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## RAPOPORT'S RULE: A COMPARATIVE ANALYSIS BETWEEN SOUTH AND NORTH AMERICAN COLUMNAR CACTI

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The geographical range of species belonging to a number of taxonomic groups tends to decrease toward the Tropics (Stevens 1989). This latitudinal pattern has been well documented over the past 30 yr, and several explanations have been put forth, including environmental history (Rapoport 1975, 1982), competition (Rapoport 1975, 1982; Rosenzweig 1975; Anderson and Koopman 1981), local climate and species environmental tolerances (Stevens 1989), the mass effect (the establishment of species in sites where they cannot self-maintain; Stevens 1989, 1992), the species dispersion capabilities and their ecophysiological properties (Stevens 1989; France 1992), and sampling bias (Colwell and Hurtt 1994). The empirical biogeographical rule that states that the latitudinal extent of the geographical range of organisms is positively correlated with the latitude at which these organisms are found was named Rapoport's rule by Stevens (1989), after the Argentine biogeographer Eduardo Rapoport, who first made reference to the correlation between range and latitude (see Rapoport 1975, 1982).

The idea that geographical ranges increase from the Tropics toward the poles has received close attention over the last several years (Stevens 1989; Pagel et al. 1991; France 1992; Rohde 1992; Rohde et al. 1993; Colwell and Hurtt 1994; Roy et al. 1994; Ruggiero 1994; Smith et al. 1994; Rohde 1996; Rohde and Heap 1996). Although Rapoport's rule has been tested on several groups in different regions, most of these studies have focused on animals (Rohde 1996; Rohde and Heap 1996), and few of them have been done for South America (Ruggiero 1994). A comparative study addressing the relationship between mean latitude and latitudinal range for one group of species in both South and North America has not been done.

The purpose of this note is to examine the validity of Rapoport's rule for species of columnar cacti along tropical-subtropical gradients in both South and North America. We chose this group of plants because they have been well col-

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lected in both continents as a result of their conspicuousness in the field. Our objective was to investigate whether the rule applied in the same manner in two continents or whether other factors such as the size or shape of the continent could introduce differences in the way the rule is expressed.

#### METHODS

Two databases, one for the 60 species of columnar cacti that occur in Mexico and the other for the 50 columnar species that occur in Argentina, were used (for the list of species, see the appendix; Mourelle and Ezcurra 1996). The first database contains 2,200 records (i.e., georeferenced localities) of Mexican species, some of which may range into border countries (the United States and Guatemala). The second database includes 1,050 georeferenced records of Argentine species, also ranging in some cases into border countries (Bolivia, Brazil, Chile, Peru, Paraguay, and Uruguay). Although it would have been desirable to expand the list of South American cacti to species not found in Argentina, for practical reasons we had to restrict the species set in South America to herbaria and published references to which we had adequate access at the time the fieldwork was done. All records came from herbarium labels or published references, and they were digitized onto  $1^\circ \times 1^\circ$  maps of North and South America.

The latitudinal range of each species was calculated as the difference between the highest latitudinal boundary of the quadrat farthest from the equator, minus the lowest latitudinal boundary of the quadrat nearest the equator. In a similar manner, we calculated for each species its longitudinal range by subtracting the lowest longitudinal boundary of the quadrat nearest to the Greenwich meridian from the highest longitudinal boundary of the quadrat farthest from the meridian. We also calculated the area occupied by each species, as the sum of the areas of each quadrat where the species was found to occur. Finally, the mean latitude of each species was calculated as the average of the latitudes of the central point of all the quadrats where the species was recorded. Thus, for both Mexican and Argentine columnar cacti, the original database was summarized into a new database in which each species was represented by its mean latitude, its latitudinal range, its longitudinal range, and its area of distribution.

This database was not suitable for regression analysis, as the dispersion of the points, taking mean latitude as the independent variable and any of the other three variables as the dependent one, failed to conform to the standard criteria of homoscedasticity (homogeneity of variances) that are required for valid regression tests (fig. 1). To obtain a set of points that conformed to the required statistical criteria, we first sorted all the species by their mean latitude, both for Mexico and Argentina. We then merged the species in groups of five, starting from the five most tropical species. For each group, we calculated the mean latitude of the group as the average of the five mean latitudes. Similarly, we calculated the mean latitudinal range, the mean longitudinal range, and the mean distribution area of each group. Finally, we included in the new database the

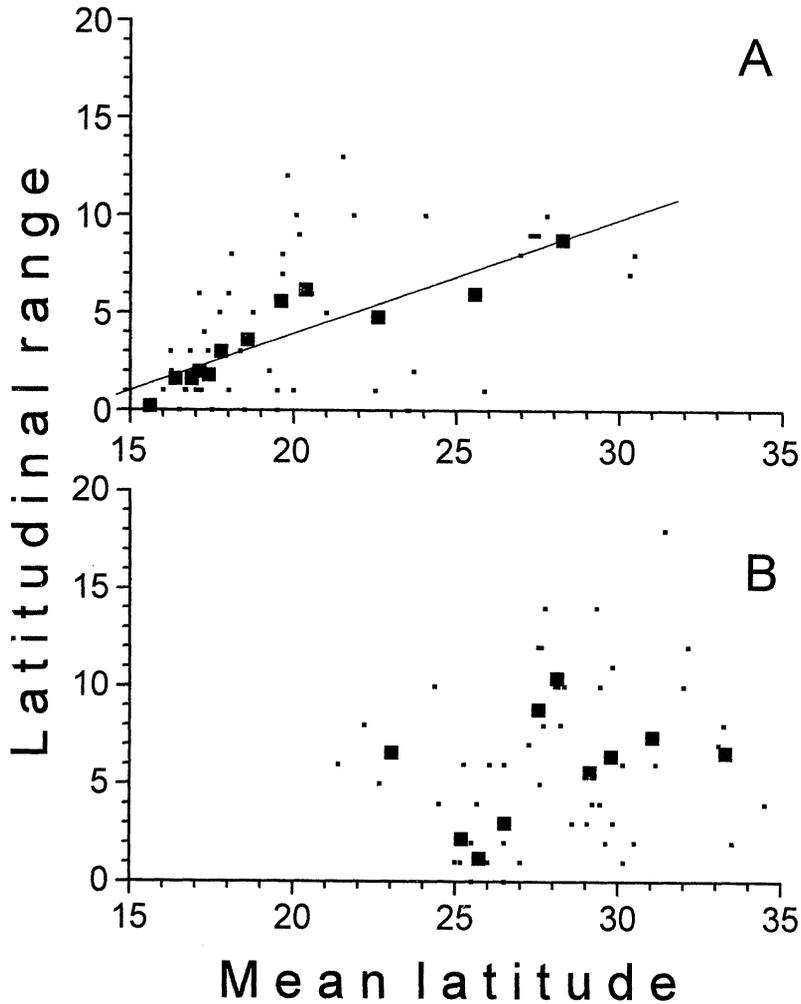


FIG. 1.—Relationship between mean latitude and mean latitudinal range for groups of five species in (A) Mexico and (B) Argentina. The significant regression line is indicated for Mexico. The smaller data points show the dispersion of the original (ungrouped) data.

standard deviation of these values. Thus, the Mexican database was reduced from 60 species to 12 mean data points, and the Argentine database was reduced from 50 species to 10 data points. With this method, each species was represented in only one data point, and the statistical problem of nonindependence criticized by Rohde et al. (1993) with Stevens's original method was thus avoided. Another source of nonindependence may arise from the fact that the species are phylogenetically related and hence may share attributes such as range size. Thus, the observed patterns could be an effect of phylogenetic rela-

tionships (see Harvey and Pagel 1991). Because the phylogeny of columnar cacti is still poorly known (particularly in South America), the potential effect of phylogenetic relatedness on the distribution of the data points was ignored in this study.

With these mean values, we performed a series of regression analyses with the mean latitude of each group of five species as the independent variable and the mean latitudinal and longitudinal ranges, the mean distribution area, and the standard deviations of these values as the dependent variables. We also included as independent variables the mean continental width and the habitat heterogeneity that corresponded to each mean latitude. The mean continental width was calculated by measuring, for each species, the nearest distances from the species center of distribution to the Atlantic and Pacific Oceans, adding these two distances and then averaging the resulting value for each group of five species. We used a map of scale 1:400,000 for North America and of scale 1:800,000 for South America. Habitat heterogeneity was estimated in two different ways: by counting the total number of phytogeographical units or provinces (to which we shall refer also as habitats) intersected by a linear transect at each mean latitude (if the same unit was found several times along a transect, it was counted each time it was found) and by counting the total number of distinct vegetational units (i.e., without repetitions). We used Cabrera and Willink's (1980) map of biogeographical provinces for South America; we used Rzedowski's (1990) phytogeographical map for Mexico, supplemented by Aldrich (1963) for the United States and by Loftas (1972) for Central America.

Finally, we counted the number of columnar cactus species in each quadrat of the  $1^\circ \times 1^\circ$  grid. To test whether a latitudinal trend in species richness existed in both North and South America, these species-richness values were regressed against quadrat latitude. For this purpose, log-linear models were used as species richness values are frequency counts (Crawley 1993; see also Mourelle and Ezcurra 1996); in the case of our species-richness data set, they showed a strongly nonnormal distribution of errors.

#### RESULTS

In Mexico, the mean latitudinal range was significantly correlated with mean latitude ( $r = 0.91$ ,  $P = .00004$ ; fig. 1A) and with mean continental width ( $r = 0.57$ ,  $P = .05$ ). Additionally, both the mean distribution area of the species and the mean longitudinal range were also significantly correlated with latitude and continental width ( $r = 0.89$ ,  $P = .0001$ , and  $r = 0.87$ ,  $P = .0002$  for distribution area against latitude and continental width, respectively;  $r = 0.60$ ,  $P = .04$ , and  $r = 0.63$ ,  $P = .03$  for longitudinal range against the same variables).

In contrast, the Argentine species did not show a significant linear association between mean latitudinal range and mean latitude ( $r = 0.38$ ,  $P = .28$ ; fig. 1B) or between latitudinal range and any other predictor. In a similar manner, the mean distributional areas and the mean longitudinal ranges were uncorrelated with the possible predictors.

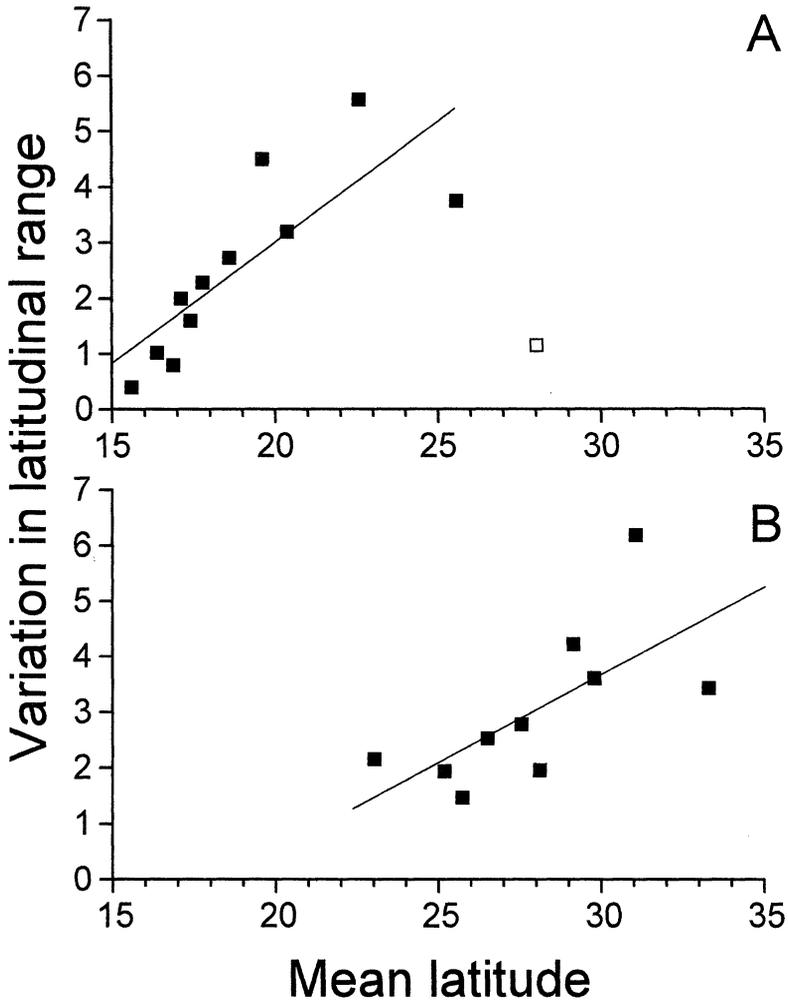


FIG. 2.—Relationship between mean latitude and the standard deviation of the mean latitudinal range for groups of five species in (A) Mexico and (B) Argentina. The significant regression lines are indicated for both countries; the outlying northernmost data point in Mexico (shown as an open square) was not included in the regression.

In both hemispheres, however, the variation of the latitudinal ranges decreased significantly toward the equator ( $r = 0.80$ ,  $P = .003$  for Mexico;  $r = 0.68$ ,  $P = .03$  for Argentina; fig. 2). In Mexico, an outlying point of low variation in latitudinal ranges was found at mean latitude  $28^{\circ}24'$ . This point corresponds to five wide-ranging species (*Pachycereus schottii*, *Bergerocactus emoryi*, *Carnegiea gigantea*, *Stenocereus gummosus*, *Stenocereus thurberii*) of the northern Sonoran Desert in Mexico and Arizona, a region where there are no microendemisms. Solely because of this point, the number of habitats was also a significant predictor of variation in latitudinal range in the Mexican columnar

cacti. If the point is removed, however, latitude becomes the best predictor of the variation in latitudinal range. That is, at higher latitudes, species with wide ranges coexist in both continents with species with restricted ranges or microendemisms. In Mexico, a similar pattern was found for the standard deviation of the distributional areas, which was significantly correlated with latitude ( $r = 0.62$ ,  $P = .03$ ). In Argentina, the variation of the distributional areas was uncorrelated with latitude. Finally, a significant inverse relationship was found between species richness and latitude in both continents when they were regressed by means of log-linear models ( $r^2 = 0.20$ ,  $P < .0001$  for Mexico;  $r^2 = 0.54$ ,  $P < .0001$  for Argentina). Species richness decreased with increasing latitude in both continents (fig. 3).

#### DISCUSSION

In Mexico, the mean latitudinal ranges of the species were positively correlated with mean latitude, which confirmed Rapoport's rule. This, however, did not occur in Argentina. Additionally, in both Mexico and Argentina the variation in the latitudinal ranges increased significantly with latitude, a fact that suggests that wide-ranging species should be more common at temperate latitudes. From this point of view, the data set of Argentine columnar cacti partially supports Rapoport's rule, in the sense that it shows that the widest-ranging species are found at higher latitudes.

Some clues to the contrasting behavior between North and South American columnar cacti can be found in Rapoport (1975). He argued that North America is wider at temperate latitudes and tends to become narrower toward the Tropics. South America, in contrast, follows an opposite trend: continental width increases toward the equator (fig. 4). Rapoport suggested that an alternative explanation of the decreasing ranges toward the Tropics could lie in the shape of the continent, as a factor restricting habitat width. In Mexico, continental width and latitude increase together. This means that if there is a trend for species ranges to increase toward the temperate regions, this trend will be enhanced even further by the combined effect of continental width. In South America, in contrast, the possible effect of greater ranges toward the temperate latitudes will tend to be counteracted by the decreasing continental width. The effect of continental width may also have operated in a historic timescale. Rohde (1996) and Rohde and Heap (1996) noted that Rapoport's rule is observed mostly in northern latitudes, where the effects of the Ice Ages have been greatest and selection for tolerance to temperature fluctuations has been intense during Pleistocene glacial events (Pielou 1979, p. 165). In agreement with this hypothesis, it is important to note that, because the land width of South America decreases toward the higher latitudes, its high-latitude climate is more buffered from extreme temperature changes than in the more continental boreal region of North America. At high latitudes, the effects of glacial events on vegetation change have been lower in South America compared with those in North America (Markgraf 1989).

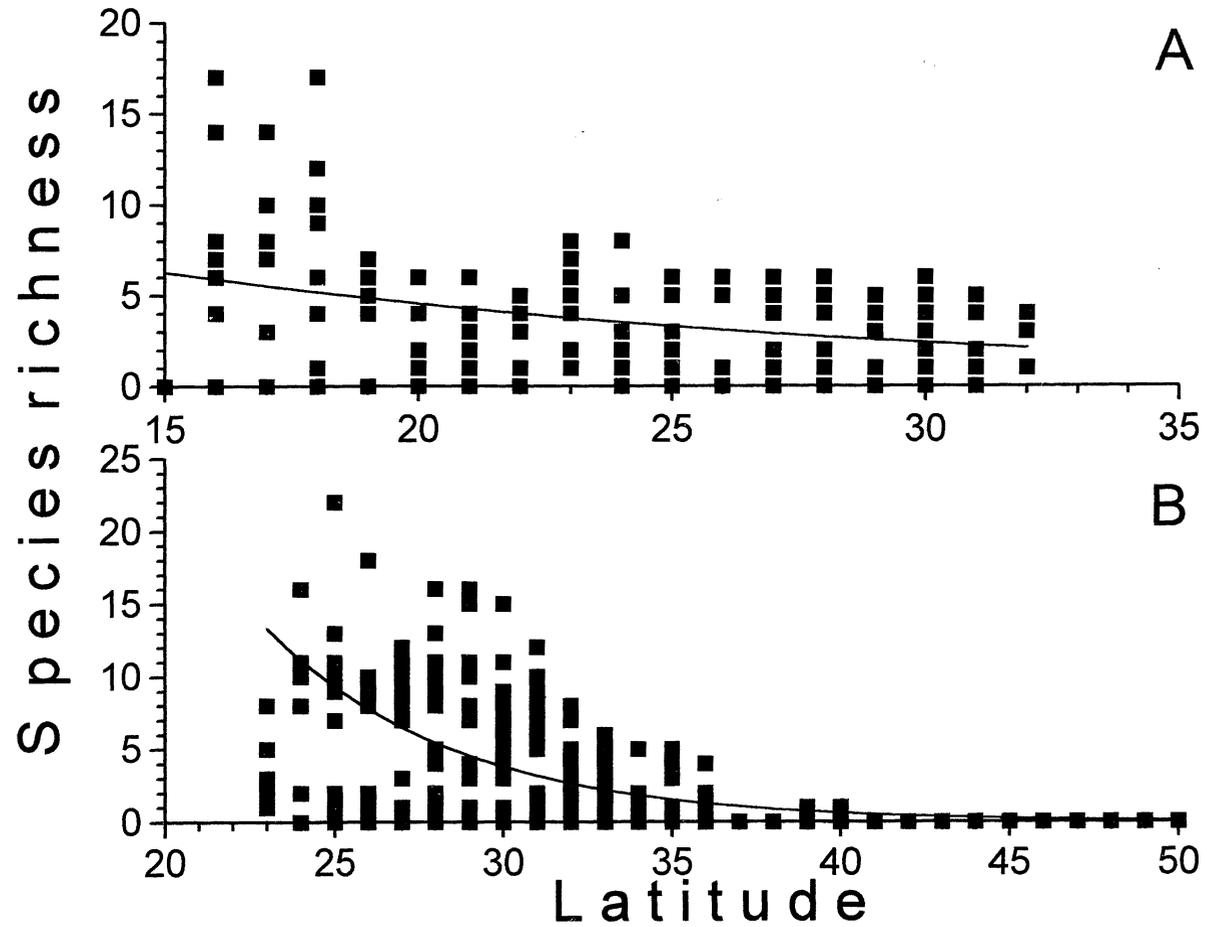


FIG. 3.—Relationship between latitude and species richness for  $1^{\circ} \times 1^{\circ}$  quadrats in (A) Mexico and (B) Argentina. The log-linear regression curves are shown for both countries.

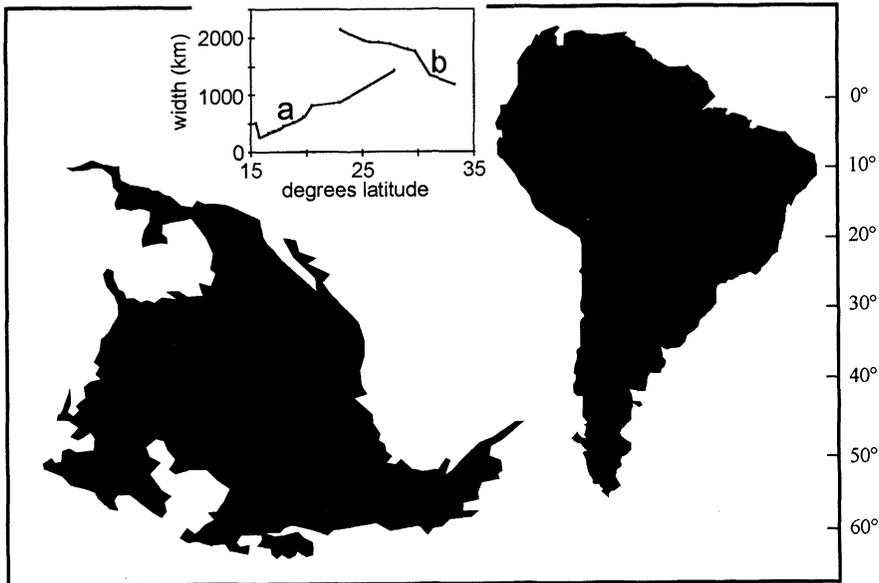


FIG. 4.—Maps of North and South America, plotted on the same latitudinal scale. The upper plot shows the relationship between continental width and latitude for (A) Mexico and (B) Argentina.

In conclusion, the evidence from columnar cacti suggests that, although Rapoport's rule seems to be an important determinant of species ranges, other effects that frequently co-vary with latitude, such as habitat width, may play an extremely important role. It is interesting, in this sense, to note that most of the support for Rapoport's rule comes from distribution data of North American species (Stevens 1989; Pagel et al. 1991; France 1992; Rohde et al. 1993). When data from South America or Australia were analyzed (Smith et al. 1994; Ruggiero 1994), the rule was not always satisfied, and other factors such as continental width and habitat heterogeneity were equally good predictors of species ranges.

According to Stevens, Rapoport's rule and the latitudinal gradient in species richness are both the outcome of the same process: temperate individuals have evolved broader tolerances to climatic factors than tropical individuals, and the broad tolerance has in turn led to wider latitudinal extent in the geographical ranges of high-latitude species than in the ranges of lower-latitude species. It is interesting to note that, while Rapoport's rule holds for the Mexican species and does not apply to the Argentine data set, species richness increased significantly toward the Tropics in both regions. This contradicts Stevens's idea that decreasing species ranges could be a principal factor explaining the temperate-tropical gradient in species diversity, as pointed out earlier by Rohde et al. (1993). In our data set from Argentina, the species-richness gradient occurs even when Rapoport's rule does not hold (Mourelle and Ezcurra 1996).

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## APPENDIX

## TABLE A1

## SPECIES LIST

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Species

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## Argentine columnar cacti:

- Cereus aethiops* Haworth
- Cereus argentinensis* Britton et Rose
- Cereus chalybaeus* Hauman (non Otto)
- Cereus dayami* Speg.
- Cereus forbesii* Haworth
- Cereus hankeanus* Web.
- Cereus stenogonus* K. Sch.
- Cleistocactus baumannii* (Lem.) Lemaire
- Cleistocactus ferrarii* R. Kiesling
- Cleistocactus jujuyensis* (Backbg.) Backbg.
- Cleistocactus smaragdiflorus* (Web.) Britton et Rose
- Denmoza rhodacantha* (SD) Britton et Rose
- Echinopsis leucantha* (Gill.) Walp.
- Echinopsis rodotricha* R. Mey
- Harrisia bonplandii* (Parmentier) Britton et Rose
- Harrisia martinii* (Labouret) Britton et Rose
- Harrisia pomanensis* (Weber) Britton et Rose
- Harrisia tortuosa* (Forbes) Britton et Rose
- Lobivia chrysochete* Werdermann
- Lobivia ferox* Britton et Rose
- Lobivia formosa* (Pfeiff.) Britton et Rose
- Lobivia koretroides* (Werd.) Backbg.
- Lobivia walteri* R. Kiesling
- Monvillea cavendishii* (Monville) Britton et Rose
- Monvillea spegazzini* (Weber) Britton et Rose
- Notocactus shumannianus* Berger
- Oreocereus celsianus* (Lemaire) Riccobono
- Oreocereus trollii* Kupp

TABLE A1 (Continued)

## Species

- Pyrrhocactus umadeave* (Werd.) Backbg.  
*Stetsonia coryne* (Salm-Dyck) Britton et Rose  
*Soehrensia brucchi* (Britton et Rose) Backbg.  
*Trichocereus andalgalensis* (Web.) Hosseus  
*Trichocereus angelesii* R. Kiesling  
*Trichocereus cabreræ* R. Kiesling  
*Trichocereus candicans* (Gillies) Britton et Rose  
*Trichocereus fabrisii* R. Kiesling  
*Trichocereus huascha* (Web.) Britton et Rose  
*Trichocereus lamprochlorus* (Lemaire) Britton et Rose  
*Trichocereus pasacana* (Web.) Britton et Rose  
*Trichocereus pseudocandicans* (Backbg.) ex R. Kiesling  
*Trichocereus rowleyi* (Friedr.) R. Kiesling  
*Trichocereus schickendantzii* (Web.) Britton et Rose  
*Trichocereus smirzianus* (Backbg.) Backeberg  
*Trichocereus spachianus* (Lem.) Ricc.  
*Trichocereus strigosus* (Salm-Dyck) Britton et Rose  
*Trichocereus tarijensis* (Vpl.) Werdermann  
*Trichocereus terscheckii* (Parm.) Britton et Rose  
*Trichocereus thelegonoides* (Speg.) Britton et Rose  
*Trichocereus thelegonus* (Web.) Britton et Rose  
*Trichocereus vatteri* Kiesling
- Mexican columnar cacti:
- Backebergia militaris* (Audot) Bravo ex Sánchez-Mejorada  
*Bergerocactus emoryi* (Engelm.) Britton et Rose  
*Carnegiea gigantea* (Engelm.) Britton et Rose  
*Cephalocereus senilis* (Haworth) Pfeiffer  
*Cephalocereus apicicephalum* Dawson  
*Cephalocereus columna-trajani* (Karw.) Schumann  
*Cephalocereus totolapensis* (Bravo et MacDougall) Buxbaum  
*Escontria chiotilla* (Weber) Rose  
*Mitrocereus fulviceps* (Weber) Backeberg ex Bravo  
*Myrtillocactus cochal* (Orcutt) Britton et Rose  
*Myrtillocactus geometrizans* (Martius) Console  
*Myrtillocactus schenkii* (Purpus) Britton et Rose  
*Neobuxbaumia euphorbioides* (Haworth) Buxbaum  
*Neobuxbaumia macrocephala* (Weber) Dawson  
*Neobuxbaumia mezcalaensis* (Bravo) Backeberg  
*Neobuxbaumia multiareolata* (Dawson) Bravo  
*Neobuxbaumia polylopha* (De Candolle) Backeberg  
*Neobuxbaumia sanchez-mejoradae* Lau  
*Neobuxbaumia scoparia* (Poselger) Backeberg  
*Neobuxbaumia squamulosa* Sheinvar et Sánchez-Mejorada  
*Neobuxbaumia tetetzo* (Coulter) Backeberg  
*Pachycereus gatesii* (M. E. Jones) D. Hunt  
*Pachycereus gaumeri* Britton et Rose  
*Pachycereus grandis* Rose  
*Pachycereus hollianus* (Weber) Buxbaum  
*Pachycereus marginatus* (DC.) Britton et Rose  
*Pachycereus pecten-aboriginum* (Engelmann) Britton et Rose  
*Pachycereus pringlei* (S. Watson) Britton et Rose  
*Pachycereus schottii* (Engelm.) Hunt  
*Pilosocereus alensis* (Web.) Byles et Rowley  
*Pilosocereus chrysacanthus* (Web.) Byles et Rowley  
*Pilosocereus collinsii* (Britton et Rose) Orcutt  
*Pilosocereus cometes* (Scheidweiler) Britton et Rose  
*Pilosocereus leucocephalus* (Poselger) Byles et Rowley

TABLE A1 (Continued)

Species
<i>Pilosocereus purpusii</i> (Britton et Rose) Byles et Rowley
<i>Pilosocereus quadricentralis</i> (Dawson) Backeberg
<i>Polaskia chende</i> (Gossel.) Gibson et Horak
<i>Polaskia chichiipe</i> Backeberg
<i>Stenocereus alamosensis</i> (J. Coulter) Gibson et Horak
<i>Stenocereus beneckeii</i> (Enrenberg) Buxbaum
<i>Stenocereus chacalapaensis</i> (Bravo) Bravo
<i>Stenocereus chrysocarpus</i> Sánchez-Mejorada
<i>Stenocereus dumortieri</i> (Scheidtweiler) Buxbaum
<i>Stenocereus eichlamii</i> (Britton et Rose) Buxbaum
<i>Stenocereus eruca</i> (Brandege) Gibson et Horak
<i>Stenocereus fricii</i> Sánchez-Mejorada
<i>Stenocereus griseus</i> (Haworth) Buxbaum
<i>Stenocereus gummosus</i> (Brandege) Gibson et Horak
<i>Stenocereus kerberi</i> (Schumann) Gibson
<i>Stenocereus laevigatus</i> (Salm-Dyck) Buxbaum
<i>Stenocereus martinezii</i> (González Ortega) Bravo
<i>Stenocereus montanus</i> (Britton et Rose)
<i>Stenocereus pruinosus</i> (Otto) F. Buxbaum
<i>Stenocereus queretaroensis</i> (Weber) Buxbaum
<i>Stenocereus quevedonis</i> (González Ortega) Bravo
<i>Stenocereus standleyi</i> (González Ortega) Buxbaum
<i>Stenocereus stellatus</i> (Pfeiffer) Riccobono
<i>Stenocereus thurberii</i> (Engelmann) Buxbaum
<i>Stenocereus treleasei</i> (Vaupel) Backeberg
<i>Stenocereus weberi</i> (Coulter) Backeberg

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