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# Comparative Serology of a Disjunct Species Group: The Prosopis juliflora-Prosopis chilensis Complex

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# COMPARATIVE SEROLOGY OF A DISJUNCT SPECIES GROUP: THE *PROSOPIS JULIFLORA-PROSOPIS CHILENSIS* COMPLEX

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## Introduction

The genus *Prosopis* is a conspicuous and dominant element of the flora of the arid scrubland of temperate North and South America (Simpson 1976). Its center of speciation is in the dry temperate areas of South America where more than 27 species are distributed primarily in Argentina but also in Chile, Peru, and Paraguay (Burkart 1940; Simpson 1976). Disjunct species or species pairs are recognized in three sections of the genus (Raven 1963). In section *Algarobia, P. chilensis* (Mol.) Stuntz, distributed in the dry temperate areas of Chile (and in more restricted areas of Argentina), is morphologically very similar to some populations of *P. juliflora* DC., sensu lato, widely distributed in the dryer regions of North and Central America (including the Caribbean) and in northern Venezuela and Colombia. Johnston (1962) indicates that among the many taxa recognized for the *P. juliflora* complex, *P. glandulosa* Torr., distributed in Texas, northeastern Mexico, Arizona, and California, is closest morphologically to *P. chilensis*.

Cytologically, all the species of *Prosopis* appear to be undifferentiated. A chromosome number of $2n = 28$ has been reported for all the species studied (Covas and Schnack 1947; Cherubini 1954; Baquar et al. 1966; Fedorov 1969; Hunziker et al. 1975). However, tetraploids ($2n = 56$) have also been reported in *P. juliflora* by Atchison (1951) and Hunziker et al. (1975), and tetraploids and octaploids ($2n = 56, \approx 112$) in *P. striata* Benth. by Castronovo (1945).

Biochemical systematic studies have been carried out recently by Carman (1973) using free amino acids and flavonoid markers. All species tested, irrespective of their taxonomic position, had very similar concentrations of the same two nonprotein amino acids: Pipecolic acid and 4-hydroxy pipecolic acid (Carman 1973; Carman et al. 1974; Simpson 1976). However, North American species of *Prosopis* of section *Algarobia* were differentiated from the South American species of the *P. chilensis* "complex" in their flavonoid patterns (Carman 1973; Simpson 1976). A high degree of intraspecific genetic variability for most species has been inferred by Solbrig and Bawa (1975) from an analysis of isozyme variation among 15 American species of the genus. However, no clear patterns of genetic differentiation between the South American and North American populations could be ascertained from such study (Simpson 1976).

A comparative serological study of selected Argentinean species of *Prosopis* has been reported by Cohen, Cei, and Roig (1966). This preliminary study involved selected species from sections *Algarobia, Strombocarpa,* and *Molinicarpa* and used both quantitative precipitin techniques (Boyden 1964; Glenn 1962) and one-dimensional diffusion techniques (Oudin 1952). Cohen et al. (1966) found that the species of section *Algarobia*: *P. chilensis, P. alpataco* Phil., *P. caldenia* Burkart, and *P. flexuosa* DC. were serologically rather similar, particularly the first two taxa. *Prosopis sericantha* Gill. ex Hook., also of section *Algarobia,* was, however, differentiated from the other species as was *P. argentina* Burkart (sect. *Molinicarpa*). There was little serological correspondence between the species of section *Strombocarpa*: *P. strombulifera* Benth. and *P. torquata* DC., and there was no serological affinity between either of these species and those of section *Algarobia.*

The purpose of this study was to investigate the relationship of related disjunct taxa of section *Algarobia* based on comparative serological analyses. Serological tests have proved useful for estimating the relationships among organisms as a complementary approach to more conventional biosystematic studies (Fairbrothers 1968; Simon 1969, 1970, 1971). The objective of this research was to discriminate between two opposed hypotheses which have been proposed to explain the presence of related or identical disjunct taxa:

a) That the taxa are the remnants of a once continuous distribution or that the species evolved from common tropical ancestors through parallel selective influences and independently in both hemispheres. Disjuncts would not be related and their morphological similarities would be the result of convergent evolution. A priori, one would expect to find conspicuous serological differences between the taxa as a result of long periods of evolution in geographical isolation (Raven 1963; Solbrig 1972).
b) The presence of similar or identical disjunct taxa is the result of more recent, postpliocene to postpleistocene, long-distance dispersal (transtropical migration) (Raven 1963). The short period of isolation between taxa should be reflected in a pattern of close serological similarity, particularly since reserve proteins of seeds of Leguminosae are reported to be conservative in their antigenic structures (Lester et al. 1965; Simola 1969; Simon 1969; Selim et al. 1977).

## Materials and Methods

Seed samples of several accessions of *P. chilensis,* "*P. juliflora,*" and other species of sections *Algarobia, Strombocarpa,* and *Cavenicarpa* were assembled for this study, as indicated in Table 1. Each accession represented pooled seeds from one tree. Antigen extracts were prepared from

seed meals according to the technique described earlier (Simon 1969, 1970, 1971) but without pre-extraction of lipids. Antisera were produced against one accession each of *P. juliflora* (Sw.) DC. (JU-1) and *P. chilensis* (CHI-1) following an immunization schedule similar to that of Simon (1970). All injections were administered intraperitoneally and pooled antisera from pairs of rabbits were used.

Immunodiffusion (ID) and Immunoelectrophoresis (IE) techniques have been used during the course of this investigation (Öuchterlony 1964; Grabar 1964). Additional information was obtained with absorbed antisera using the double immunodiffusion technique of Öuchterlony (1964) as described by Simon (1969). Immunoelectrophoresis was carried out, according to the technique of Lester, Alston, and Turner (1965), to further establish the identity of some antigen-antibody reactions remaining after absorption. The interpretation of the comparative precipitation patterns follows Öuchterlony (1964) as described by Simon (1969).

## Results

Antisera produced against *P. juliflora* (JU-1) reacted similarly against extracts of the five accessions of this species complex. Öuchterlony plates disclosed a complex pattern of six to eight precipitin bands showing that the five accessions are serologically very similar (Table 2). Extracts of *P. chilensis* and of other South American species shared only one to four bands with Ju-1 indicating clear-cut differences between the disjunct species complexes (Table 2).

These differences were confirmed in absorption tests because three to five precipitin bands were present in the ID plates after test-reactions with anti-JU-1 serum absorbed with CHI extracts. On the other hand, no consistent reactions were observed when the absorption of the anti-JU-1 serum was performed with extracts of other accessions of JU (Table 2).

IE tests confirmed and clarified the patterns of serological differentiation between the taxa. IE plates with anti-JU-1 serum showed that the five accessions of that species were serologically similar but not identical (Fig. 1a). At least seven immunoprecipitin arcs were discernible in the test reaction and the IE spectra of JU-1 and JU-2 were qualitatively identical. The other three accessions, however, were distinguished from JU-1 and JU-2 by differences in the mobility of the anodal bands. Furthermore JU-4 and JU-5 spectra lacked one of the arcs (located close to the origin) which was present in the spectra of the other accessions (Fig. 1a). The two most extreme IE patterns obtained in reactions between anti-JU-1 serum and CHI antigens indicated that these taxa shared only three to four antigens with JU. In addition, the intensity of the arcs was reduced and their positions in the electric field indicated that the proteins had dissimilar electrophoretic mo-

Table 1. Locality of collection of seed samples of *Prosopis*.

| Species sensu Burkart (1940) and Johnston (1962) | Locality of collection | Section of genus | Abbreviation as used in text |
|---|---|---|---|
| *P. laevigata* (Humb. & Bonpl. ex Willd.) Johnst. | Rt. 150, beyond Tecamachalco, 37 mi from Tehuacan, Prov. Puebla, Mexico. *Solbrig 4113.* | *Algarobia* | JU-1 |
| *P. laevigata* | Ixmiquilpan, Prov. Hidalgo, Mexico. Coll. by J. Rzedowski, *No. 271.* | *Algarobia* | JU-2 |
| *P. glandulosa* Torr. var. *glandulosa* | 1 mi N of La Esperanza, Monterrey, Prov. Nuevo Leon, Mexico. *Solbrig 4101.* | *Algarobia* | JU-3 |
| *P. glandulosa* var. *torreyana* (L. Benson) Johnst. | 6 mi N of Camargo on Hy. 45, Prov. Chihuahua, Mexico, *Solbrig 4129.* | *Algarobia* | JU-4 |
| *P. glandulosa* var. *torreyana* | Rancho Santa Ana Botanic Garden, Claremont, Calif., U.S.A. *No. 7023.* | *Algarobia* | JU-5 |
| *P. chilensis* (Mol.) Stuntz | Rio Huasco, 5 mi W of Vallenar, Prov. Atacama, Chile. Coll. S. Lailhacar, *No. 434.* | *Algarobia* | CHI-1 |
| *P. chilensis* | Near San Luis, Prov. San Luis, Argentina. Coll. D. E. Anderson, *No. 521.* | *Algarobia* | *CHI-2* |
| *P. chilensis* | Quebrada de la Plata, La Rinconada, Maipú, Prov. Santiago, Chile. Coll. G. Pincheira, *No. 417.* | *Algarobia* | *CHI-3* |
| *P. chilensis* | San Pedro de Atacama, Prov. Antofagasta, Chile. Coll. S. Lailhacar, *No. 435.* | *Algarobia* | *CHI-4* |
| *P. chilensis* | Rt. 60, 10 km E of San Felipe, Prov. Aconcagua, Chile. Coll. J.-P. Simon, *No. 412.* | *Algarobia* | *CHI-5* |
| *P. chilensis* | Rt. 60, 3 km W of Los Andes, Prov. Aconcagua, Chile. Coll. J.-P. Simon, *No. 365.* | *Algarobia* | *CHI-6* |
| *P. chilensis* | Rt. 57, 6 km S of Pocuro, Prov. Aconcagua, Chile. Coll. J.-P. Simon, *No. 401.* | *Algarobia* | *CHI-7* |

Table 1. Continued.

| Species sensu Burkart (1940) and Johnston (1962) | Locality of collection | Section of genus | Abbreviation as used in text |
|---|---|---|---|
| *P. chilensis* | Rt. 5, 1 km N of Rungue, Prov. Santiago, Chile, Coll. J.-P. Simon, *No. 351.* | *Algarobia* | *CHI-8* |
| *P. alba* Gris | 10 km E of Salta, Provincia de Salta, Argentina, Coll. J.-P. Simon, *No. 514.* | *Algarobia* | *ALB* |
| *P. nigra* (Gris) Hiéron | Near San Luis, Prov. de San Luis, Argentina. Coll. D. E. Anderson, *No. 194.* | *Algarobia* | *NIG* |
| *P. caldenia* Burk. | San Luis, Prov. de San Luis, Argentina. Coll. D. E. Anderson, *No. 218.* | *Algarobia* | *CAL* |
| *P. alpataco* Phil. | Pailemán, Dept. Valcheta, Prov. Rio Negro, Argentina. Coll. J. Hunziker, C. A. Naranjo, & R. A. Palacios, *No. 8663.* | *Algarobia* | *ALP* |
| *P. patagonica* Speg. | 71 km W of La Grande, Dept. Valcheta, Prov. Rio Negro, Argentina. Coll. J. Hunziker, C. A. Narango, & R. A. Palacios, *No. 8712.* | *Algarobia* | *PAT* |
| *P. pubescens* Benth. | Rancho Santa Ana Botanic Garden, Claremont, Calif., U.S.A. *No. 7873.* | *Strombocarpa* | PUB |
| *P. tamarugo* Phil. | Canchones, Dept. Iquique, Prov. Tarapaca, Chile. Coll. F. Sudsuki, *No. 624.* | *Cavenicarpa* | TAM |

Table 2. Number and type of precipitin bands produced in reactions between anti-Ju-1 or anti-Chi-1 sera unabsorbed and absorbed, and extracts of taxa of *Prosopis*. (Tests performed in Öuchterlony plates).

| Antigen & Absorbant* | Anti-JU-1 serum | | Anti-CHI-1 serum | |
|---|---|---|---|---|
| | Unabsorbed | Absorbed with: | Unabsorbed | Absorbed with: |
| JU-1, JU-3, JU-5 | 7–8 | 0 | 2(1) | 6–7 |
| JU-2, JU-4 | 6(1)** | 0 | 1(2) | 6–8 |
| CHI-1, CHI-2, CHI-4 CHI-6, CHI-8 | 3–4(1) | 3 | 8–10 | 0 |
| CHI-3 | 3(1) | 4 | 8(2) | 0 |
| CHI-5 | 3(2) | 3 | 8(1) | 0 |
| CHI-7 | 3(1) | 4 | 8(1) | 1 |
| ALB | 4 | 4 | 5(2) | 3 |
| ALP | 2(1) | 3 | 6(1) | 4 |
| NIG | 1 | 4 | 5(2) | 3–4 |
| CAL | 1(1) | 4 | 5(1) | 3 |
| PAT | 0 | 6 | 0 | 8 |
| PUB | 0 | 5 | 0 | 7–8 |
| TAM | 0 | 6–7 | 0 | 8–9 |

* Extracts used to absorb the antisera before performing test-reactions.

** Numbers in parenthesis refer to type III precipitin bands; partial identity bands according to Öuchterlony (1964).

bilities to those of JU antigens. Absorption tests (Fig. 2a) corroborated the serological differences since about six immunoprecipitin systems remained in the homologous reaction after absorption of anti-JU-1 serum with extracts of *P. chilensis* and *P. alpataco*.

Antisera prepared against *P. chilensis* (CHI-1) produced a complex of eight to ten precipitin bands in ID plates when reacted against the eight accessions of the species (Table 2). Reactions involving this antiserum and other South American taxa such as *P. alba, P. nigra, P. alpataco,* and *P. caldenia* produced between four and seven bands of which one or two were partial identity (Type III of Öuchterlony 1964) reactions giving rather faint bands (Table 2). Accessions of *P. juliflora* gave only two to three precipitin bands of which one or two were also Type III bands (Table 2).

Absorption tests indicated that, with the exception of CHI-3, all accessions of the species were serologically similar. One precipitin band remained in homologous reactions involving anti-CHI-1 serum absorbed with CHI-3. The absorption tests showed that South American species of section *Algarobia* were serologically more similar to *P. chilensis* than taxa of the North American *P. juliflora* complex since fewer bands were seen in homologous reactions with anti-CHI-1 serum absorbed with extracts of South American species (Table 2).

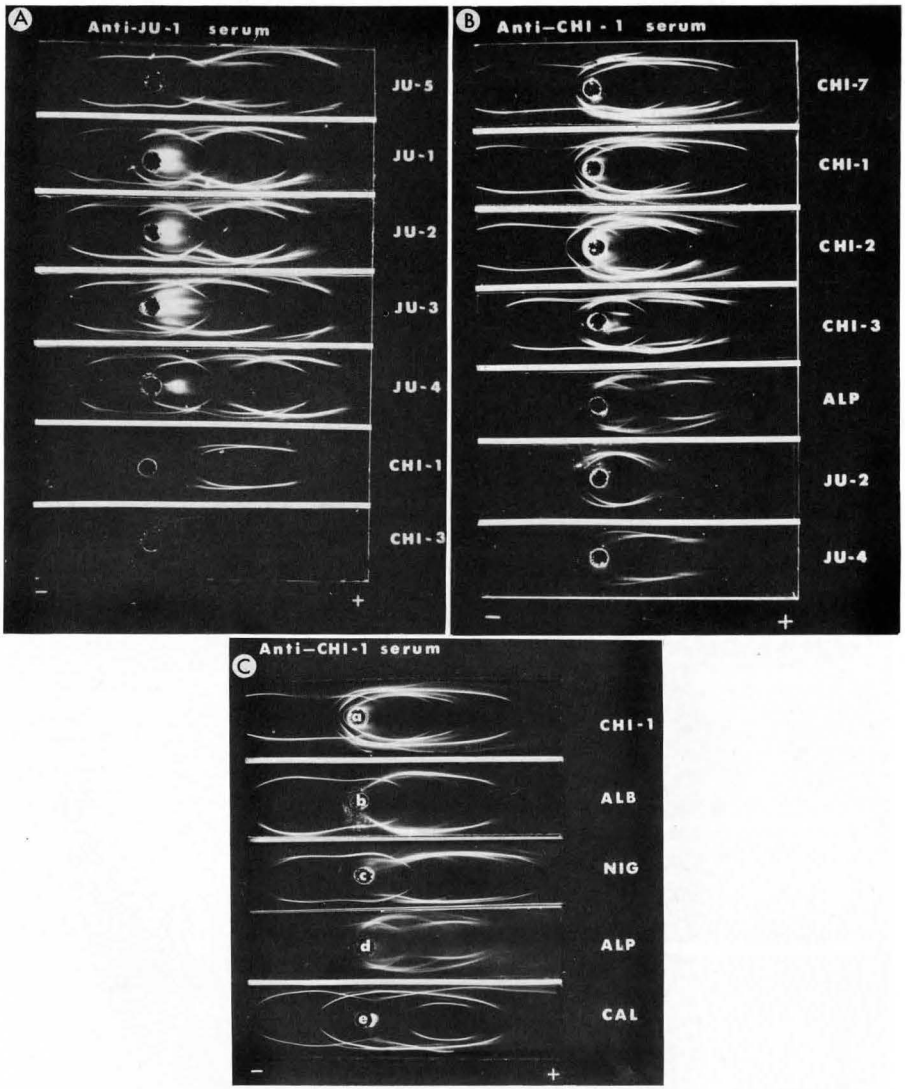


Fig. 1. A. IE spectra resulting from reactions between anti-JU-1 serum and antigen extracts of *Prosopis*.—B. IE spectra resulting from reactions between anti-CHI-1 serum and antigen extracts of species of *Prosopis*.—C. IE spectra resulting from reactions between anti-CHI-1 serum and South American species of *Prosopis* section *Algarobia*. (For explanation of symbols, see Table 1.)

A more discriminatory analysis of serological affinities was obtained from IE tests (Fig. 1b, c; 2b; 3a, b). Reactions involving anti-*P. chilensis* serum and *P. chilensis* extracts indicated that these shared at least eight antigens in the IE spectra (Fig. 1b). The IE pattern of CHI-3 appeared slightly dif-

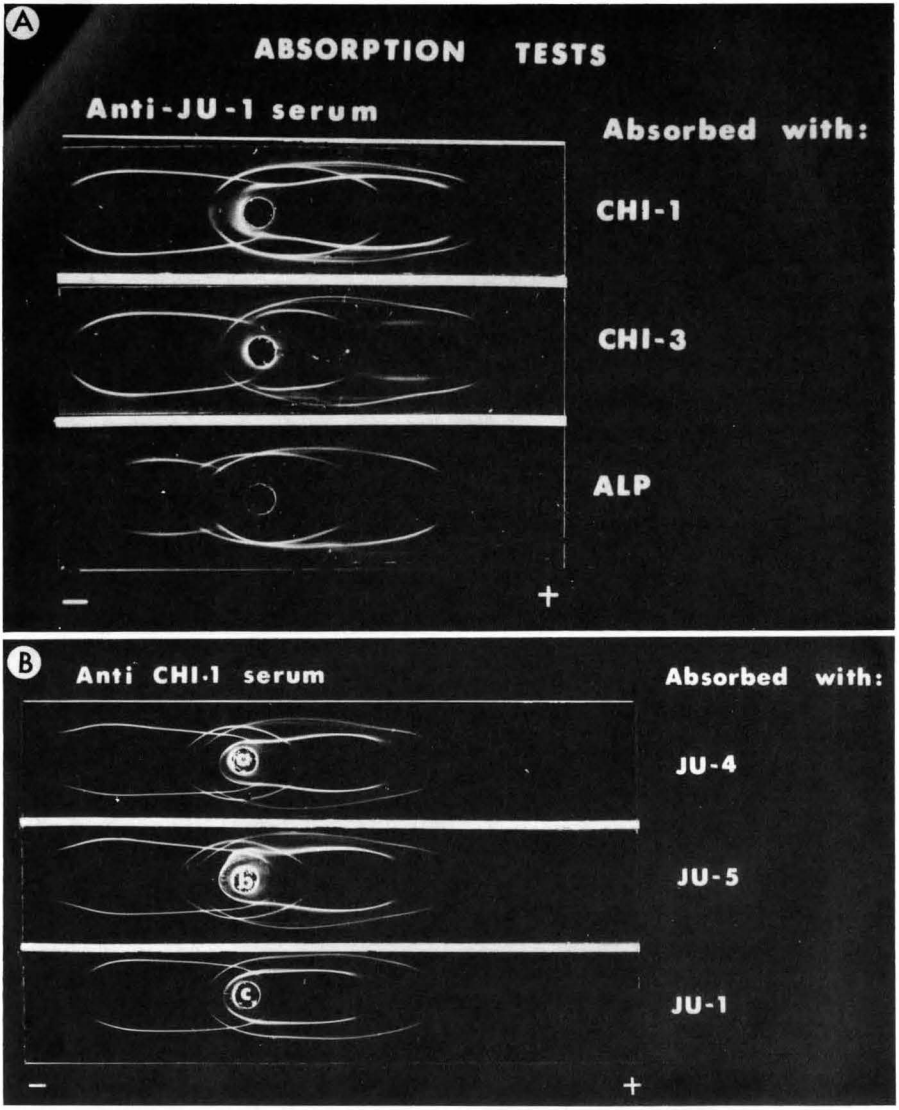


Fig. 2. A. IE spectra resulting from test-reactions with anti-JU-1 serum preabsorbed with antigen extracts of different *Prosopis* species.— B. IE spectra resulting from test-reactions with anti-CHI-1 serum preabsorbed with antigen extracts of various *Prosopis* species. (For explanation of symbols, see Table 1.)

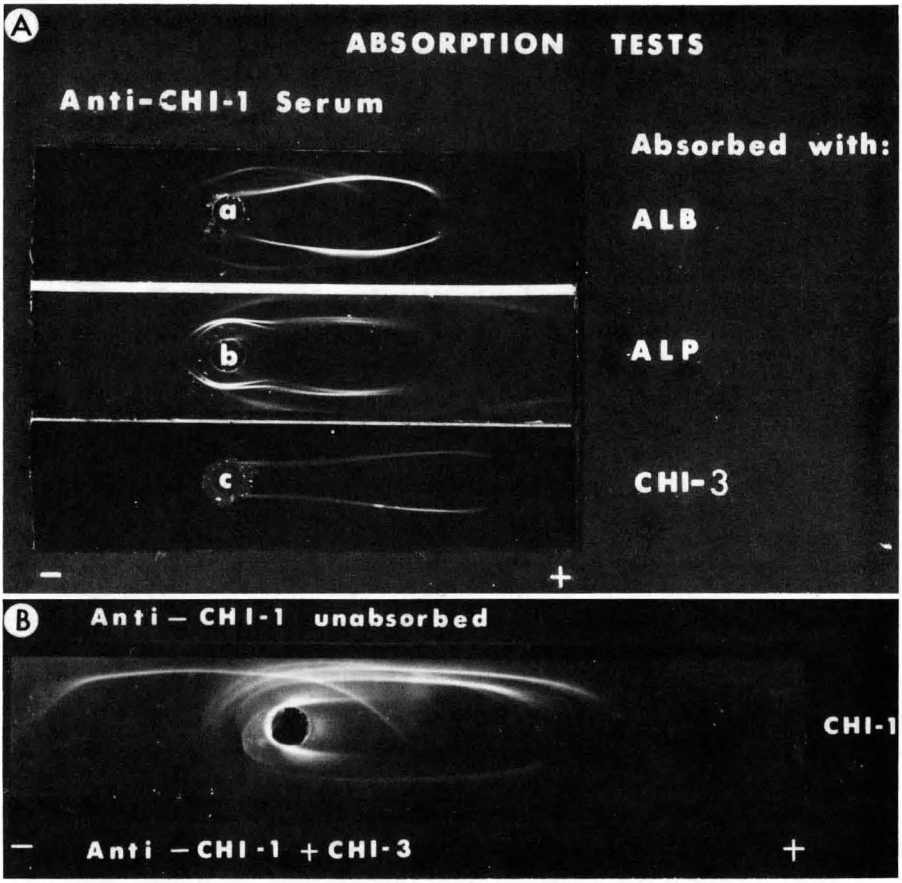


Fig. 3. A. IE spectra resulting from test-reactions with anti-CHI-1 serum preabsorbed with antigen extracts of South American species of *Prosopis* section *Algarobia*.—B. IE spectrum resulting from a test-reaction combining absorbed and unabsorbed anti-CHI-1 serum. Absorption was carried out with CHI-3 extract (For explanation of symbols, see Table 1.)

ferent from the others in that one arc close to the origin was missing and there were shifts in the position of several of the immunoprecipitin systems (Fig. 1b). The spectra of *P. alba, P. nigra, P. alpataco,* and *P. caldenia,* although distinct from that of CHI, indicate a rather close serological relationship with *P. chilensis* (Fig. 1c). Only four to five weak arcs were produced in reactions between anti-CHI-1 serum and the various JU extracts (Fig. 1b). Further insight into the serological differences between *P. juliflora* and *P. chilensis* was obtained from absorption tests which showed that four to five antigens were specific to *P. chilensis* (Fig. 2b). *Prosopis juliflora*

shared only three to four such systems while the South American species of section *Algarobia* had a more substantial pool of antigens in common with *P. chilensis,* since fewer precipitin bands remained after absorption (Fig. 3a). Slight intraspecific differences were also observed in *P. chilensis.* Absorption tests disclosed that CHI-3 was serologically differentiated from the other seven accessions since one immunoprecipitating system was not shared by this accession (Fig. 3b).

The results indicate that taxa of the North American complex *Prosopis juliflora* are serologically very similar to each other but are differentiated from South American species closely related to *P. chilensis.* The data also show that *P. chilensis* genotypes share a substantial pool of seed antigens with closely related South American species of section *Algarobia.* By contrast, seed extracts of other South American species belonging to the same section (*P. patagonica*) or to other sections of the genus: *P. pubescens* (sect. *Strombocarpa*) and *P. tamarugo* (sect. *Cavenicarpa*) did not react with the antisera. However, extracts of *Acacia greggi* Gray produced one faint anodal arc in reactions with either antiserum.

## Discussion

The serological data indicate close similarities among accessions of the *P. juliflora* complex and a similar pattern is repeated for the *P. chilensis* samples analysed in this study. The close serological similarity of the *P. juliflora* accessions was unexpected in view of the considerable morphological variability and ecological amplitude shown by the taxa of the complex (Simpson 1976). Phenological and ecophysiological differences resulting in ecotypic differentiation have been reported within *P. glandulosa* and *P. laevigata* (McMillan and Peacock 1964; Peacock and McMillan 1965). Despite these differences, the evidence to date supports a close phyletic relationship for all members of the complex. The serological similarity reported here parallels the results of Bragg et al. (1978) who found little differentiation in flavonoid patterns among 114 tree samples representing the five taxa of the complex. Our sampling, admittedly more restricted, represented however three of the taxa recognized by Johnston (1962) for the complex and were collected over a range of more than 2700 km encompassing 15° latitude.

Serological differences among the 8 accessions of *P. chilensis* were also minimal despite the fact that samples were collected over a 1,300-km range covering 11° latitude. Carman (1973) found no intraspecific variability in flavonoid patterns for the species and Solbrig and Bawa (1975) reported similar isozyme frequencies for four enzyme systems in Chilean samples of the species collected from two different localities.

It could be argued that the serological similarities found among taxa of

the *P. juliflora* complex or among accessions of *P. chilensis* may be indicative of the extreme conservatism of seed antigenic proteins in legumes (Lester et al. 1965; Simola 1969; Simon 1969; Selim et al. 1977) rather than an expression of close phyletic relationship. However, the fact that these similarities are also found among flavonoid patterns, reputed to be more variable at the intraspecific level (Carman 1973; Alston and Turner 1963) makes this proposition less likely.

As indicated by Bragg et al. (1978), it is possible that flavonoid and seed protein chemistry were not affected by selective processes leading towards the adaptation and niche differentiation that now exist for these taxa. However, it is also likely that the biochemical similarities may be a consequence of the high level of intra- and interspecific hybridization reported to be prevalent among taxa of section *Algarobia* in both hemispheres (Hunziker et al. 1975; Simpson 1976). Another factor which may have contributed to the uniformity of flavonoid and serological patterns in the *P. juliflora* complex may be the rapid expansion and colonization of members of this taxon in North America (Simpson 1976). Rapid colonization may be effected by the selection of a flexible genotype endowed with a high level of phenotypic plasticity in morphological and growth characteristics (Bradshaw 1965; Harper 1977) as has been demonstrated recently in *Xanthium* (Moran and Marshall 1978). The isozyme data of Solbrig and Bawa (1975) indicate the presence of differences for two of the four enzyme systems analysed among taxa of the *P. juliflora* complex. The genetic basis of these differences remains to be determined.

*Prosopis chilensis* shares a number of seed antigens with other South American species of section *Algarobia* such as *P. alba, P. nigra, P. alpataco,* and *P. caldenia.* A close relationship is inferred from the serological data since extracts of these species removed most of the antibodies from *P. chilensis* antisera during absorption. This group of species is morphologically closely related to *P. chilensis,* in particular *P. alba, P. alpataco,* and *P. nigra* and interspecific hybridization occurs in areas of sympatry (Burkart 1952, 1976; Hunziker et al. 1975; Simpson 1976). My serological results are similar to those of Cohen et al. (1966) which were based on different serological techniques. Close serological affinities between *P. chilensis, P. alpataco,* and *P. caldenia* were reported by these authors but no information was available for *P. alba* and *P. nigra.*

In contrast with the close serological relationships obtained for samples of the *P. juliflora* complex and among accessions of *P. chilensis,* the serological data indicate that these two disjunct taxa are well differentiated from each other. Four particularities of the biochemical data in *Prosopis* suggest that the low degree of serological affinity found between these two species complexes is likely to be indicative of a long period of evolution in geographical isolation.

1) The serological similarities among accessions of each disjunct suggest that seed antigens are not modified rapidly by natural selection under differential selective pressures imposed by the variable environments found in the area of distribution of each taxon.
2) The serological differences between these two disjuncts are of higher magnitude than those separating many of the South American species of section *Algarobia* which are morphologically more diverse to each other as a group.
3) A high degree of conservatism of seed antigens among genera of the Leguminosae is inferred from the serological analyses carried out to date (Kloz 1971). For instance, very close serological affinities have been reported for American and Old-World *Lathyrus* species by Simola (1969). Annual and perennial species of *Medicago,* that evolved in isolation in central Asia and the Mediterranean basin, could not be differentiated consistently (Simon 1969) and the genus has strong serological affinities with taxa of other genera such as *Trigonella* and *Melilotus* (Simon, in preparation). Comparable results were obtained by Lester et al. (1965) in a survey of the genus *Baptisia* and recent studies by Selim et al. (1977) indicate that a similar situation is found in *Trifolium*.
4) Results obtained by Carman (1973) from the analysis of flavonoid patterns in these disjunct taxa are consistent with the serological data reported here. The *P. chilensis* samples did not share any of the identified flavonoid glycosides that were found to be consistently present in leaves of four taxa of the *P. juliflora* complex (Carman 1973; see also table 3–5 of Simpson 1976).

The clear-cut differentiation between the *P. juliflora* complex and *P. chilensis* contrasts with the chemical identity found in North and South American populations of another disjunct taxon: *P. reptans* Benth., belonging to section *Strombocarpa* (Carman and Mabry 1975). The flavonoid patterns of Texan and Argentinean populations of this species were identical and only slight differences in leaf morphology were found. The most likely explanation for the *P. reptans* disjunction is that of recent long-distance dispersal since the area colonized by the species in the Gulf coast region of Texas is of very recent geological origin (Carman and Mabry 1975).

The *P. reptans* and the *P. juliflora-P. chilensis* situations are likely to represent extremes in the timing of disjunctions in *Prosopis*. Raven (1963) and Solbrig (1972) have suggested that the genus *Prosopis* may have had a tropical origin with subsequent migration and speciation north and south. The biochemical evidence suggests that taxa of the *Prosopis juliflora* complex may have evolved in isolation early in the Tertiary, even before desert habitats were available in both hemispheres (Vuilleumier 1971).

## Summary

Protein extracts of seeds from several accessions of the two disjunct species complexes: *Prosopis juliflora* DC. (North America) and *P. chilensis* (Mol.) Stuntz (South America) were compared serologically using both immunodiffusion and immunoelectrophoretic techniques. Only slight differences were found among accessions of each taxon, using unabsorbed and absorbed antisera produced against *P. juliflora* and *P. chilensis*. However, the complexes were well differentiated from each other since they shared only 20–30% of the reacting antigens. Close serological affinities were found between *P. chilensis* and other South American species of section *Algarobia* but other species belonging to this section or to other sections of the genus did not react with the antisera. The results suggest that taxa of the two complexes may have evolved in isolation from common tropical ancestors, possibly during the early Tertiary. The morphological similarities may be due to parallel or convergent evolution under similar desert environments in the two hemispheres.

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