY 00832553)	West base of Warner Ridge, 2.4 km SSE of Beehive Dome, 11 km SE of St. George, Washington Co., Utah

Potential groups of populations were assessed using cluster analysis conducted with nearest neighbor linkage and principal factor analysis (PFA), and pre-classified groupings of populations were assessed using discriminant function analysis (DFA). All multivariate analyses were performed using SPSS 20 (IBM, Inc., Armonk, NY). An attempt was made to normalize values for discrete data with log transformations and for continuous data with square root transformations.

Potential correlations among characters were assessed using the linear regression and regression curve estimation functions of SPSS 20. Regression analyses were performed with stem diameter as the independent

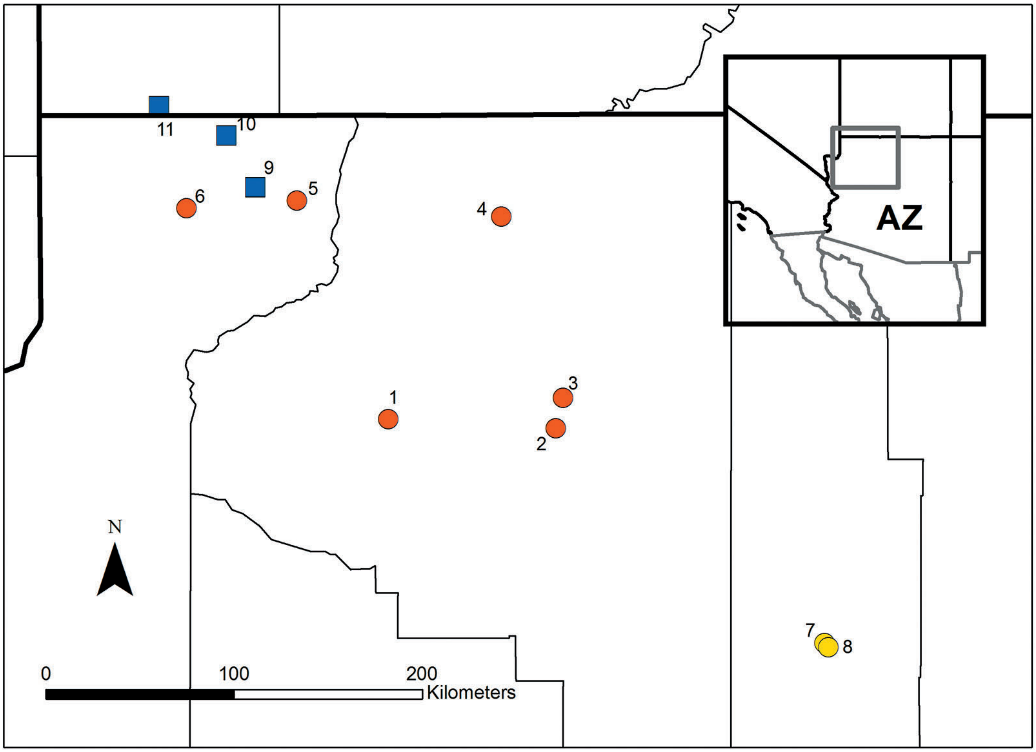


Fig. 4. Locations of study populations for the morphological study of *Pediocactus peeblesianus*. Numbers correspond to those in Table 1. Yellow circles represent *Pediocactus peeblesianus* subsp. *peeblesianus*; red circles *P. peeblesianus* subsp. *fickeiseniorum* Lüthy; and blue squares *P. sileri* as circumscribed by Parfitt and Gibson (2003). Inset map shows the general location of the study sites within the Four Corners area.

variable and each of the remaining characters as independent variables. These tests were made in order to determine whether the values for any characters correlated with plant size.

RESULTS

Cluster analysis conducted with nearest neighbor linkage failed to group individuals of *Pediocactus peeblesianus* into geographically coherent groups but placed all individuals of *P. sileri* within their own group. There was little difference between analyses using transformed or untransformed data. Similarly, PFA showed little correlation between geography and morphology among individuals of *P. peeblesianus*, with overlap among individuals belonging to the type localities for *P. peeblesianus* and *P. peeblesianus* var. *fickeiseniae* (Fig. 5). Individuals of *P. sileri* were clearly separated from those of *P. peeblesianus*. When the PFA was run without the outgroup (populations 9–11), individuals tended to cluster by population, probably owing to a combination of local genetic and environmental influences. However, individuals of the two populations historically classified as *P. peeblesianus* var. *peeblesianus* did not cluster together (Fig. 6). Character loadings (Table 3) suggested that at least some of the characters correlated with stem size were also important in the PFA results and, indeed, when individuals are plotted by stem diameter size classes (10, 20, 30, 40 and 50mm), individuals within their respective size classes are fairly well grouped and formed a cline from the smallest to the largest (Fig. 7). Discriminant function analysis (DFA) indicated what might appear to be an acceptable classification of Benson's subspecific groups within *Pediocactus peeblesianus*, with only 10.7% misclassification of individuals between pre-classified *P. peeblesianus* subsp. *peeblesianus* and *P. peeblesianus* subsp. *fickeiseniorum* (Table 4,

Table 2. Explanation of morphological characters measured for the multivariate analyses. Except for number of stems and stem diameter at base, all characters were repeated five times on the stem, with each repeat from a separate areole. All measurements were made to the nearest mm except for angles, which were measured to the nearest degree, and spine widths and thickness, which were measured by digital calipers to the nearest 0.01mm. Characters radial spine thickness 1 and 2 were omitted from the multivariate analyses but were used to generate radial spine sponginess, which was used in the analysis.

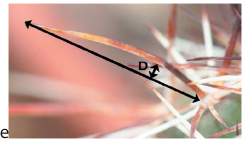
Number of stems	Number of connivent stems, not including branches arising from areoles above substrate surface. Connivent stems may or may not be joined below.
Stem diameter at base	Diameter of the stem at the substrate surface. Note that the maximum diameter of an individual may potentially be below substrate surface.
Tubercle height	Height of a mature tubercle, not including the areole.
Tubercle width	Width of a mature tubercle from sinus to sinus.
Length between areoles	Distance from the top of an areole to the top of another areole along the same spiral.
Number of central spines	Number of central spines within a single areole as determined by position and morphology.
Number of radial spines	Number of radial spines within the same areole measured for central spines.
Central spine length	Length of longest central spine. Note that an attempt was made to straighten curved spines for a more accurate measurement.
Central spine angle	Angle formed between the largest central spine and the upper surface of the stem, porrect spines being 90°, upwardly appressed spines 0°, and downwardly appressed spines 180°.
Central spine curvature	Curvature of largest central spine measured as the maximum distance (D) perpendicular to a line between the base and apex of the spine. Example on right is from *Echinocereus fendleri*. 
Radial spine length	Length of longest radial spine.
Radial spine angle	Angle of largest radial spine. See central spine angle.
Radial spine curvature	Curvature of largest radial spine. See central spine curvature.
Central spine width	Width of largest central spine at its midpoint. Note that the calipers were areole surface.
Radial spine width	Width of largest radial spine.
Radial spine thickness 1	Thickness of largest radial spine where calipers are applied without pressure. Note that the calipers were placed perpendicular to the areole surface.
Radial spine thickness 2	Thickness of largest radial spine where calipers are applied with pressure until value stabilizes. Note that calipers are in the same exact position and location as spine thickness 1.
Spine sponginess	Derived from radial spine thickness 1 minus radial spine thickness 2.

Fig. 8). None of the individuals of the outgroup, *P. sileri*, were misclassified. However, the best statistical grouping of *P. peeblesianus* populations consisted of populations 1, 4, 7, and 8 versus populations 2, 3, 5, and 6, which correlates poorly with geography (Table 5).

MANOVA using Benson's (1982) taxonomy indicated that most characters were significantly different between *Pediocactus peeblesianus* var. *peeblesianus* and *P. peeblesianus* var. *fickeisenii* (Table 6). Ironically, central spine number, which was the primary character used by Benson to separate the two varieties, was not significantly different. For a MANOVA comparing the two artificial *P. peeblesianus* population groups (populations 1, 4, 7, and 8 versus populations 2, 3, 5, and 6), the same character means were significantly different for all of those in the MANOVA using Benson's taxonomy, with tubercle height also being significantly different (Table 7). In addition, the differences in means were greater in the artificial grouping for seven of the nine characters.

Linear regression analyses indicated that values for four characters showed marked and significant correlation to values for stem diameter ($p<0.0005$, Table 8). These included tubercle height (Fig. 9), distance between tubercles (Fig. 10), central spine length (Fig. 11), and central spine angle (Fig. 12). The independent variables explain nearly 50% of the variability of the dependent variable tubercle height. The weakest correlation among the four dependent variables is for central spine angle, where the independent variables explain only 28% of the variability.

DISCUSSION

Our evidence does not support the recognition of subspecific taxa within *Pediocactus peeblesianus*. There was an artificial morphological grouping of populations that included the type locality of *P. peeblesianus*, but the

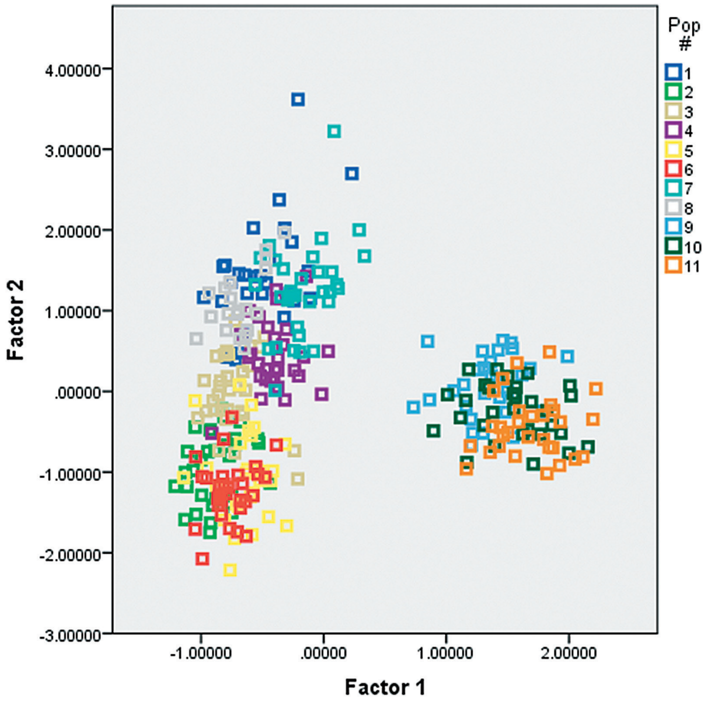


Fig. 5. Scatterplot of PFA factors 1 and 2 showing individuals by population, with the outgroup (populations 9–11) included.

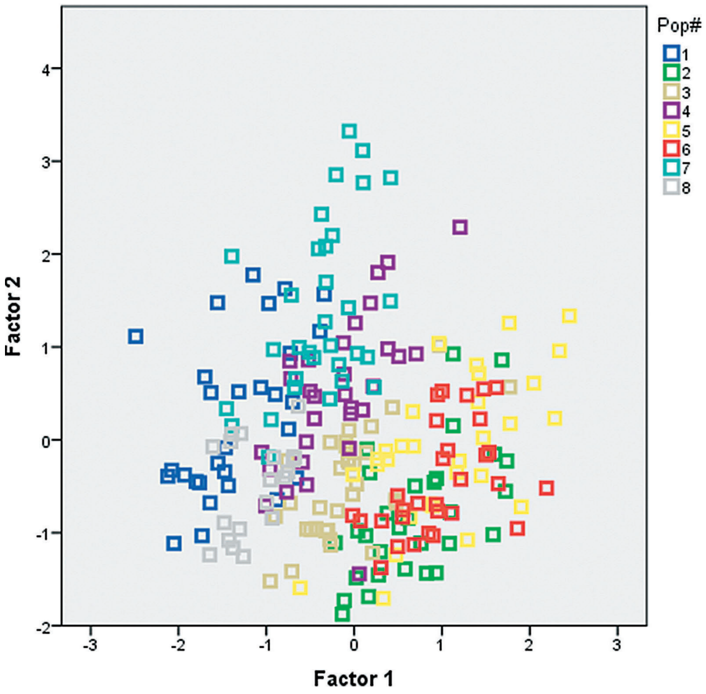


Fig. 6. Scatterplot of PFA factors 1 and 2 showing individuals by population, with the outgroup excluded.

TABLE 3. Character loadings by factor for PFA, excluding outgroup populations. Characters in bold are those that were most significant in the regression analysis.

Character	Factor			
	1	2	3	4
Central spine length	0.801	0.257	0.162	0.372
Radial spine number	0.765	-0.369	0.013	-0.034
Central spine curvature	0.728	0.136	0.174	0.410
Central spine angle	0.713	0.080	-0.053	0.357
Tubercle height	0.699	0.414	-0.154	-0.344
Radial spine width	-0.674	0.625	0.014	0.102
Radial spine thickness 1/ thickness 2	-0.584	0.533	-0.113	0.155
Distance between areoles	0.579	0.540	-0.016	-0.456
Central spine number	0.529	-0.144	0.370	-0.023
Central spines width	-0.070	0.676	0.240	0.308
Radial spine length	0.134	0.635	-0.370	0.115
Tubercle height	0.585	0.618	-0.014	-0.333
Radial spine curvature	-0.467	0.533	0.215	-0.013
Radial spine angle	-0.222	0.104	0.849	-0.214
Percent of variance explained	34.3	20.1	8.5	7.6

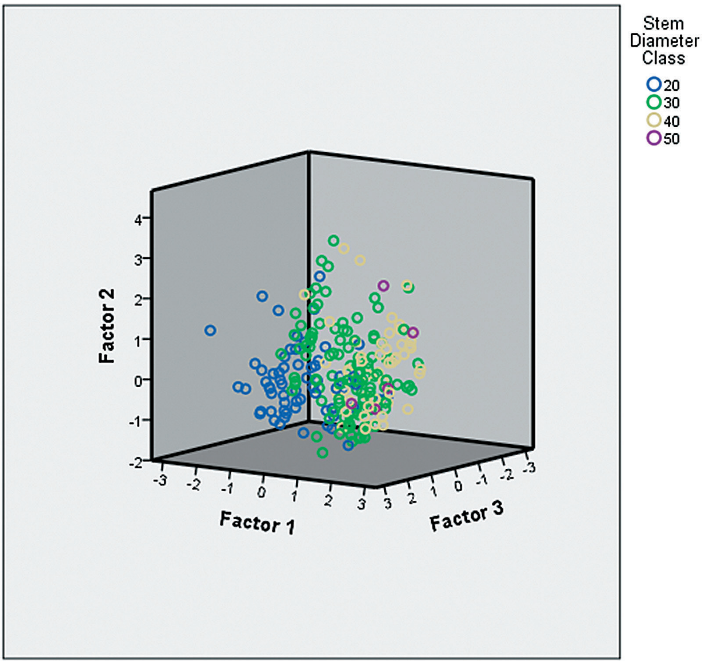


FIG. 7. Scatterplot of PFA factors 1–3 showing individuals by stem diameter class, with the outgroup excluded.

Table 4. DFA classification results using Benson's taxonomy. 94.1% of original grouped cases correctly classified, and 89.3% cases correctly classified between varieties of *P. peeblesianus.*

			Predicted Group Membership			Total
			P. peeblesianus* var. *peeblesianus	***P. peeblesianus* var. *fickeisenii***	***P. sileri***	
Original	Count	*P. peeblesianus* var. *peeblesianus*	44	8	0	52
		P. peeblesianus var. *fickeisenii*	11	170	0	181
		P. sileri	0	0	90	90
	%	*P. peeblesianus* var. *peeblesianus*	84.6	15.4	0.0	100.0
		P. peeblesianus var. *fickeisenii*	6.1	93.9	0.0	100.0
		P. sileri	0.0	0.0	100.0	100.0

Table 5. DFA classification results using the best statistical grouping of populations. 97.8% of original grouped cases correctly classified, and 97.0% cases correctly classified between group one (populations 1, 4, 7, 8) and group two (populations 2, 3, 5, 6).

			Predicted Group Membership			Total
			***P. peeblesianus* population group one**	***P. peeblesianus* population group two**	***P. sileri***	
Original	Count	*P. peeblesianus* population group one	108	4	0	112
		P. peeblesianus population group two	3	118	0	121
		P. sileri	0	0	90	90
	%	*P. peeblesianus* var. *peeblesianus*	96.4	3.6	0.0	100.0
		P. peeblesianus var. *fickeisenii*	2.5	97.5	0.0	100.0
		P. sileri	0.0	0.0	100.0	100.0

Table 6. Significantly different character means between *Pediocactus peeblesianus* var. *peeblesianus* and *P. peeblesianus* var. *fickeisenii***.**

Character	Character means, in mm except for angles, which are in degrees		
	P. peeblesianus* var. *peeblesianus	***P. peeblesianus* var. *fickeisenii***	**Difference between means**
Radial spine number	3.4	4.9	1.5
Central spine length	11.5	15.6	4.1
Central spine angle	51	65	14
Central spine curvature	2.5	4.2	1.7
Radial spine angle	169	149	20
Radial spine curvature	1.0	0.3	0.7
Central spine width	0.75	0.65	0.1
Radial spine width	0.55	0.38	0.17
Radial spine sponginess	0.17	0.14	0.03

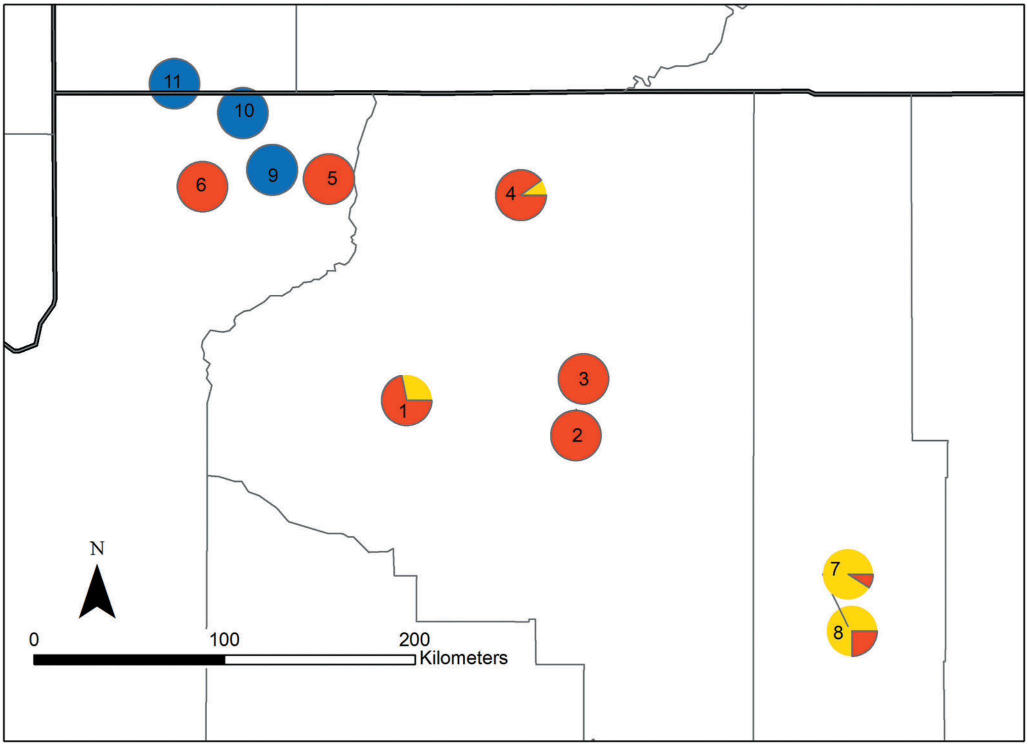


Fig. 8. Classification results, by population, from DFA following Parfitt and Gibson (2003). Yellow represents percentage of individuals classified as *Pediocactus peeblesianus* subsp. *peeblesianus*; red *P. peeblesianus* subsp. *fickeiseniorum* Lüthy; and blue *P. sileri*.

Table 7. Significantly different character means between *Pediocactus peeblesianus* populations 1, 4, 7, 8 and populations 2, 3, 5, 6.

Character	**Character means, in mm except for angles, which are in degrees**		
	P. peeblesianus var. *peeblesianus*	*P. peeblesianus* var. *fickeisenii*	Difference between means
Tubercle height	4.7	5.7	1
Radial spine number	3.4	5.2	1.8
Central spine length	10.9	16.7	5.8
Central spine angle	47	70	23
Central spine curvature	2.2	4.6	2.4
Radial spine angle	164	147	17
Radial spine curvature	0.95	0.17	0.78
Central spine width	0.73	0.64	0.09
Radial spine width	0.58	0.33	0.25
Radial spine sponginess	0.19	0.12	0.07

Table 8. Model summaries for linear regression analyses. Stem diameter is the predictor or independent variable.

	R	**R^2**	**Adjusted R^2**	**Std. Error of the Estimate**
Tubercle height	0.705	0.497	0.495	0.8689
Length between areoles	0.604	0.365	0.362	1.1364
Central spine length	0.577	0.332	0.330	5.6788
Central spine angle	0.528	0.278	0.275	19.5134

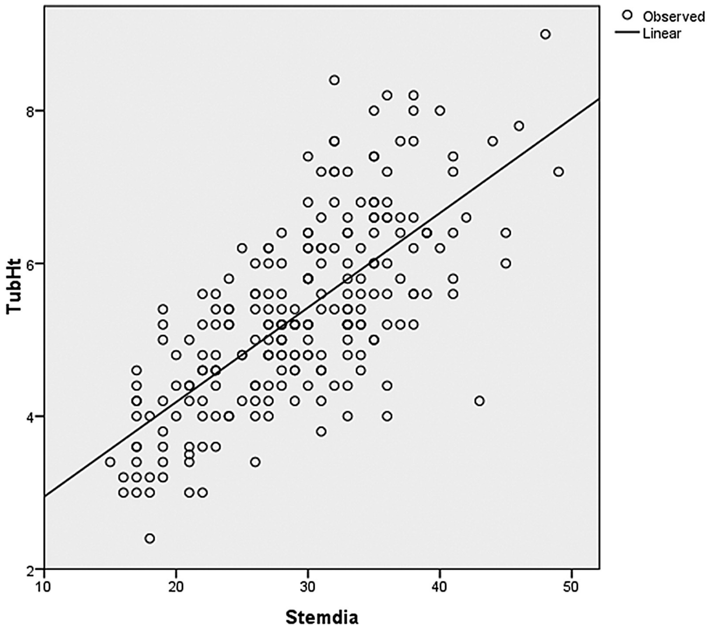


Fig. 9. Regression curve estimation between stem diameter (independent) and tubercle height (dependent).

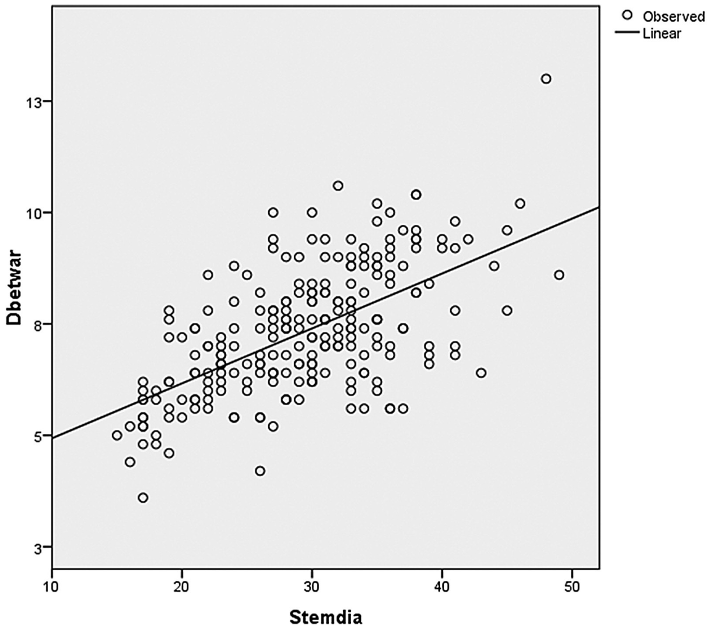


Fig. 10. Regression curve estimation between stem diameter (independent) and distance between areoles (dependent).

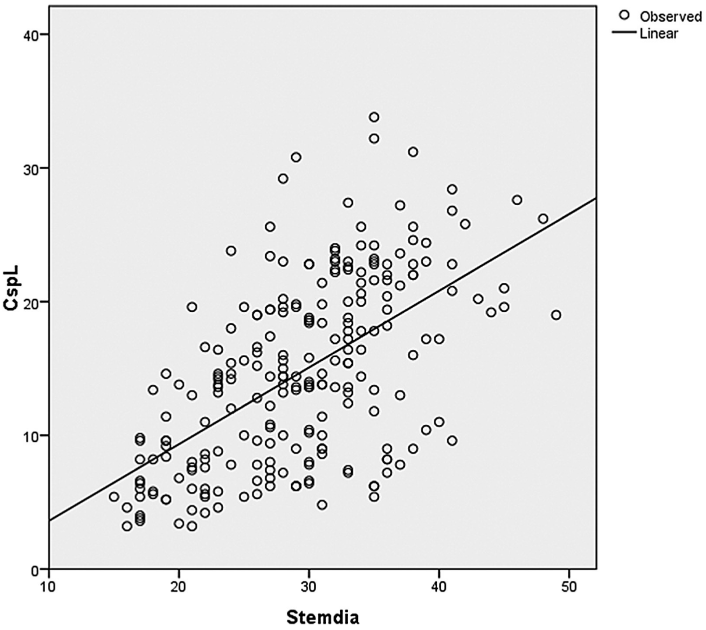


Fig. 11. Regression curve estimation between stem diameter (independent) and central spine length (dependent).

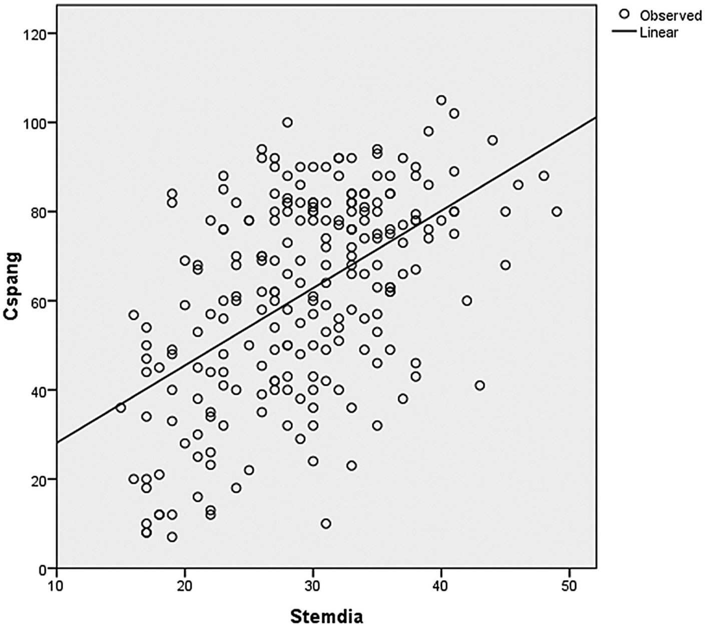


Fig. 12. Regression curve estimation between stem diameter (independent) and central spine angle (dependent).

populations correlated poorly with geography. This is a good example of the power of DFA to produce groupings that are statistically different from one another and cautions against the acceptance of *a priori* groups without testing the significance of other possible groupings, especially those that may be indicated by cluster analysis or PFA. Although Porter's DNA data suggested the recognition of *P. peeblesianus* var. *fickeisenii* as genetically distinct from the typical variety, his data can at best be considered preliminary, due to previously-discussed sample size issues.

Individuals at the type locality (population 4) of *Navajoa peeblesiana* subsp. *menzelii* appear to be closely allied morphologically to those of Benson's *Pediocactus peeblesianus* var. *peeblesianus* (populations 7 and 8) or Parfitt and Gibson's (2003) *P. peeblesianus* subsp. *peeblesianus*. This is best shown by the number of individuals in population four classified by DFA as *P. peeblesianus* subsp. *peeblesianus*. Hochstätter (2007) defines *N. peeblesiana* subsp. *menzelii* by its brownish flower and more robust habit. Photographs by Greg Goodwin indicate that flower color of individuals in that area vary from pale yellow-pink to pale pink (Fig. 13A, B), while individuals near the lectotype locality for *P. peeblesianus* var. *fickeisenii* vary from yellow-pink to pale yellow (Fig. 13C, D). From the small number of observations recorded, it appears that the Cataract Canyon individuals tend to have yellow-pink flowers, and individuals in at least some of the other populations tend to have pale yellow flowers. However, this correlation appears weak given that such flower color variation occurs within other species of *Pediocactus* (Butterworth 2012; Heil & Porter 2003). With respect to the putative robust habit of the Cataract Canyon population, individuals sampled from that population in the present study were smaller than those in most of the other populations. The mean stem diameter for the Cataract population was 22.3 mm, while those of the remaining populations, except the easternmost, varied between 28.9 and 32.6 mm. Only the mean for population 8 (Joseph City 2) was smaller, at 21.9 mm.

At least some of the morphological variation within *Pediocactus peeblesianus* is attributable to maturity, as values for several characters are correlated with those of stem diameter. Larger plants have significantly longer tubercles, distances between tubercles, longer central spines, and larger central spine angle. Also, PFA indicated that plant size (stem diameter) had a much greater influence on the clustering of individuals of *P. peeblesianus* than did current taxonomic lines. Thus, some of the taxonomic confusion may be attributed to neoteny, which occurs in other genera, such as *Coryphantha* (Zimmerman 2003). Parfitt and Gibson (2003) note that within the subfamily Cactoideae, flowering may begin before individuals attain their adult stem morphology, and that such neotenous individuals have sometimes been misidentified and even named as new species based on their juvenile morphology. Habitat appears to play a role with respect to neoteny in *P. peeblesianus*, where individuals growing in shallow soils tend to maintain their juvenile morphology long after they first flower, while individuals in deeper soils tend to become much larger and develop a more typical adult morphology before or soon after they first flower. This phenomenon is especially apparent in the populations near Joseph City but also occurs in other areas.

CONCLUSION

In conclusion, based on our morphological data, there is no practical manner in which to segregate groups of populations within *Pediocactus peeblesianus* to form any natural taxonomic boundaries. There is a weak morphological cline from the west to the east, in which central spines increase in number and length, and radial spines decrease in thickness. Populations of typical *P. peeblesianus* were based on neotenous individuals that probably occurred on very shallow soils, while those of *P. peeblesianus* var. *fickeisenii* occurred on deeper soils farther west along the east-west cline. The creation of artificial taxonomic groups based solely on either geography, a single morphological character, or a combination of overlapping morphological characters that are not correlated with geography defeats the true nature of taxonomy, which is to provide names for recognizable entities of common evolutionary descent. In the case of *P. peeblesianus*, of the several possible morphological groupings of populations, none are markedly distinctive. Although taxonomy at the subspecific level is concerned with detecting nearly independent biological lineages, many of which can be morphologically cryptic, the definition of an independent biological lineage is a matter of degree. In Cactaceae,

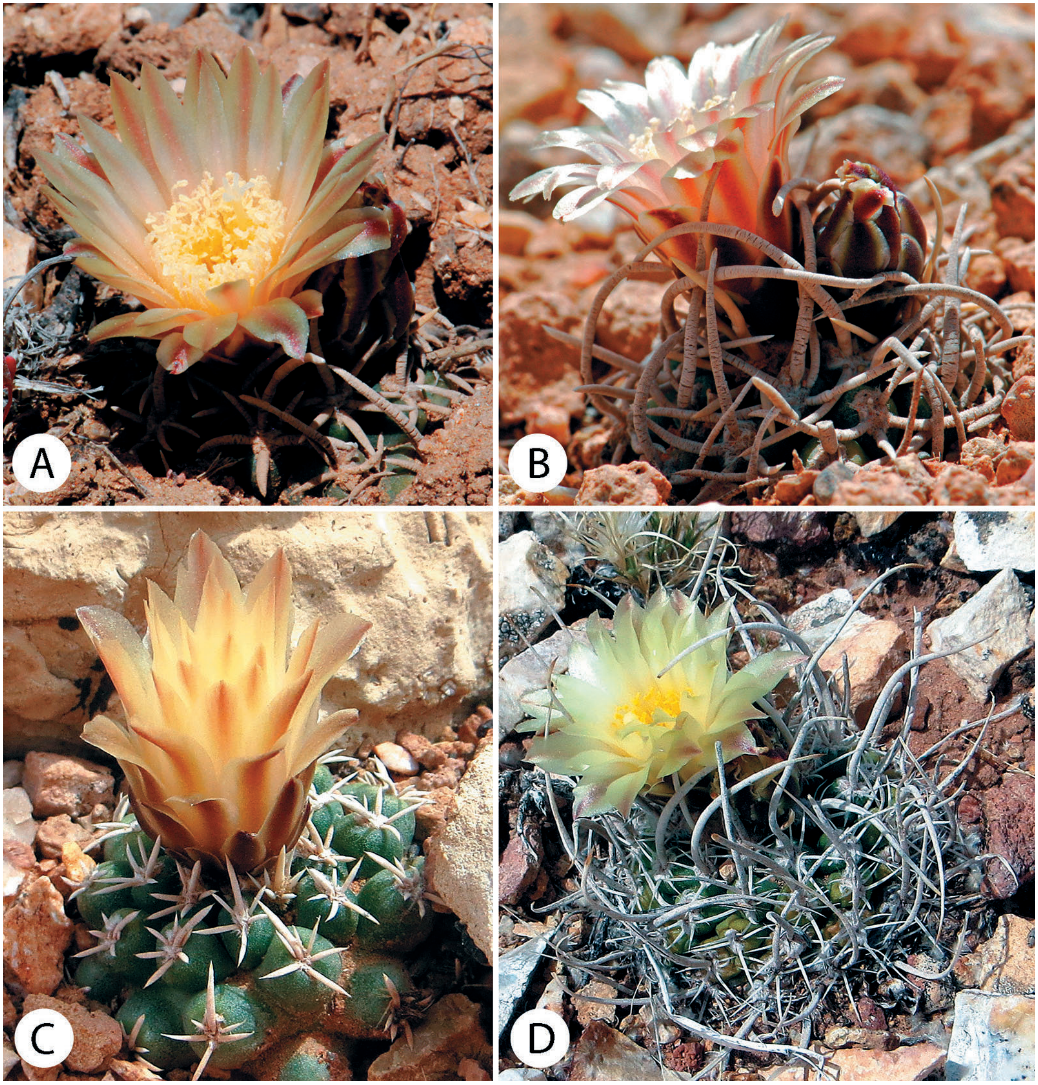


Fig. 13. *Pediocactus peeblesianus* variation in flower color and habit. **A.** Flowering individual of *P. peeblesianus* from Cataract Canyon (Population 1). Photograph by Greg Goodwin. Notice remarkable resemblance to Croizat's type specimen of *Navajoa peeblesianus* (Fig. 3); **B.** Flowering individual of *Pediocactus peeblesianus* from Cataract Canyon (Population 1). Photograph by Greg Goodwin; **C.** Flowering individual of *Pediocactus peeblesianus* from the Little Colorado Gorge (Population 3). Photograph by Michelle Cloud-Hughes; **D.** Flowering individual of *Pediocactus peeblesianus* from the Little Colorado Gorge (Population 3). Photograph by Michelle Cloud-Hughes.

populations circumscribed within a single taxon are often geographically isolated from one another and, at best, rarely exchange genes. If every such population were named based on slight but consistent genetic differences, the taxonomy for many genera within the family would become unmanageable.

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