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# PROSOPIS PALMERI: A RELICT OF AN ANCIENT NORTH AMERICAN COLONIZATION

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Baja California has long been recognized as the home of many endemic and often bizarre plant taxa (Shreve and Wiggins, 1964; Humphrey, 1970). Even the genus *Prosopis* (Leguminosae, Mimosoideae), usually thought of in terms of commonplace mesquites and screwbeans, has a singular representative, *P. palmeri* S. Wats., restricted to the lower Sonoran Zone (Shreve and Wiggins, 1964). Because of its confusing characters and scarcity in collections, this taxon has been placed in various sections of *Prosopis* (Watson, 1889; Burkart, 1940; Schuster, 1969) or in a monotypic genus *Sopropis* (Britton and Rose, 1928). The most recent treatment of the Leguminosae by Hutchinson (1964) returned *P. palmeri* to a monotypic genus. We report here results of an overall study of *Prosopis* (Carman, 1973; Burkart, in press) that indicate *P. palmeri* should not only be retained in *Prosopis* but should also be placed in a section to which it has not previously been referred. In addition, our study of *P. palmeri* helps to confirm a decision to unite two former sections of the genus (Burkart, in press) and provides clues for the evolutionary history of *Prosopis*.

In a current revision of *Prosopis,* Burkart (in press) has separated the genus into five sections based on the morphological characters shown in Table 1. The largest section, *Algarobia,* contains the 29 species known as mesquites in North America and algarrobos in South America. The second largest section, *Strombocarpa,* formerly contained only the screwbeans (Burkart, 1940) but has been modified to include the two species

† Deceased

of the former section *Cavenicarpa*. Two screwbeans, *Prosopis pubescens* Benth. and *P. reptans* Benth., have traditionally been considered the only two native species of this section to occur in North America. The remaining species in sect. *Strombocarpa* (including *Cavenicarpa*) were previously thought to occur only in arid and semiarid areas of Central and southern South America. A third New World section containing only *P. argentina* Burk., a species restricted to the base of the Andes of northwestern Argentina, has only recently been circumscribed (Burkart, in press).

The remaining two sections of *Prosopis* are Old World. The four species of sect. *Prosopis* are scattered across Iran, Afghanistan, and India. *Prosopis africana* (Guill. & Perr.) Taub., the only member of sect. *Anonychium,* is common in the savannas of west-central Africa east to Ethiopia.

Many earlier treatments that dealt with *Prosopis* did not include *P. palmeri* because they restricted themselves to the species in the United States (Benson, 1941; Isely, 1972) or to only the taxa of sect. *Algarobia* (Johnston, 1962). The treatment of *Prosopis* by Shreve and Wiggins (1964) considered *P. palmeri* a *Prosopis* but did not indicate sectional affinities. In an earlier treatment, Burkart (1940) tentatively suggested a placement of *P. palmeri* near *P. africana,* and at least one subsequent author (Schuster, 1969) formally placed it with that species in sect. *Anonychium*. Finally, Hutchinson (1964) resegregated *P. palmeri* in the monotype *Sopropis* because its spines do not match those of species with similar fruits (sect. *Prosopis*) and the fruits do not match those of species with similar spine development (sect. *Strombocarpa*). In addition, Hutchinson (1964) decided that the partial fusion of the petals in *P. palmeri* was a unique character. It is noteworthy that he did not entertain the idea that *P. palmeri* might be allied to *P. africana,* a species with which he was very familiar.

## Morphology

An examination of Table 1, which enumerates morphological characters of all of the currently recognized sections of *Prosopis,* clearly shows that the majority of features found in *P. palmeri* (fig. 1), including sympetally (fig. 1, d) are similar to those found in sect. *Strombocarpa*. Although absence of spines in *P. africana* does not, by itself, preclude a close relationship with *P. palmeri,* distinct differences in the internal fruit structure (fig. 1, e), *P. africana*'s dense rather than loose arrangement of flowers along the inflorescence (fig. 1, b), and the lack of conspicuous stipular spines that are present in *P. palmeri* (fig. 1, c) argue against any such alignment.

## Palynology

A survey of the pollen of species of all sections of *Prosopis* using the scanning electron microscope reveals a uniformity of size and shape

TABLE 1. CHARACTERISTICS OF THE SECTIONS OF PROSOPIS COMPARED WITH P. PALMERI.

| Section or taxon | Spines | Stipules | Inflorescence | Flower | Ovary |
|---|---|---|---|---|---|
| *Prosopis* | aculei along the branches | foliaceous | spicate, fls. loosely arranged | glabrous petals; white; free | glabrous |
| *Anonychium* | absent | inconspicuous | spicate, fls. loosely arranged | glabrous petals; white; free | villous |
| *Algarobia* | paired or single formed by lateral branches | inconspicuous | spicate, fls. densely or loosely arranged | pubescent petals; white, yellow or red; free | villous |
| *Prosopis argentina* Burk. (new section, Burkart, in press) | single, axillary and terminal | inconspicuous | spicate, fls. loosely arranged | pubescent petals; color uncertain; almost free | villous |
| *Strombocarpa* | paired, thin, white, or thick, yellow | forming the paired spines | spicate or globose; if spicate, fls. loosely arranged | pubescent or villous petals; yellow, reddish; fused | villous |
| *Prosopis palmeri* S. Wats. | paired, thin, white | forming the spines | spicate, fls. loosely arranged | glabrous petals; yellow; fused | villous |

TABLE 1. *Continued.*

| Section or taxon | Fruit shape | Mesocarp | Endocarp | Seeds | Chemistry |
|---|---|---|---|---|---|
| *Prosopis* | thick, slightly flattened, straight or arched | not developed | degenerates | end to end | M–3–0–g |
| *Anonychium* | thick, terete, straight | spongy | horizontally septate | end to end | no M–3–0–g |
| *Algarobia* | slightly flattened, straight or arched or twisted | spongy | stony, horizontally septate | end to end | M–3–0–g in only 2 of 29 species |
| *Prosopis argentina* Burk. (new section, Burkart, in press) | beaded, straight | reduced red | stony, horizontally septate | end to end | no M–3–0–g |
| *Strombocarpa* | spirally twisted or short, terete | disintegrates or dense, spongy | horizontally or transversally septate | end to end or stacked | M–3–0–g |
| *Prosopis palmeri* S. Wats. | slightly flattened, straight or slightly arched | disintegrates | disintegrates | end to end | M–3–0–g |

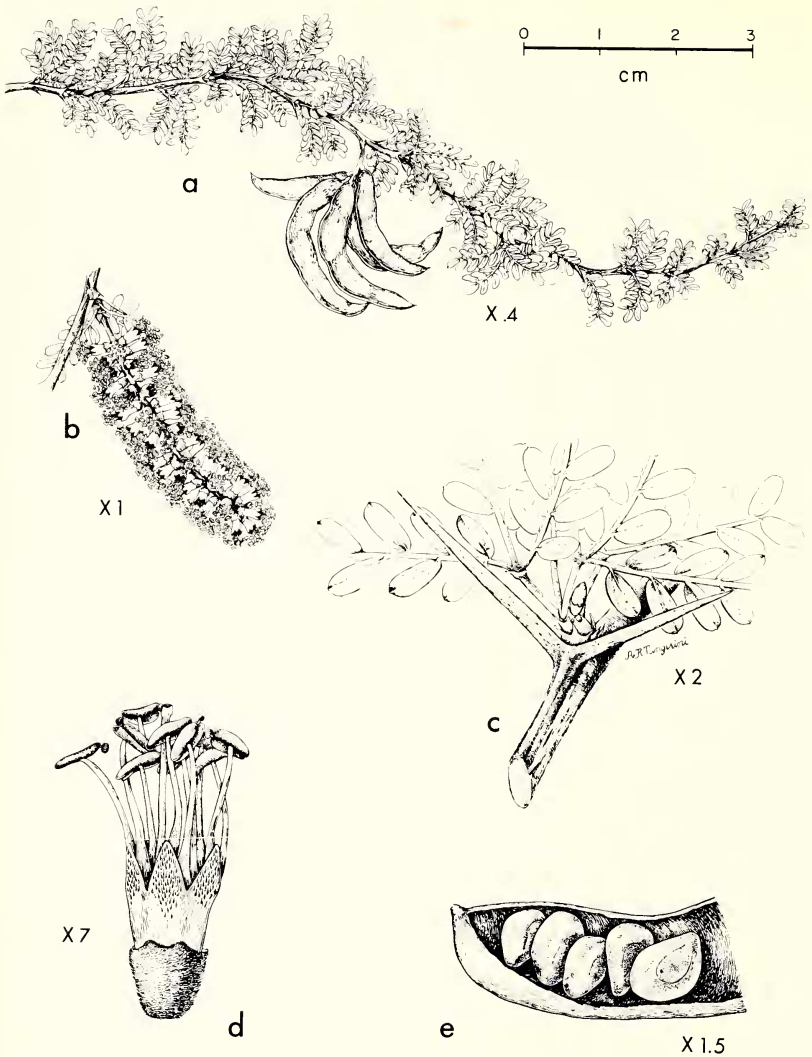


Fig. 1. Morphological features of *Prosopis palmeri* S. Wats. a, flowering branch of a tree 4m tall showing the clustering of the leaves on short shoots along the branch and the straight or slightly curved aspect of the pods. b, an inflorescence with the flowers rather loosely arranged along the spike. c, a pair of spines with axillary buds and shoots above demonstrating that the spines are formed from a pair of stipules. d, a flower illustrating the cuplike stigma and the anther glands found in all *Prosopis* species and the sympetalous corolla restricted to a few species. e, a cut-away section of a mature fruit that illustrates that the meso- and endo-carp have disintegrated. The seed on the far right has shaken loose and is upside down. The circular markings on the seeds are found throughout *Prosopis* and mark a weak region facilitating seed germination. Drawn from *Carter 2477* and *4275* (US) by Alice Tangerini.

throughout the genus. Slight variations that are present include a tendency for members of sect. *Algarobia* with single axillary spines to have more prolate pollen with smoother exines than grains of species of other groups. Pollen of sect. *Prosopis* is also very prolate but is punctate or rugose. Pollen of *P. palmeri* most closely resembles that of *P. pubescens* (sect. *Strombocarpa*) although both are similar to that of most species in the genus.

## Natural Products Chemistry

As part of a study of the flavonoid chemistry of *Prosopis* (Carman, 1973), flavonoid compounds from the leaves of *Prosopis palmeri* were chromatographically and spectrally compared with those obtained from species in various sections. Results from the chemical analyses definitely indicate that *P. palmeri* belongs in *Prosopis*. The chemistry further supports exclusion of *P. palmeri* from sect. *Algarobia* or sect. *Anonychium*. Except for *P. alba* Griseb. and *P. chilensis* (Mol.) Stuntz (sect. *Algarobia*), the species of these two sections do not contain myricetin 3–0–glycosides, which are abundant in leaf extracts of *P. palmeri*. However, species of sects. *Adenopis* and *Strombocarpa* all produce a number of myricetin 3–0–glycosides (Table 1). Of the species in these two sections, only *P. pubescens* has a flavonoid pattern nearly identical to that of *P. palmeri* (fig. 2). Both have patterns relatively distinct from that of *P. reptans*, the second North American screwbean.

## Conclusions

On the basis of similarities in floral morphology, pollen type, vegetative structure, and flavonoid chemistry (Table 1), *Prosopis palmeri* definitely belongs within *Prosopis* and should not be considered generically distinct. Presence of paired stipular spines (fig. 1, c) and of myricetin substituted glycosides indicates that it belongs in sect. *Strombocarpa*. The horizontal arrangement of the seeds (fig. 1, e) indicates its relationship within this section to the screwbeans. (These species are placed together in a series of sect. *Strombocarpa* and those species formerly placed in sect. *Cavenicarpa* in a second series, cf. Burkart, in press). The lack of coiling of the fruit is, however, novel in this group although *P. torquata* (Cav. ex Lag.) DC., a screwbean of northwestern Argentina and Chile, has fruits that only loosely spiral. In terms of flavonoid chemistry, pollen morphology, and leaf morphology, *P. palmeri* is most similar to *P. pubescens*. Nevertheless, the straight or arched fruit (fig. 1, a) with its disintegrating mesocarp and endocarp (fig. 1, e) is very different from that of the latter. The distinctness of the natural products chemistry between *P. pubescens* and *P. reptans* has already led to the postulation that these two North American representatives of sect. *Strombocarpa* represent two independent introductions from South America (Carman and Mabry, in press). The differences in the fruit

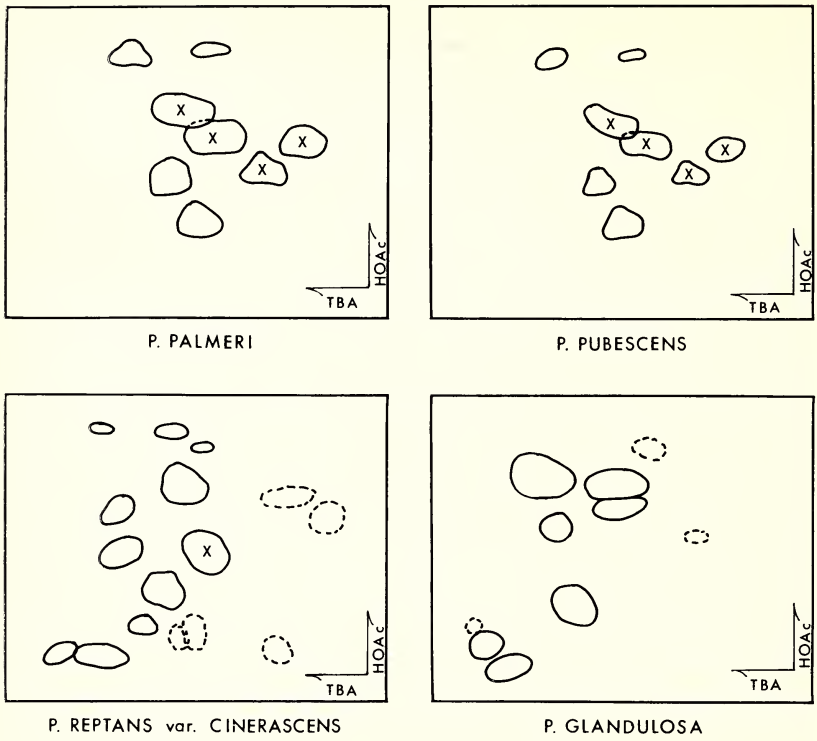


Fig. 2. Chromatograms showing flavonoid patterns of three members of sect. *Strombocarpa* (*Prosopis palmeri*; its nearest apparent relative, *P. pubescens*; and another North American species, *P. reptans* var. *cinerascens*) and also a member of section *Algarobia*, the common North American honey mesquite, *P. glandulosa*. Data from Carman, 1973, and *in litt.*

morphology between *P. palmeri* and either of these two species indicate a third and probably early independent colonization. The marked morphological differences between *P. palmeri* and the screwbeans and the presence of some similarities with Old World species imply that it reached North America early in the evolution of the genus and may have diverged little from the basal stock that subsequently gave rise to sect. *Strombocarpa*.

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# DISTRIBUTION, CHROMOSOMES, AND TAXONOMY OF PARTHENICE MOLLIS (COMPOSITAE)

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*Parthenice* is a little-known genus native to southern Arizona and northwestern Mexico. Its single species, *P. mollis* A. Gray, is a rank-smelling, weedy annual bearing a superficial resemblance to *Iva xanthifolia* (marsh elder).

In 1851, Charles Wright made the first known botanical collection of *P. mollis* near the Mexican town of Santa Cruz, Sonora. Since that time the plant has been rather sporadically collected in Arizona as well as in several states in Mexico (fig. 1). In addition, *P. mollis* has been reported from New Mexico and Colorado in several western United States floras. Weber (1966) stated, however, that he was unable to verify the report of *P. mollis* in Colorado and suggested that the record should be rejected. The report from New Mexico also seems doubtful; there are no supporting records in herbaria of that state. It is interesting to note that the type specimen bears the handwritten inscription "collected in N. Mex.", which may have been interpreted to mean New Mexico instead of northern Mexico thereby giving rise to the report from that state.

In Arizona, the Ajo Mountains represent the western limit of distribution; the Patagonia Mountains limit it to the east and the Tortolito Mountains are the most northern site. The rather colonial populations