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THE TAXONOMIC RELATIONSHIP
BETWEEN *PROBOSCIDEA LOUISIANICA* AND
PROBOSCIDEA FRAGRANS (MARTYNIACEAE)

P. K. BRETTING

ABSTRACT.—Based upon a numerical index constructed from five characters, *Proboscidea louisianica* from the Great Plains and the midwestern United States is clearly differentiable from *P. fragrans* from central Mexico. In contrast, these taxa intergrade in Trans-Pecos Texas and northcentral Mexico, where their variational pattern resembles a mosaic of both intermediate forms and plants readily assigned to a species. Because of this intergradation, and many other biological similarities between them, these taxa are reduced to subspecies. As delimited here, *P. louisianica* ssp. *louisianica* is a relatively homogeneous taxon distinguished from the extremely variable, polymorphic *P. louisianica* ssp. *fragrans* by leaf form and by the color of the corolla, anthers, and hypocotyls/cotyledons.

Proboscidea louisianica (Miller) Thellung and *P. fragrans* (Lindley) Decaisne are weedy summer annuals that reproduce sexually; disperse zoochorously by their indurate, uncinata fruit; and colonize disturbed soil (Bretting, 1981). *Proboscidea fragrans* is native to arid Trans-Pecos Texas in the United States, and the Mesa Central of Mexico; *P. louisianica* is endemic to the southern Great Plains and Texas northeast of the Pecos river, and occurs as a probable escape from cultivation in California and the midwestern United States. These species have long been cultivated, primarily as ornamentals, in Europe and the United States (Van Eseltine, 1929; Lawrence; 1957; Bretting, 1981).

These taxa have heretofore always been considered separate species. The type collections and cultivated lines of *P. fragrans* and *P. louisianica* stem from, respectively, Hidalgo, Mexico (Lindley, 1840; 1841) and the eastern United States (Linnaeus, 1753; Miller, 1768). Populations from these regions exhibit striking morphological differences: the leaves of *P. louisianica* have entire margins, and the corollas are creamy-white tinged with lavender; leaves of *P. fragrans* are 3-5 lobed with roughly serrate margins and the corollas are dark-medium purple. Most keys to species of *Proboscidea* have relied upon these characters to differentiate *P. louisianica* from *P. fragrans* (e.g., Van Eseltine, 1929; Hevly, 1970).

Statistical analyses of forty morphological characters during a generic revision of *Proboscidea* (Bretting, 1981) showed that *P. louisianica* and *P. fragrans* were more similar to each other than to any other species. Additional biosystematic studies revealed that the species share identical flavonoid patterns, a facultatively outbreeding system, and chromosome number of $2n = 30$ (Bretting, 1981). Fertile interspecific hybrids (F_1 and F_2) were readily secured.

Considering these species' many biological similarities and their contiguous geographical ranges, the taxonomic importance of corolla color and leaf form come into question. The present investigation examines the

variation of these, and several other morphological characters, across the geographical range of both taxa in order to assess the taxonomic relationship of *P. fragrans* and *P. louisianica*.

MATERIALS AND METHODS.—Replicate sets of seven geographically and morphologically representative populations (five-ten plants) per species (Appendix 1) were grown in greenhouses and outdoor gardens at Indiana University, Bloomington, Indiana. Several qualitative characters that were constant within populations and under different environments were identified. Several quantitative characters with coefficients of variation less than 15.0 were also noted (Appendix 2). Simpson, Roe, and Lewontin (1960) recommended using characters with coefficients of variation less than 10 in systematic zoology. Because of the greater inherent morphological variability of plants, a slightly higher coefficient was used here.

Characters were scored from the greenhouse/garden plants, and when possible from the more than five hundred herbarium samples (ca. two hundred-fifty per species) cited by Bretting (1981). Qualitative characters were then directly coded into character states. Those states present in cultivated lines or midwestern populations of *P. louisianica* were given a score of 1, those present in cultivated lines or southcentral Mexican populations of *P. fragrans* were assigned a 3, and when possible a 2 represented values intermediate between these extremes. The range of variation of each quantitative character was subdivided into three states as with the qualitative characters, and was also coded as 1, 2, or 3.

Scores for each character except anther and hypocotyl/cotyledon colors (often unobservable from herbarium specimens) were summed for each population or herbarium sample, the total was divided by the maximum possible total (three times the number of characters scored), and the resulting ratio was multiplied by 100. Using this index, a sample that resembled *P. louisianica* in all measurable characters would score 33, an intermediate form would score about 66, and samples resembling southern populations of *P. fragrans* would score 100.

RESULTS.—*Greenhouse-garden population.*—Populations of *P. fragrans* from the Mexican states of Zacatecas, Querétaro, and México scored close to the *P. fragrans* pole of variation (ca. 100), as did one population from Trans-Pecos Texas. Another population from Trans-Pecos Texas, and those from Chihuahua and San Luis Potosí, Mexico had intermediate scores. All these plants had white anthers and, with the exception of one Trans-Pecos population, they also had leaves that were somewhat 3-5 lobed and serrate or crenate, and hypocotyls/cotyledons that were pink. The intermediate Trans-Pecos population, with its entire leaves, lavender corollas, white anthers, and maroon hypocotyls/cotyledons, scored close to the *P. louisianica* pole (ca. 33) on the numerical index.

Populations of *P. louisianica* exhibited much less variation than did those of *P. fragrans*. All had entire leaves, white corollas, magenta anthers, maroon hypocotyl/cotyledons, and scored ca. 33 on the numerical index.

Herbarium specimens. Index values are presented in Fig. 1. The irregular polygon labelled " > 87 " bounds a block of populations of *P. fragrans* with medium-dark corollas, small fruits with abscising pedicels, and 3-5 lobed, serrate leaves. The diagonal line labelled " ≤ 50 " signifies that to the north and east of that line, populations of *P. louisianica* all had white corollas and entire, smooth-margined leaves. Between the zones of relative homogeneity (i.e., numerical index values of ≤ 50 for *P. louisianica* and > 87 for *P. fragrans*) lie populations from Trans-Pecos Texas and northcentral Mexico with scores that were usually intermediate (50-70), but sometimes quite high or low. The intermediate plants cannot be assigned to either species with confidence. These specimens exhibit a wide variety of leaf,

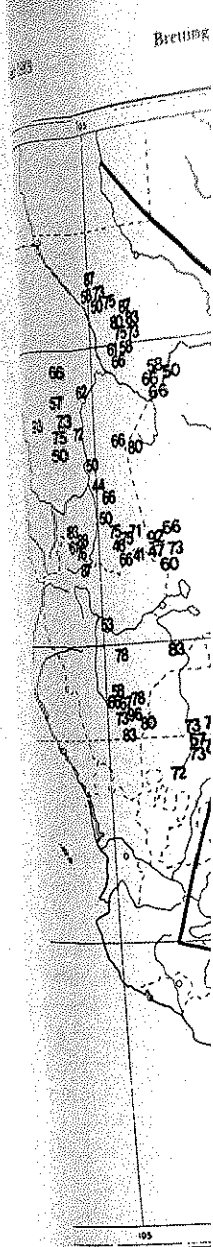


FIG. 1.—Geographical plot of herbarium samples.

and fruit morphology from Durango, Mexico.

DISCUSSION.—Two geographically coherent greenhouse/garden forms were assignable to *P.*

cal and morphological poles lay intermediate populations distributed, along with the two extreme variants, in a pattern resembling a patchwork of intergradation (Fig. 1).

Their intergradation, their many biological similarities cited previously, and the morphological dissimilarity of variants from the extreme northern and southern sectors of their combined range, strongly suggest that *P. louisianica* and *P. fragrans* should be considered subspecies. This taxonomic change necessitates a new nomenclatural combination. The basionym of *P. louisianica*, *Martynia louisianica* Miller in Gard. Dict. n.p. (Corrigenda #3) 1768, has priority over the basionym for *P. fragrans* so the correct new combination is **Proboscidea louisianica** (Miller) Thellung ssp. **fragrans** (Lindley) Bretting comb. et stat. nov., basionym: *Martynia fragrans* Lindley in Bot. Reg. 26:85 (Misc. Item #206). 1840.

The question of how to treat the intermediate populations remains. Van Eseltine (1929) subsumed them and the associated epithet, *P. violaceae* (Engelmann) Decaisne (basionym: *Martynia violaceae* Engelmann in Wisliz. Mem. Tour N.M.:101. 1848.) under what is here considered *P. louisianica* ssp. *fragrans*. Evidence from artificial hybridizations support Van Eseltine's action. Hybrids (F₁) between several populations of *P. louisianica* ssp. *louisianica* and an intermediate population were partially pollen sterile, whereas F₁ hybrids between the intermediate population and other populations of *P. louisianica* ssp. *fragrans* were completely fertile (Bretting, 1981). Considering these data, and the likelihood that intermediate "forms" are polytypic (intermediate populations from Trans-Pecos Texas, San Luis Potosí, and Chihuahua have different character combinations), formal taxonomic recognition does not now seem prudent. The wise precedent of Van Eseltine is followed here, and the intermediate form is provisionally subsumed under *P. louisianica* ssp. *fragrans*.

As delimited here, *P. louisianica* ssp. *louisianica* is composed of plants with predominantly white corollas, entire leaves, magenta anthers, and maroon cotyledons/hypocotyls. It is a relatively homogeneous taxon that comprises one extreme of a complex, polymorphic series of populations, the bulk of which has been referred to *P. louisianica* ssp. *fragrans*. The latter may be characterized by the following character combinations: white anthers, pink or maroon hypocotyls/cotyledons, unlobed to 3-5 lobed, entire or serrate-margined leaves, and dark purple to lavender (or very rarely white) corollas. A complete list of exsiccatae is given in Bretting (1981). The intergradation between the subspecies may be a result of hybridization of previously differentiated species, primary differentiation of an ancestral species into dissimilar forms, or several other phenomena (Grant, 1971). As such, this variational pattern represents an intriguing evolutionary pattern for further study.

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APPENDIX 1.—GREENHOUSE-GARDEN POPULATIONS.—*P. louisianica*: UNITED STATES: Park Seed Co. s.n. KANSAS: Russell Co.: 2 mi. N of Bunker Hill, Dilcher s.n. NEW MEXICO: Chaves Co.: along US Hwy. 380, .25 mi. W of Caprock, Bretting 369. Lea Co.: along US Hwy. 82, W of Lovington, Nabhan 922. OKLAHOMA: Marshall Co.: N shore of Lake Texoma, Phillippi s.n. Tillman Co.: 5 mi. W of Manitor, Cooper s.n. TEXAS: Mason Co.: 1.2 km. E of Katency, Rowell s.n. *P. fragrans*: MEXICO: CHIHUAHUA: along Rte. 16, 19.7 mi W of General Trias, Wagner 4354. MEXICO: Texcoco, Bretting M218. QUERÉTARO: banks of Rio Moctezuma, San Juan del Rio, Bretting 352. SAN LUIS POTOSÍ: Mpio. de Villa de Reyes, Bretting M213. ZACATECAS: Mpio. de Calera, Banda BF 1123. UNITED STATES: TEXAS: Culberson Co.: along runway of county airport, E of Van Horn, Bretting 312. Presidio Co.: along Hwy. 17, 8 mi. N of Marfa, Bretting 319.

Voucher specimens have been deposited at IND or CHAPA.

APPENDIX 2.—MORPHOLOGICAL CHARACTERS AND CHARACTER STATES OF *P. LOUISIANICA* AND *P. FRAGRANS*.—The number in parentheses following each character state is used to construct the numerical index used in the text and Fig. 1. *Leaf lamina*: entire (1); 3-5 lobed, margins crenate/serrate (2); 3-5 lobed, margins irregularly serrate (3). *Mature fruit*: rostrum longer than 13.0 cm., rostrum length-capsule length ratio greater than 2.0, pedicel thickening in fruit (1); rostrum 10.0-12.0 cm. long, rostrum length-capsule length ratio 1.75-2.0, pedicel thickening in fruit (2); rostrum shorter than 10.0 cm., rostrum length-capsule length ratio less than 1.5, pedicel abscising or not thickening in fruit (3). *Adaxial sepal length-total calyx length ratio*: 0.38 or greater (1); 0.37-0.34 (2); 0.33 or less (3). *Calyx color*: green with dark green venation (1); green with purple venation (2); lavender-purple with purple venation (3). *Corolla color*: white-cream, streaked with pale lavender, no purple splotches on adaxial lobes (1); lavender, with purple splotches on adaxial lobes (2); medium-dark purple with purple splotches on adaxial lobes (3).

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