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SYSTEMATICS OF PALAFOXIA (ASTERACEAE:HELENIEAE)¹

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The genus *Palafoxia* was proposed by Lagasca (1816) who applied the generotype to a plant originally collected in "New Spain" and which Cavanilles (1794) had at first termed *Ageratum lineare* and later (1797) *Stevia linearis*. Cassini (1818) placed *Palafoxia linearis* in synonymy under his own *Paleolaria carnea* which cannot be recognized since Lagasca's earlier name has priority.

Since Cassini's work, *Palafoxia* has been split into as many as three genera, although Bentham and Hooker (1873), Hoffmann (1894), Cory (1946), and Shinnars (1949) recognized only the single genus. *Polypteris* was proposed by Nuttall (1818) and subsequently sanctioned by Gray (1884), Bush (1904), Rydberg (1914) and Baltzer (1944), the last three of whom also sustained Rafinesque's (1836) segregate genus, *Othake*.

In our opinion, *Polypteris* and *Othake* cannot be retained apart from *Palafoxia* because they are too inextricably bound as a phyletic group to be treated as segregate genera. To place emphasis on putative diagnostic characters such as comparative length of corolla parts and phyllary texture, as was done by the several authors men-

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tioned, appears biologically unsound because it stresses cryptic differences and ignores the presence of an overwhelming multitude of morphological and cytological similarities which collectively suggest that the three taxa belong within the confines of a single generic unit.

In the present account, *Palafoxia* is treated as composed of 12 species (and 6 varieties), 9 annuals and 3 perennials, occurring mostly in sandy soils of southwestern United States and Mexico, although *P. feayi* and *P. integrifolia* are indigenous to Florida. While most of the taxa are locally very common and widespread, six are rare and/or endemic: *P. reverchonii*, *P. hookeriana*, *P. arida* var. *gigantea*, *P. riograndensis*, *P. texana* var. *robusta*, and *P. lindenii*.

GENERIC POSITION

Palafoxia has been classically treated as a member of the tribe Helenieae and the sole representative of the subtribe Palafoxianae. The phyletic affinities of *Palafoxia* to other genera in the Helenieae are controversial (Turner and Powell, 1977). Most workers recognize *Palafoxia* as distinct from, but closely related to, *Bahia*, *Florestina*, *Hymenothrix*, and *Schkuhria*, all members of the subtribe Bahiinae. Turner's (1963) hypothetical diagram, illustrating the relative relationships of these 5 helenioid genera, suggests that *Florestina* is the most closely allied member of the Bahiinae to *Palafoxia*. However, we disagree with Shinnars' (1949, 1952) expanded concept of *Palafoxia* which includes *Florestina*. Although the two genera are quite similar with respect to habit and inflorescence type, they differ markedly in certain floral structures. The disc corollas of *Palafoxia* are regular, but irregular in *Florestina*; the style branches of *Palafoxia* are linear, revolute, and hispidulous whereas those in *Florestina* are flattened with cuspidate appendages and tend to be glabrous.

In spite of the seemingly close relationship of *Palafoxia* to *Florestina*, Turner and Powell (1977) reckon *Palafoxia* to be sufficiently remote to be included, along with *Marshallia*, as members of the subtribe Palafoxianae and positioned in the tribe Eupatorieae.

FLAVONOID CHEMISTRY

Intra- and inter-populational samples of selected species of *Palafoxia* were analyzed for flavonoid content. Dried leaves and stems of these samples were finely ground in a Waring Blender and extracted at room temperature in cold 85% methanol (aq.) for 24 hours. The resultant crude extract was subsequently concentrated, spotted on Whatman 3MM chromatography paper, and developed two-dimensionally in tertiary butyl alcohol (TBA) and acetic acid (HOAc) solvent systems.

All of the flavonoid spots from each of the plant samples were found to be purple under UV light, but extremely faint suggesting very low compound concentration. Furthermore, the color of each spot changed to yellow-green when subjected to ammonia and viewed under UV light. With respect to spot color and also R_f values, each of the observed flavonoids could be classified as being either flavonol monoglycosides or diglycosides with hydroxyl functions at both the 4' and 5 positions.

CHROMOSOME NUMBERS

Meiotic chromosome counts, available from 11 of 12 species and 4 of 6 varieties of *Palafoxia*, were found to be $n = 10$, 11, and 12 (Table 1). Both meiotic and mitotic material were stained with acetocarmine and all configurations were quite clear. At diakinesis and metaphase I, bivalents with two chiasmata were normally formed while mitotic figures showed large well-differentiated chromosomes (Figs. 1-2). All of the 86 collections examined were found to be diploid.

Table 1. Collections of *Palafoxia* examined for chromosome number.

Species	Locality and voucher*	<i>n</i> = number
<i>P. arida</i> var. <i>arida</i>	Ariz. MOHAVE CO.: <i>T.</i> 4787.	12
	Ariz. YUMA CO.: <i>T.</i> 4756.	12
	Calif. IMPERIAL CO.: <i>T.</i> 4758.	12
	Calif. RIVERSIDE CO.: <i>P. & S.</i> 1383.	12
	Calif. IMPERIAL CO.: <i>R.</i> 11506A.	12
	Mex. BAJA CALIF. <i>S & B.</i> 298.	12
	Mex. BAJA CALIF. <i>P. & T.</i> 1705.	12
	Mex. BAJA CALIF. <i>P. & T.</i> 1730.	12
	Mex. BAJA CALIF. <i>P. & T.</i> 1818.	12
	Mex. SONORA. <i>R.</i> 11677A	12
	Mex. SONORA. <i>S. & B.</i> 167a.	12
<i>P. arida</i> var. <i>gigantea</i>	Calif. IMPERIAL CO.: <i>R.</i> 12910A.	12
	Calif. IMPERIAL CO.: <i>T.</i> 4757.	12
	Calif. IMPERIAL CO.: <i>T.</i> 4759.	12
<i>P. callosa</i>	Tex. BANDERA CO.: <i>T.</i> 3840.	10
	Tex. FAYETTE CO.: <i>T.</i> 4452.	10
	Tex. KENDALL CO.: <i>T.</i> 3834.	10
	Tex. LAMPASAS CO.: <i>T.</i> 4587.	10
	Tex. LLANO CO.: <i>T.</i> 3483.	10
	Tex. MC CULLOCH CO.: <i>Smith</i> 232 (KANU) ^B	10
	Tex. VAL VERDE CO.: <i>T.</i> 3252	10
	Tex. VAL VERDE CO.: <i>T.</i> s.n.	10
	Tex. COLEMAN CO.: <i>T.</i> 4860.	10
	Mex. COAHUILA: <i>P. et al.</i> 1587	10
	Mex. COAHUILA: <i>P. et al.</i> 1411C.	10
<i>P. feayi</i>	Fla. LAKE CO.: <i>T.</i> 4663.	12
	Fla. COLLIER CO.: <i>Plettman & T.</i> F-15	12
<i>P. hookeriana</i> var. <i>hookeriana</i>	Tex. BASTROP CO.: <i>Smith</i> 555 (KANU) ^B (reported as <i>P. sphacelata</i>)	12
	Tex. LAVACA CO.: <i>T.</i> 3273.	12
	Tex. LIBERTY CO.: <i>T.</i> 4617.	12
	Tex. WASHINGTON CO.: <i>T.</i> 3917.	12
<i>P. hookeriana</i> var. <i>minor</i>	Tex. FREESTONE CO.: <i>T.</i> 4449.	12
	Tex. FREESTONE CO.: <i>T.</i> 4443.	12
	Tex. LEON CO.: <i>T.</i> 4429.	12
<i>Palafoxia integrifolia</i>	Fla. LEON CO.: <i>T.</i> 4657.	12
<i>Palafoxia lindenii</i>	Mex. VERACRUZ: <i>King</i> 2418.	11

Table 1 (continued)

Species	Locality and voucher*	<i>n</i> = number
<i>Palafoxia reverchonii</i>	Tex. ANDERSON CO.: <i>T.</i> 5743.	12
	Tex. HENDERSON CO.: <i>T.</i> 5742.	12
	Tex. HOUSTON CO.: <i>T.</i> 5746.	12
	Tex. UPSHUR CO.: <i>King</i> 2182.	12
<i>Palafoxia riograndensis</i>	Mex. COAHUILA: <i>Flyr</i> 247.	12
<i>Palafoxia rosea</i> var. <i>macrolepis</i>	N. Mex. ROOSEVELT CO.: <i>T.</i> 4720.	10
	Tex. ANDREWS CO.: <i>Melchert</i> 228.	10
	Tex. ANDREWS CO.: <i>Melchert</i> 225.	10
	Tex. COCHRAN CO.: <i>T.</i> 4718.	10
	Tex. FAYETTE CO.: <i>Smith</i> 552 (KANU) ^B (reported as <i>P. integrifolia</i>)	10
	Tex. LIVE OAK CO.: <i>Thompson & T.</i> 12.	10
	Tex. LLANO CO.: <i>T.</i> 2512.	10
	Tex. MEDINA CO.: <i>Johnston et al.</i> 3438.	10
	Tex. MOTLEY CO.: <i>Tomb</i> 148.	10
	Tex. WILSON CO.: <i>T.</i> 4423.	10
	Tex. WILSON CO.: <i>Sullivan & T.</i> 1.	10
<i>Palafoxia rosea</i> var. <i>rosea</i>	Tex. FREESTONE CO.: <i>T.</i> 4447.	10
	Tex. GALVESTON CO.: <i>T.</i> 3070.	10
	Tex. LEON CO.: <i>T.</i> 4437.	10
<i>Palafoxia sphacelata</i>	Mex. CHIHUAHUA: <i>Stuessy</i> 1115.	12
	N. Mex. DE BACA CO.: <i>T.</i> 5672.	12
	N. Mex. LEA CO.: <i>T.</i> 2945. (SMU)	12
	Okla. WOODS CO.: <i>Tomb</i> 593.	12
	Tex. CRANE CO.: <i>AVERETT</i> 213, 214C.	12
	Tex. PECOS CO.: <i>Watson</i> 142	12
	Tex. WARD CO.: <i>Melchert</i> 251.	12
<i>Palafoxia texana</i> var. <i>ambigua</i>	Tex. ARANSAS CO.: <i>T.</i> 5035.	11
	Tex. HIDALGO CO.: <i>T.</i> 4481.	11
	Tex. KARNES CO.: <i>T.</i> 5017.	11
	Tex. NUECES CO.: <i>T.</i> 3961.	11
<i>Palafoxia texana</i> var. <i>texana</i>	Mex. COAHUILA: <i>Flyr</i> 236, 237.	11
	Mex. COAHUILA: <i>P.</i> 501, 503, 519.	11
	Mex. COAHUILA: <i>Rock</i> M-488.	11
	Mex. COAHUILA: <i>T.</i> 2981, 6007.	11
	Mex. NUEVO LEON: <i>McGregor</i> 16752 (KANU).	11
	Mex. TAMAULIPAS: <i>King</i> 2209.	11

Table 1 (continued)

Species	Locality and voucher*	<i>n</i> = number
<i>Palafoxia texana</i>	Tex. ATASCOSA CO.: <i>T.</i> 4982.	11
var. <i>texana</i>	Tex. FRIO CO.: <i>Sullivan & T.</i> 15.	11
	Tex. FRIO CO.: <i>Sullivan & T.</i> 18.	11
	Tex. FRIO CO.: <i>T.</i> 4558.	11
	Tex. HIDALGO CO.: <i>T.</i> 4481.	11
	Tex. HIDALGO CO.: <i>Strother</i> 82.	11
	Tex. MEDINA CO.: <i>T.</i> 4561.	11
	Tex. MC MULLEN CO.: <i>Flyr</i> 168.	11
	Tex. STARR CO.: <i>T.</i> 4512.	11
	Tex. STARR CO.: <i>T.</i> 4501.	11
	Tex. VAL VERDE CO.: <i>Melchert</i> 263.	11
	Tex. VAL VERDE CO.: <i>P. & Watson</i> 1399C.	11
	Tex. WEBB CO.: <i>Melchert</i> 272.	11
	Tex. ZAVALA CO.: <i>T.</i> 5001.	11

*Except where spelled out, collectors are abbreviated as follows: *B* for Babcock; *P* for Powell; *R* for Raven; *S* for Sikes; *T* for Turner. Unless specified, voucher specimens are deposited in TEX.

^ARaven, P. H. and D. W. Kyhos, *In*: Am. J. Bot. 48:842-850. 1961.

^BSmith, E. B. and R. R. Johnson, *In*: Madrono 17:268. 1964.

^CPowell, A. M. and S. Sikes, *In*: Southwest. Naturalist 15:175-186. 1970.

Except in synthetic interspecific hybrids between *P. rosea* ($n = 10$) and *P. callosa* ($n = 10$), meiosis was nearly always regular and fragments were only infrequently observed. Meiotic figures from F_1 hybrids between the single synthetic cross attempted showed bridges and fragments in about 50% of the cells examined; the remaining 50% appeared normal.

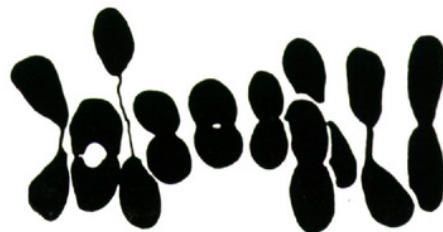


Fig. 1. Meiotic chromosomes of *Palafoxia rosea* var. *rosea* ($n = 10$); $\times 3400$.



Fig. 2. Mitotic chromosomes of *Palafoxia rosea* var. *rosea* ($2n = 20$); $\times 3400$.

GENERIC ORIGIN

Although phylogenetic histories of a genus are necessarily hypothetical, certain geobotanical considerations correlated with cytological data provide interesting clues to the origin of *Palafoxia* and attendant species. The ancestral prototype of *Palafoxia* probably originated in tropical America from Eupatorioid stock or derivations thereof. According to Shinnars (1952), *Palafoxia* evolved during the Miocene as an autochthonous element of the Texas-North Mexican (Mexican Plateau) flora which migrated northeastward to the Edwards Plateau and Trans-Pecos regions of present-day Texas. If Shinnars is correct, it is very possible that the genus became initially established within an area now generally known as south-central Texas from where the incipient stages of evolutionary divergence occurred.

We view the origin of the group somewhat differently. It is surmised that the rayed species of *Palafoxia*, *P. reverchonii*, *P. sphacelata*, and *P. hookeriana*, each possessing the base chromosome number, $x = 12$, represent the most primitive members of the genus and constitute a closely related monophyletic unit from which the remaining nine eradiate species ultimately had their origin. This being so, we visualize the primitive species as being relictual elements of a neotropical flora which occupied much of the southeastern United States during the early Terti-

ary. The peripheral, more advanced taxa such as *Palafoxia texana* ($n = 11$), *P. lindenii* ($n = 11$), *P. rosea* ($n = 10$), and *P. callosa* ($n = 10$) were evidently derived by progressive aneuploid reduction from the ancestral base of $x = 12$, the first 3 species adapting to sandy soils, *P. callosa* to limestone soils. *Palafoxia lindenii*, an endemic to the sand dunes of Veracruz, Mexico and vicinity, is very closely related to *P. texana* and is, presumably, a recent insular-type derivative from the latter species. Insular adaptation of divergent *Palafoxia* populations to sand dune habitats is not an uncommon phenomenon and has probably occurred independently in the genus several times. With respect to *P. linearis*, *P. arida*, *P. riograndensis*, *P. feayi*, and *P. integrifolia*, populations representing their differentiating gene pools could have been subjected to disruptive selection pressures which eventually led these evolving groups to occupy ecologically similar (sandy), but spatially disjunct habitats.

Table 2. Selected characteristics of *Palafoxia* listed according to their adjudged primitive and advanced states.

Primitive Characters	Advanced Characters
Heads rayed	Heads eradiate
$n = 12$	$n = 11, 10^*$
Annual	Perennial
Outer disc florets regular	Outer disc florets irregular
Leaves petioled	Leaves sessile
Lobes of disc corollas longer than throat	Lobes of disc corollas shorter than throat
Phyllaries tending to be broadened: ovate, obovate, lanceolate	Phyllaries tending to be narrowed: oblong, elliptic, linear
Pappus of outer disc florets monomorphic	Pappus of outer disc florets dimorphic
Phyllaries green, foliaceous	Phyllaries white, membranous

*Highly advanced

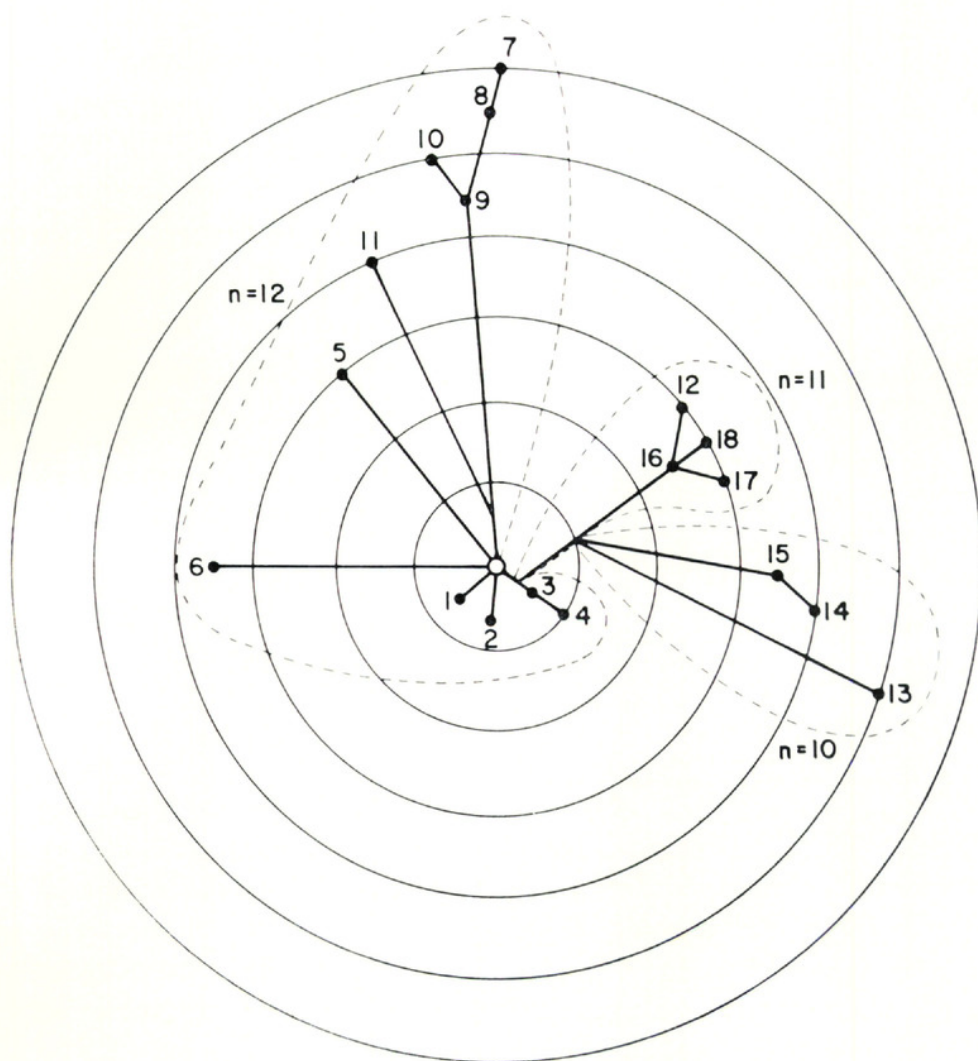


Fig. 3. Hypothetical phylogenetic diagram showing the species and varieties of *Palafoxia* as indicated by number: (1) *reverchonii*; (2) *sphacelata*; (3) *hookeriana* var. *hookeriana*; (4) *hookeriana* var. *minor*; (5) *feayi*; (6) *integrifolia*; (7) *linearis* var. *linearis*; (8) *linearis* var. *glandulosa*; (9) *arida* var. *arida*; (10) *arida* var. *gigantea*; (11) *riograndensis*; (12) *lindenii*; (13) *callosa*; (14) *rosea* var. *rosea*; (15) *rosea* var. *macrolepis*; (16) *texana* var. *texana*; (17) *texana* var. *ambigua*; (18) *texana* var. *robusta*. The common ancestor is represented by the origin and each consecutive, concentric level symbolizes an incremental advancement of 1.0 (e.g., outermost circle = 6.0).

Table 2 lists certain characteristics according to their adjudged states of primitiveness and advancement. "Generalized" characters were not necessarily considered to be primitive. Numerical values of 0 and 1 were assigned to characters deemed primitive and advanced, respectively. Highly advanced characters were assigned a value of 2. Each species and variety was arranged according to its hypothetical phylogenetic relationships (Fig. 3).

TAXONOMY

PALAFXIA Lagasca

Palafoxia Lagasca, Elench. Pl. Hort. Matr. 26. 1816; Gen. et Sp. Nov. 26. 1816.

Paleolaria Cassini, Bull. Soc. Philom. 198. 1816; Dict. Sci. Nat. 1, Suppl. 59. 1816.

Polypteris Nuttall, Gen. N. Am. Pl. 2: 139. 1818.

Lomaxeta Rafinesque, New Fl. Am. 4: 72. 1836.

Othake Rafinesque, New Fl. Am. 4: 73. 1836.

Taprooted annuals or perennials; stems erect or ascending, brittle-herbaceous, suffruticose to woody in certain species, variously branched to nearly simple, densely glandular-pubescent to almost glabrous; leaves alternate (usually opposite at first), firm-membranous, petiolate (rarely sessile); blades linear to broadly lanceolate, entire; heads irregularly corymbiform at the top of the plant, 3-28 mm high; involucre cylindric to broadly turbinate; receptacle flat, naked; phyllaries 2-3 seriate, subequal, linear to obovate, green, thickish to membranous, the margins often tinged red-purple, pubescence when present commonly interspersed with glandular trichomes; ray flowers absent or present, when present pale to dark violet, prominently 3-toothed terminally, pistillate, fertile; disk flowers white to violet, perfect, fertile, corollas regular or irregular, 5-lobed terminally; style branches linear, spreading or revolute, hispidulous; achenes 4-angled, obpyramidal; pappus

of 4-10 scales, varying from a minute callosity to a long acuminate hyaline-margined callose midrib, prominently dimorphic in certain species; gametic chromosome numbers, $n = 10, 11, 12$. Type species: *Palafoxia linearis* (Cav.) Lagasca.

KEY TO SPECIES AND VARIETIES OF PALAFOXIA

- A. Heads with conspicuous rays B.
- B. Leaves linear, narrowly lanceolate, 2-4(-6) mm wide; stems not glandular except for inflorescence; achenes 5-6 mm long; involucre bracts 6-7(-8) mm long 1. *P. reverchonii*
 - B. Leaves lanceolate to ovate-lanceolate, 3-20 mm wide; stems usually glandular for some distance below inflorescence, often conspicuously so; achenes 6-9 mm long; involucre bracts 7-20(-25) mm long .. C.
 - C. Heads narrowly turbinate to cylindric; involucre bracts 2.0-2.5(-3) mm wide; ligule of ray mostly 10 mm long or less; stems not robust, branching at or below middle (except in immature or depauperate specimens); species of western Texas, New Mexico, and adjacent Mexico 2. *P. sphacelata*
 - C. Heads broadly turbinate to campanulate; involucre bracts 2-5 mm wide; ligule of ray mostly 10 mm long or more; stems robust, branched at or above middle (except in mowed or injured specimens); species of eastern Texas D.
 - D. Stems densely glandular-pubescent throughout; involucre, in flower, 10-16 mm high; florets 50-90 per head 3a. *P. hookeriana* var. *hookeriana*
 - D. Stems glandular-pubescent only in the upper portions; involucre, in flower, 7-12 mm high; florets 25-50 per head 3b. *P. hookeriana* var. *minor*

- A. Heads without rays (peripheral florets inconspicuously zygomorphic in *P. riograndensis*) E.
- E. Species of southeastern U. S. (principally Florida) F.
- F. Involucral bracts linear, herbaceous, green; spindly shrubs 1-3 m tall 4. *P. feayi*
- F. Involucral bracts narrowly elliptic to obovate, membranous, white; perennial herbs 0.3-1.0 m tall 5. *P. integrifolia*
- E. Species of southwestern U. S. (west of Mississippi River) and Mexico G.
- G. Corolla lobes short, about $1/5$ as long as the elongate throat; species of Sonoran and Mojave deserts (southwestern-most Utah to southern-most Baja California, Mexico) H.
- H. Leaves linear, obtuse or rounded at apex; sprawling shrublets of southern Baja California (occasional adventive in dune sand along beaches of Sonora, Mexico) I.
- I. Mid-stem foliage (and most others) rather evenly pubescent with appressed white hairs and without glandular trichomes 6a. *P. linearis* var. *linearis*
- I. Mid-stem foliage (and most others) densely covered with a rough glandular pubescence 6b. *P. linearis* var. *glandulosa*
- H. Leaves linear-lanceolate, acute at apex; strictly erect, taprooted annuals of more northern distribution J.
- J. Plants not robust, 0.3-0.9 m tall, the primary stem 0.5 cm thick or less; heads (including disc florets), 20-25(-28) mm long; widespread in the Sonoran desert 7a. *P. arida* var. *arida*
- J. Plants robust, 0.9-1.5 m tall, the primary stem 0.5-1.0 cm thick; heads 28-35 mm long; endemic to large sand dunes west

- of Yuma, Arizona
 7b. *P. arida* var. *gigantea*
- G. Corolla lobes longer than throat; species of the Chihuahuan desert, Mexico, and eastward . . K.
- K. Involucre cylindric; corolla of outermost florets zygomorphic; achenes (7-)8-11 mm long 8. *P. riograndensis*
- K. Involucre turbinate; corollas regular; achenes 4-7 mm long L.
- L. Leaf blades greyish puberulent, widest at or near the middle; achenes glabrous or nearly so 9. *P. lindenii*
- L. Leaf blades greenish, often whitish canescent; achenes pubescent M.
- M. Leaves mostly linear to narrowly lanceolate, 2-6 mm wide; chromosome number, $n = 10$; species of southcentral to western Texas and northward N.
- N. Involucral bracts narrowly linear, 0.6-1.3 mm wide; pappus 0.5-2.0 mm long; species on predominantly limestone soils 10. *P. callosa*
- N. Involucral bracts linear to obovate, mostly 1.2-2.5 mm wide; pappus 1.0-8.0 mm long; species on predominantly sandy soils O.
- O. Pappus scales mostly short, obtuse to acute, 1.0-3.0 mm long; involucral bracts 5-7 mm long; plants of southcentral Oklahoma and eastern Texas 11a. *P. rosea* var. *rosea*
- O. Pappus scales mostly long, acute to long acuminate, 3.0-8.0 mm long; involucral bracts 7-10 mm long 11b. *P. rosea* var. *macrolepis*
- M. Leaves mostly broad lanceolate, 6-15 mm wide; chromosome number, $n = 11$, species of southcentral Texas and southward P.
- P. Pappus scales of inner achenes 3-5(-6) mm long; involucral bracts broadly linear to oblanceolate, pubescence interspersed with glandular trichomes; main stem usually branched below; usually occur-

- ring in rocky limestone soils
 12a. *P. texana* var. *texana*
- P. Pappus scales of inner achenes 1-3(-4) mm long; involucre bracts linear, usually lacking glandular trichomes; main stem usually unbranched below (except following injury); usually occurring in silty alluvial or sandy soils Q.
- Q. Achenes 4.0-5.5 mm long; plants of southernmost Texas and adjacent Mexico
 12b. *P. texana* var. *ambigua*
- Q. Achenes 6-7 mm long; plants of coastal sand dunes of central Tamaulipas, Mexico
 12c. *P. texana* var. *robusta*



Fig. 4. *Palafoxia reverchonii*. A. Whole plant, $\times \frac{1}{4}$. B. Ray floret, $\times 3$. C. Disc floret, $\times 3$.

1. *Palafoxia reverchonii* (Bush) Cory, *Rhodora* 48:86. 1946. *Fig. 4*

Othake reverchonii Bush, *Trans. Acad. Sci. St. Louis* 14: 180. 1904. TYPE: UNITED STATES. **Texas:** UPSHUR CO.: Big Sandy, *Reverchon* 3289 (Holotype, MO!; isotypes, NY!, 2 sheets). *Polypteris reverchonii* (Bush) Small, *Fl. S.E. U. S.* ed. 2, 1373. 1913.

Annual herbs 10-90 cm tall; stems brittle, dark green, rather evenly appressed pubescent throughout with short white hairs, without glandular trichomes except in the inflorescence; leaves opposite at first but soon alternate; mid-stem leaves narrowly lanceolate, 2-4(-6) mm wide, 30-90 mm long, petioles 3-10 mm long, blades appearing 1-nerved beneath, sparsely appressed hispid on both surfaces, the apices slender, acute; inflorescence an open corymb with 5-40 heads; heads turbinate 1.0-1.5 cm high, 15-35 flowered, on ultimate peduncles 1.5-8.0 cm long; principal involucre bracts 8-12, linear-lanceolate to somewhat obovate, 6-8 mm long, 1.5-3.0 mm wide, usually green and membranous along the margins, but occasionally purplish, pubescent with short, appressed hairs, these sparsely to densely interspersed with glandular trichomes; ray florets pale to dark violet, 15-25 mm long, the ligules with 3 linear lobes, these 4-5 mm long, 2-3 mm wide; disc corollas violet, regular, 5-8 mm long, the tube 3-5 mm long, abruptly flaring into a short throat 0.5-1.0 mm long, the lobes linear 2-3 mm long; achenes 5-6 mm long, uniformly short pubescent; pappus of disc florets composed of ca. 8 scarious, lanceolate, attenuate scales, 3-6 mm long, the mid-portion darker and somewhat indurate; ray pappus of 8 short, obovate scales ca. 0.5 mm long; chromosome number, $n = 12$.

Distribution: Sandy soils in upland pine and oak woodlands of eastern Texas. Flowering, Sept.-Oct. *Fig. 5*.

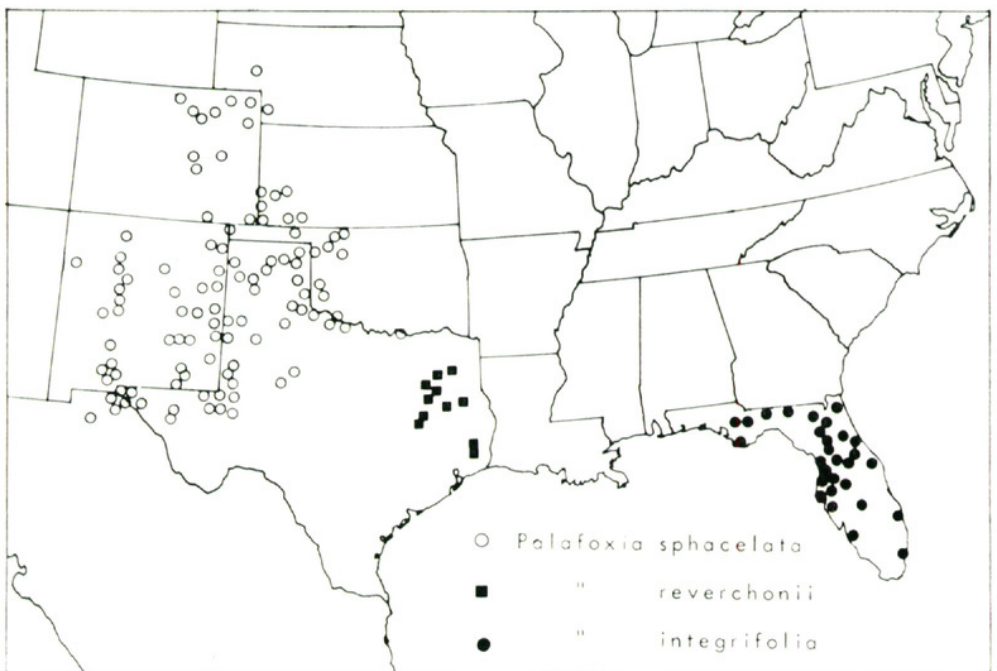


Fig. 5. Distribution of *Palafoxia sphacelata*, *P. reverchonii*, and *P. integrifolia*.

REPRESENTATIVE SPECIMENS: UNITED STATES. Texas: ANDERSON CO.: 6 miles NW Tennessee Colony, *Marsh, Jr.* 278 (TEX); Engeling area, *Marsh, Jr.* 56-43 (TEX); HARDIN CO.: 7.5 miles W of Silsbee, *Cory* 11327 (GH); HENDERSON CO.: Athens, *Turner* 5742 (TEX); HOUSTON CO.: Grapeland, *Palmer* 12834 (ARIZ, GH, NY, UC, US); LEON CO.: Centerville, *Fisher* (F); NACOGDOCHES CO.: Cushing, *Tharp & Brown* s.n. (TEX); UPSHUR CO.: 1.5 miles E of Big Sandy, *King* 2182 (SMU, TEX).

The species is most closely related to the allopatric *Palafoxia hookeriana* and might with some justification be treated as no more than a variety of that taxon. *Palafoxia reverchonii* is a much more delicate plant (with smaller heads, narrower leaves and fewer glands) than *P. hookeriana*. Through several years of field work, attempts at finding mixed populations of these two taxa were never successful. The taxa occur in seemingly pure populations near each other in Houston County, but were not found growing together.

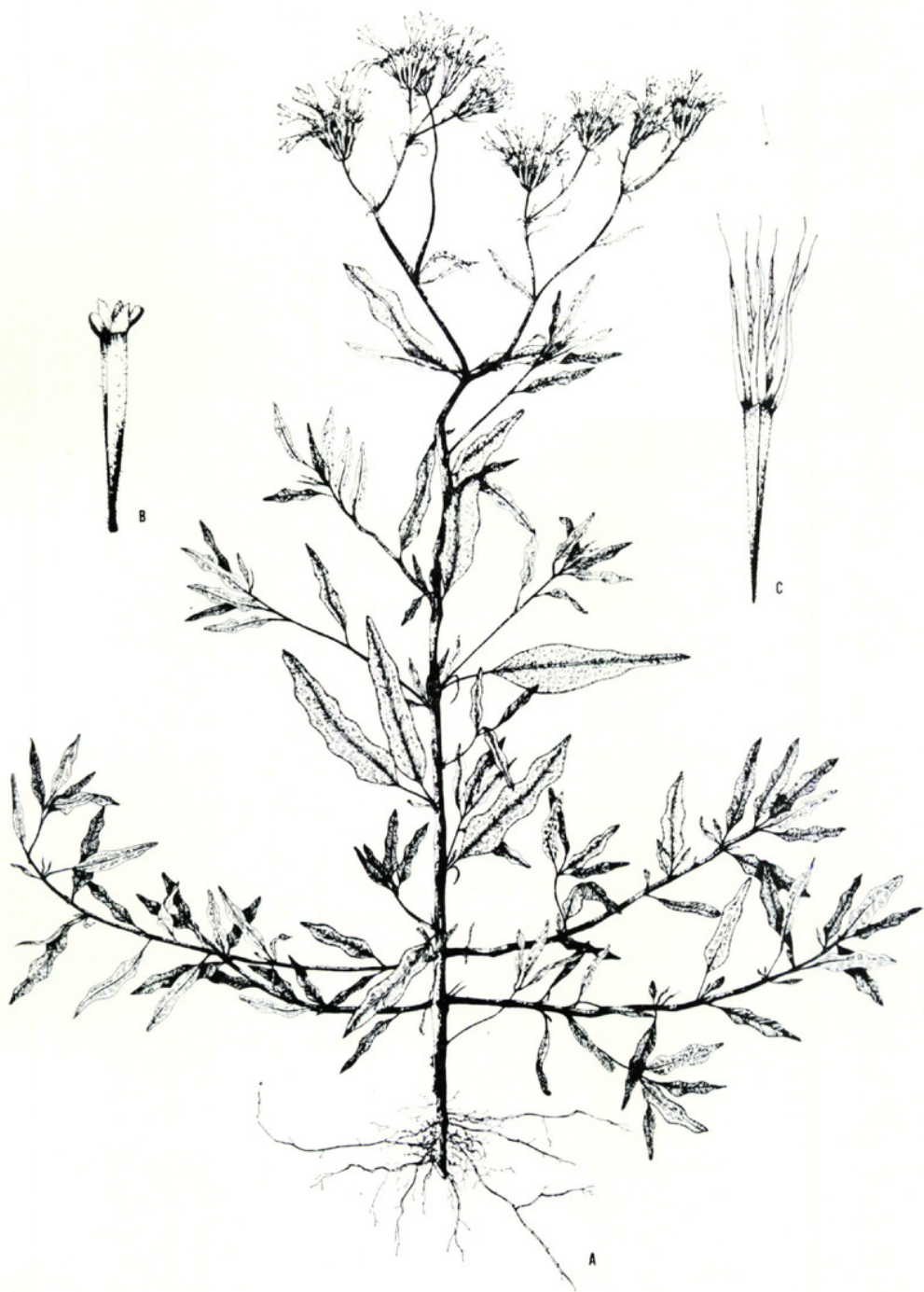


Fig. 6. *Palafoxia sphacelata*. A. Whole plant, $\times \frac{1}{4}$. B. Ray achene and pappus, $\times 3$. C. Disc achene and pappus, $\times 3$.

2. *Palafoxia sphacelata* (Nutt. ex Torr.) Cory, *Rhodora* 48: 86. 1946. *Fig. 6*.

Stevia sphacelata Nutt. ex Torr., *Ann. Lyc. N.Y.* 2:214. 1828. TYPE: UNITED STATES. Without date or specific locality, probably in southeastern Colorado, *James*, (Holotype, NY!). *Palafoxia hookeriana* var. *subradiata* T. & G., *Fl. N. Am.* 2:368. 1842. *Polypteris sphacelata* (Nutt. ex Torr.) Trel. ex Branner & Cov., *Ann. Rep. Geol. Surv. Arkansas* 1888, 1:197. 1891. *Othake sphacelatum* (Nutt.) Rydb., *Bull. Torr. Bot. Club* 37:332. 1910. *Palafoxia hookeriana* Hook., *In: Curtis's Bot. Mag.* 91:t.5549. 1865. *non Palafoxia hookeriana* T. & G., 1842.

Annual herbs, 10-90 cm tall; stems brittle, becoming white and much-branched with age, merely hispid below, the upper portions densely glandular-pubescent; leaves simple, opposite at first but soon becoming alternate; mid-stem leaves broadly to narrowly lanceolate, even in the same population, 3-20 mm wide, 30-90 mm long, petioles 5-25 mm long, blades prominently 3-nerved beneath, roughly hispid on both surfaces, the apices acute; inflorescence corymbose with 3-20 heads; heads narrowly to broadly turbinate, 1-2 cm across, 1-2 cm high (including the exserted disc florets), 20-40 flowered, on ultimate peduncles 1.0-4.5 cm long; principal involucre bracts 10-12, linear-lanceolate, 9-12 mm long, 1.5-3.0 mm wide, usually purplish along the membranous margins, pubescent with short rough hairs, these interspersed with glandular-capitate trichomes; ray florets pale to dark violet, 15-25 mm long, the ligules with 3 narrow lobes 4-8 mm long, 1.5-3.0 mm wide; disc corollas pale violet, regular, 10-14 mm long, the tube 6-8 mm long, abruptly flaring into a short throat 1-2 mm long, the lobes linear, 3-5 mm long; achenes 6-9 mm long, uniformly short pubescent; pappus of disc florets composed of ca. 8 scarious, lanceolate, attenuate scales 7-9 mm long, the mid-portion darker and somewhat indurate; ray pappus of 8 short, obovate, erose scales, 0.2-0.7 mm long; chromosome number, $n = 12$.

Distribution: Mostly in sandy soils from northeastern Colorado south to trans-Pecos Texas and adjacent Mexico. Flowering, May-Nov. Fig. 5.

REPRESENTATIVE SPECIMENS. UNITED STATES. Colorado: BACA CO.: 4 miles N of Okla. line, *Rogers* 6418 (US); EL PASO CO.: between Drennen and Ellicott, *Bacigalupi* 858 (DS, GH, UC); LARIMER CO.: Ft. Collins, *Baker* 806 (MICH); LAS ANIMAS CO.: 3 miles SW of Tobe, *Rogers* 6128 (US); WELD CO.: Roggen, *Ramaley* 15136 (CAS, US); YUMA CO.: Wray, *Eggleson* 15535 (F). **Kansas:** MORTON CO.: S of Cimarron River, *Gates* 16175 (F); SEWARD CO.: Arkalon, *Kellerman* s.n. (US). **New Mexico:** BERNALILLO CO.: Isleta, *Arsene* 17503 (F, US); CHAVES CO.: 35 miles W of Roswell, *Earle & Earle* 381 (MO, US); DONA ANA CO.: Mesilla Valley, *Wootton* s.n. (ARIZ, DS, UC); EDDY CO.: Carlsbad, *Tracy* 8163 (F, GH, MO, US); GUADALUPE CO.: vicinity of Santa Rosa, *Arsene & Benedict* 16714 (F); MC KINLEY CO.: near Ft. Wingate, *Rusby* 211 (MICH); QUAY CO.: Nara Visa, *Fisher* 150 (US); ROOSEVELT CO.: 2.5 miles S of Tolar, *Tucker* 2959 (US); SANDOVAL CO.: Jemez Springs, *Nelson* 11680 (GH, MO, UC); SAN MIGUEL CO.: near Las Vegas, *Cockerell* (CAS); SIERRA CO.: near Elephant Butte Dam, *Archer* 408 (MICH); SOCORRO CO.: San Acacia, *O'Byrne & Magner* 3440-1 (MO); UNION CO.: 22 miles SW of Clayton, *Waterfall* 12283 (TEX); VALENCIA CO.: 8 miles S of Bellen, *Parker* 2408 (ARIZ, CAS). **Oklahoma:** BEAVER CO.: near Beaver, *Palmer* 41895 (MO, UC); BECKHAM CO.: SE part of county, *Eskew* 1524 (GH, MO, US); CIMARRON CO.: 1 mile W & 4 miles S of Kenton, *Waterfall* 8685 (MO); ELLIS CO.: Wolf Creek, near Shattuck, *Stevens* 2908 (DS, MO, US); TILLMAN CO.: Frederick, *Duncan* s.n. (MO); WOODS CO.: Waynoka dunes, north at Cimarron R. near Highway 281, *Hansen* s.n. (US); WOODWARD CO.: w/o locality, *White* s.n. (MO). **Texas:** ANDREWS CO.: W of Andrews, *Gentry* 1928 (ARIZ); BAILEY CO.: 2 miles S of Muleshoe, *Ferris & Duncan* 3411 (CAS, DS, MO); CHILDRESS CO.: 10½ miles N of Childress, *Cory* 50140 (DS, GH, US); COLLINGSWORTH CO.: 10 miles NE of Wellington, *Cory* 50166 (GH, US); CRANE CO.: near Crane, *Cutak* 6 (MO); CULBERSON CO.: 13 miles E of Van Horn, *Waterfall* 5473 (CAS, GH, MO); DALLAM CO.: Texline, *Howell* 147 (US); ECTOR CO.: Odessa, *Harad* s.n. (US); EL PASO CO.: 25 miles E of El Paso, *Gooding & Hardies* 2860 (ARIZ); GAINES CO.: Seminole, *Tharp* 4558 (TEX, US); GRAYSON CO.: Denison, *Letterman* s.n. (F); HARDEMAN CO.: 7.2 miles N of Quanah on Red River, *Whitehouse* 10751 (UC, US); HARTLEY CO.: 10 miles E of Romero, *Cory* 16468 (GH); HEMPHILL CO.: near Canadian, *Eggert* s.n. (MO); HUDSPETH CO.: 4 miles E of Hueco, *Waterfall* 3865 (ARIZ, GH, MO); LAMB CO.: 16 miles N of Littlefield, *Turner & Melchert* 4829 (TEX); LIPSCOMB CO.: Lipscomb, *Howell* 56 (US); LOVING CO.: 3 miles E of Red Bluff

Lake, *Hinckley & Hinckley* 351 (TEX); LUBBOCK CO.: Lubbock, *Tharp* s.n. (MO, TEX); MITCHELL CO.: 2½ miles N of Colorado City, *Shinners* 8395 (GH, MO); MOTLEY CO.: 5 miles N of Matador, *Cory* 16096 (GH); OLDHAM CO.: 1 mile N of bridge over Canadian R. on Amarillo-Dalhart Rd., *Ferris & Duncan* 3501 (CAS, DS, MO); POTTER CO.: Amarillo, along R. R., *Palmer* 12543 (GH, MO, US); ROBERTS CO.: 28 miles S of Perryton, *Wallis* 7908 (TEX); WARD CO.: 3½ miles NW of Monahans, *Cory* 51973 (US); WILBARGER CO.: *Reverchon* 1230 (F); WINKLER CO.: 9 miles E of Kermit, *Correll* 15190 (US).

MEXICO. **Chihuahua:** 8 miles S of Samalayuca, *Johnston* 3005 (TEX); sand dunes, *Le Sueur* 65 (CAS, F, GH, MO, TEX, US); near Lake Santa Maria, *Nelson* 6404 (GH, US); Colonia Diaz, *Nelson* 6463 (GH, US); sand hills near Paso del Norte, *Pringle* 761 (F, GH, MICH, MO, UC, US); E of Santa Maria, *Schott* s.n. (GH); 36 miles S of Ciudad Juarez, *Shreve* 7921 (ARIZ).

Palafoxia sphacelata is sympatric over part of its range with the eradiate *P. rosea* var. *macrolepis*. In fruiting specimens it is difficult to distinguish between these taxa. However, they are quite distinct, the former possessing dimorphic achenes (the pappus of the ray and disc florets differ) and a chromosome number of $n = 12$; the latter having uniform achenes and a chromosome number of $n = 10$. This, of course, largely precludes serious consideration of Shinners' suggestion (1952) that *P. sphacelata* is "Perhaps better regarded as a third variety of *P. texana*, from which it is very difficult to distinguish after the ray florets have fallen."

Early workers, as indicated by the synonymy above, frequently confused the allopatric *Palafoxia sphacelata* and *P. hookeriana*. Indeed, the species are quite similar and, except for the lower habit and western distribution of the former, are difficult to distinguish. Both species are diploid with $n = 12$, and are probably derived from the same phyletic stock. For additional discussion see *P. hookeriana*.

3. *Palafoxia hookeriana* T. & G. Fl. N. Am. 2: 368. 1842.

TYPE: UNITED STATES. Texas, *Drummond* II. 136 (Holotype, K!; Isotypes, GH!, NY!, TEX!).

Polypteris hookeriana (T. & G.) Gray, Proc. Am. Acad. 19:30. 1883. *Othake hookerianum* (T. & G.) Bush, Trans.

Acad. Sci. St. Louis 14:177. 1904. Hooker (1837) first described and pictured this plant, but erroneously assumed that Drummond's collection was *Palafoxia texana* DC. In his description of the specimen which accompanies the plate, he states: "Flowers large, handsome, distinctly rayed, of which circumstance DeCandolle takes no notice; but in other respects his description is so accurate that I cannot but think the two plants are the same." Gray, in describing the plant as a new species, typified the taxon by reference to Hooker's plate which was made from the Drummond collection cited above.

Polypteris maxima Small, Fl. S.E. U. S. 1288. 1903. TYPE: UNITED STATES. Texas, without date or collection number, but collected probably in Austin Co., near Industry, August, 1844, *Lindheimer* (Holotype, NY!; probable isotypes, MO!, NY!). *Othake maximum* (Small) Bush, Trans. Acad. Sci. St. Louis 14:179. 1904.

3a. *Palafoxia hookeriana* T. & G. var. *hookeriana*. Fig. 7.

Plants annual, 25-180 cm tall; stems erect, sparingly branched (except following injury), densely glandular-pubescent (viscid) throughout; midstem leaves narrowly to broadly lanceolate, 4-25 mm wide, 50-100 mm long, with petioles 5-25 mm long, blades gradually tapering into an acute apex, scabrous on both surfaces and usually glandular-pubescent, especially along the margins; inflorescence a few-flowered cyme of 3-8 heads; heads radiate, broadly turbinate, 15-20 mm across (excluding the projecting rays), 15-20 mm high, 30-80 flowered, on densely glandular peduncles 2-10 cm long; principal involucre bracts 10-15, broadly linear to narrowly obovate, 10-15 mm long, 3-5 mm wide, scabrous to densely glandular pubescent, the outer-most rarely becoming somewhat foliaceous; ray florets 8-13, deep pink, 10-20 mm long, the ligule prominently 3-lobed, to 12 mm long and 4 mm wide, the tube narrowly cylindric, 6-9 mm long; disc florets deep pink, 10-12 mm long, tube cylindric ca. 5 mm long, the 5 linear lobes united for ca. $1/3$ to $2/5$ their length into a funnelform throat;

style branches 3-5 mm long; achenes black, narrowly obpyramidal, 6-8 mm long, sparsely pubescent to nearly glabrous; pappus scales dimorphic, those of the ray obovate, truncate, 0.5-0.7 mm long, those of the disc linear-lanceolate, 5-8 mm long, with pronounced midribs; chromosome number, $n = 12$.



Fig. 7. *Palafoxia hookeriana* var. *hookeriana*. A. Whole plant, $\times \frac{1}{4}$. B. Ray floret, $\times 2$. C. Disc floret, $\times 3$.

Distribution: Relatively light, sandy soils in pine and oak woodlands of southcentral and eastern Texas. Flowering, Aug.-Nov. Fig. 8.

REPRESENTATIVE SPECIMENS. UNITED STATES. Texas: AUSTIN CO.: Industry, *Lindheimer* (MO); BASTROP CO.: Bastrop, *Tharp* 44499 (GH, TEX); BURLESON CO.: Lyons, *Martin* 6235 (TEX); CALDWELL CO.: near Luling, *Schulz* s.n. (F); GOLIAD CO.: Goliad, *Williams* 121 (F);

GONZALES CO.: *Whitehouse* s.n. (MO, UC); GRIMES CO.: Navasota, *Fisher* 32153 (ARIZ, CAS, MICH, US); HARRIS CO.: Crosby, *Fisher* 31 (US); HILDALGO CO.: Edinburg, *Shiller* 837 (US); JACKSON CO.: w/o locality, *Drushel* s.n. (TEX); KENEDY CO.: 25 miles S of Sarita, *Webster & Wilbur* 3089 (US); LAVACA CO.: 14 miles SE of Yoakum, *Turner & Tharp* 3273 (TEX); LEE CO.: *Knoblock* s.n. (TEX); LIBERTY CO.: Romayer, *Fisher* 33209 (ARIZ, CAS, F, TEX); NUECES CO.: Flour Bluff, *Parks* s.n. (MO); SAN PATRICIO CO.: 2½ miles NE of Calallen, *Cory* 20678 (GH); STARR CO.: 2.9 miles SW of Santa Elena, *Johnston* 541430 (TEX); VICTORIA CO.: Victoria, *Bindewald* s.n. (TEX); WASHINGTON CO.: 5 miles NE of Brenham, *Turner* 3917 (TEX); WILSON CO.: Cover Ranch, Kicaster, *Parks* 1504 (MO).

This is a handsome species, and while it shows great variation in growth habit, it is nonetheless restricted in its habitat to the forested, deep sandy soils of southcentral and east Texas. It can apparently survive and spread into other areas for, in 1955, the senior author found the species growing as a weed locally in Lucedale, Mississippi, where it was introduced by seed obtained from natural populations in Texas by the local Methodist preacher.

Early workers tended to confuse *Palafoxia hookeriana* with *P. sphacelata*, the latter being a much smaller plant confined to the sandy grasslands of more western regions. Nevertheless, the rayed species, *P. hookeriana* ($n = 12$), *P. sphacelata* ($n = 12$) and *P. reverchonii* ($n = 12$) are clearly related and probably form a monophyletic unit from which the aneuploid derivatives, *P. texana* ($n = 11$), *P. rosea* ($n = 10$), and *P. callosa* ($n = 10$) had their origin, presumably by aneuploid reduction from an ancestral base of $x = 12$.

Palafoxia hookeriana var. *hookeriana* is a relatively rare taxon as is the var. *minor*. We have not seen the two taxa growing together (although Shinnars, 1952, indicates they do) and it appears that the latter occurs more often in central Texas while var. *hookeriana* is more widespread, especially to the south.

It is suspected that the rare hybrid between *Palafoxia hookeriana* and *P. reverchonii* must occur since their

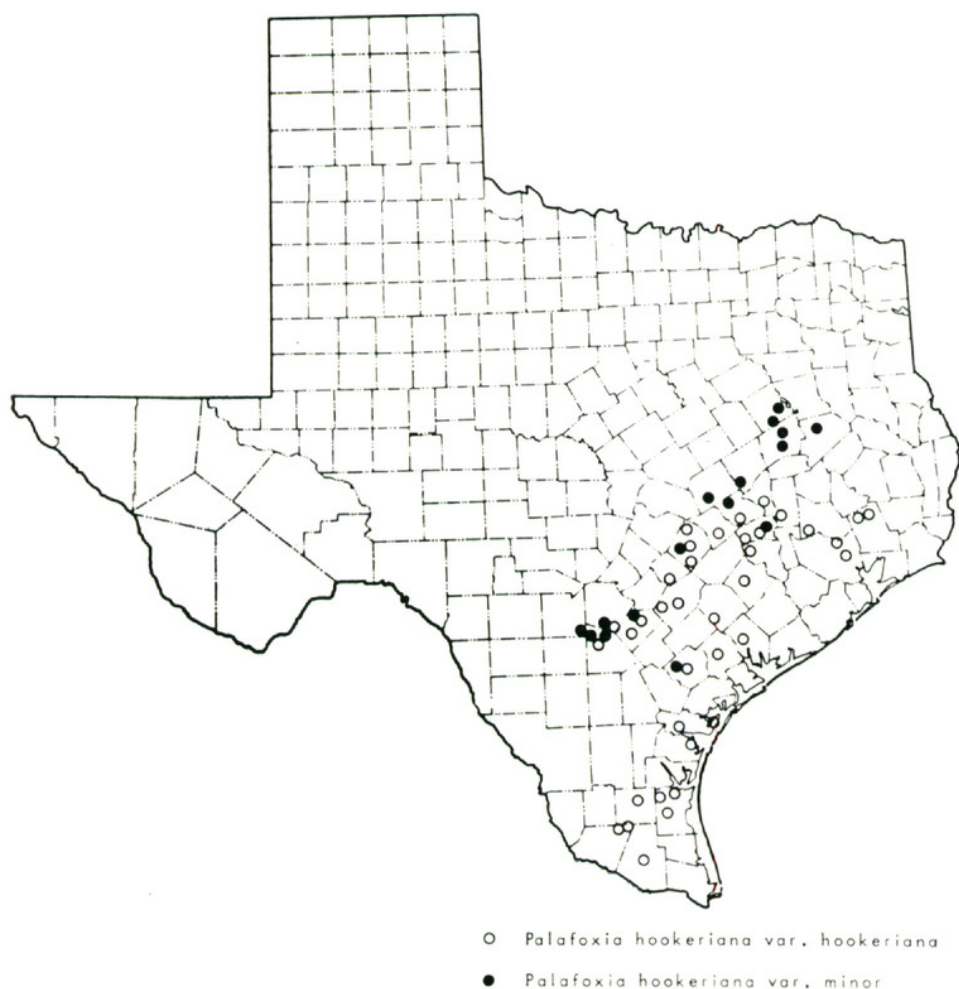


Fig. 8. Distribution of *Palafoxia hookeriana* var. *hookeriana* and *P. hookeriana* var. *minor*.

ranges overlap to the northeast, although we have not found evidence for this in the field. It may be, however, that the less glandular, smaller-headed plants, here recognized as *P. hookeriana* var. *minor*, are from populations which show introgression from *P. reverchonii* into *P. hookeriana*. In the early stages of the present study it was thought possible that the plants called *P. reverchonii* were hybrids between *P. rosea* ($n = 10$) and *P. hookeriana* ($n = 12$), but more recent field work has indicated that these taxa, while often growing near each other, do not hybridize to any detectable extent.

3b. *Palafoxia hookeriana* var. *minor* Shinnars, Field & Lab. 20:98. 1952. TYPE: UNITED STATES. Texas: HARRIS CO.: Channelview, *Fisher* 50717 (Holotype, SMU!).

Similar to var. *hookeriana* except that the plants are not as robust, possessing smaller heads and less glandular-pubescent stems.

Distribution: Southcentral and eastern Texas on light sandy soils in pine and oak woodland. Flowering, Sept.-Oct. Fig. 8.

REPRESENTATIVE SPECIMENS. UNITED STATES. Texas: ATASCOSA CO.: Pleasanton, *Palmer* 10781 (DS, MO, US); 12 miles N of Pleasanton, *Cory* 15564 (GH); Poteet, *Parks* 1270, 1277, 1278, 1416 (MO); BASTROP CO.: W of Cistern, *Tharp & Graham* s.n. (TEX); BEXAR CO.: Applewhite road, 18 miles S of San Antonio, *Clare* 448 (CAS, UC); FREESTONE CO.: 11 miles ESE Fairfield, *Turner* 4443 (TEX); GOLIAD CO.: near Goliad, *Williams* 74 (F, MO); LEON CO.: 5 miles E of Buffalo, *Gould* 7273 (TEX); MEDINA CO.: 3 miles SW of Devine, *Cory* 11756 (GH); MILAM CO.: Milano, *Joor* 54 (MO, UC, US); ROBERTSON CO.: Hearne, *White* s.n. (TEX); WASHINGTON CO.: w/o locality, *Tharp* s.n. (TEX, US); WILSON CO.: Sutherland Springs, *Parks* 15463 (GH).

Shinnars (1952), in his key to species, describes the stems of both var. *hookeriana* and var. *minor* as being "glandular-pubescent throughout with widely spreading hairs." Actually the lower half of the main stem of var. *minor* is usually without glandular trichomes and we find this character to be an easy one for distinguishing between the taxa. Also, occasional plants (*Cory* 15563, TEX; *Cory* 15564, GH) may be found without glands on their stems (or involucre!) but these cannot be confused with the more eastern *Palafoxia reverchonii* because they invariably have much broader leaf blades and a coarser, more hispid pubescence. Such plants may represent the occasional hybrid of *P. hookeriana* ($n = 12$) with *P. rosea* ($n = 10$) or *P. texana* ($n = 11$), but we have not observed the former growing together with either of the latter in the field. Baltzer annotated such specimens (e.g., *Palmer* 10781) as *P. sphacelata*, but that is a species of more western distribution.

4. *Palafoxia feayi* Gray, Proc. Am. Acad. 12:59. 1877. *Fig. 9.* TYPE: UNITED STATES. **Florida:** S. Florida, *Feay* s.n. (Holotype, GH!). On the same sheet with collections of the species by Chapman and Curtis.

Spindly shrubs, 1-3 m tall; stems sparingly branched, strigillose to nearly glabrous; leaves simple, opposite or subopposite at first, becoming alternate; mid-stem leaves ovate to narrowly elliptic, 2-6 cm long, 0.5-2.5 cm wide, petioles 2-6 mm long, blades thick, scabrous or roughly hispid on both surfaces, rounded or broadly obtuse at the apex; inflorescence corymbose with 10-50 heads; heads turbinate, 1-2 cm across, 2.0-2.5 cm high (including the exerted florets), 15-25 flowered, on ultimate peduncles 1-4 cm long; principal involucral bracts 9-12, linear to oblong, 5-9 mm long, 1.0-1.5 mm wide, membranous to somewhat thickened, strigillose, usually purplish-tinged; florets regular, white at first, becoming pinkish, corolla about 10 mm long, tube 2 mm long, the throat elongate, cylindric, 4.5-6.0 mm long, the lobes equal, 1.0-1.5 mm



Fig. 9. *Palafoxia feayi*. A. Top of plant, $\times \frac{1}{4}$. B. Head, $\times 1$.

long; style branches 5 mm long, otherwise as described for the genus; achenes obpyramidal, linear, 6-8 mm long, 4-sided, sparingly pubescent with short, spreading hairs; pappus scales 8, 1.5-2.0 mm long, acute to narrowly obtuse at the apex, those on the angles longer; chromosome number, $n = 12$.

Distribution: Sandy soils of pinelands in central and southern Florida usually in open fields with secondary shrubby growth. Flowering, Apr.-Nov., but most commonly in the summer and fall. Fig. 10.

REPRESENTATIVE SPECIMENS. UNITED STATES. Florida: BREVARD CO.: Merritts Island, w/o collector, C21264 (US); COLLIER CO.: Marco, *Hitchcock* 159 (F, GH, MO, US); DADE CO.: Arch Creed Prairie, *Small et al.* 6811 (GH, US); DIXIE CO.: Manatee, *Tracy* 6357 (MO, US); HIGHLANDS CO.: Archbold Biological Station, 10 miles S of Lake Placid, *Brass* 15233 (GH, US); HILLSBOROUGH CO.: Riverview, *Blanton* 6718 (DS, F); LAKE CO.: 1 mile E of Lisbon, *Turner* 4663 (TEX); LEE CO.: Fort Myers, *Buswell* 0061 (ARIZ); MANATEE CO.: Palma Sola, *Tracy* 6932 (F, MO, US); ORANGE CO.: Clarcona, *Meislahn* 73a (US); PALM BEACH CO.: w/o locality, *Randolph* 157 (GH); PINELLAS CO.: near St. Petersburg, *Deam* 2814 (MICH); POLK CO.: Winter Haven, *McFarlin* 3325 (MICH); VOLUSIA CO.: near Seville, *Curtis* 6688 (GH, MO, UC, US).

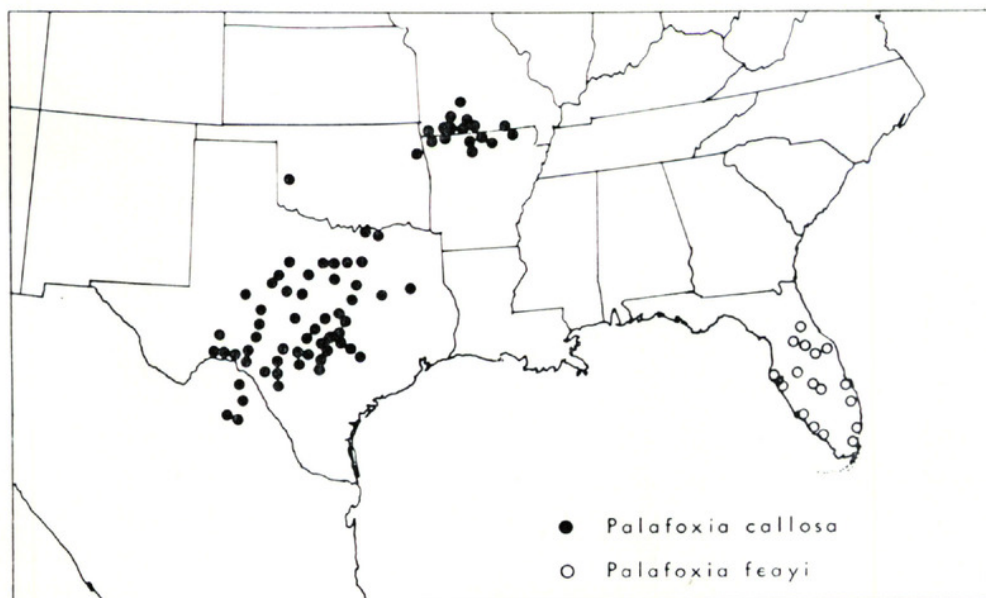


Fig. 10. Distribution of *Palafoxia callosa* and *P. feayi*.

Baltzer (1944) stated that "this species is intermediate between the genera *Polypteris* and *Palafoxia*, but is placed in the latter group because of the floret characters." In our opinion, the species is perhaps as close to *Othake* as it is to *Polypteris* (which includes only *P. integrifolia*).

Palafoxia feayi is a brittle-stemmed shrub up to 3 meters tall. Judging from its restriction to sandy soils on the Florida Peninsula, we believe that its woody nature is secondary, this having developed because of ancestral insular conditions to which it became adapted. Similar robust habits in coastal or active inland dunes have apparently developed independently in *P. texana* var. *robusta* and *P. arida* var. *gigantea*, and it seems almost certain that the robust *P. lindenii* developed from an ancestral stock not too unlike the herbaceous *P. texana*. Nonetheless, *P. feayi* must be older than any of these insular taxa since it has floral features which mark it as quite removed from any of the extant species of *Palafoxia*. In any case it is quite removed geographically from its most closely related taxa, *P. riograndensis* and *P. arida*.

5. ***Palafoxia integrifolia*** (Nutt.) Torr. & Gray, Fl. N. Am. 2:368. 1842. *Fig. 11*.

Polypteris integrifolia Nutt., Gen. N. Am. Pl. 2:139. 1818. *non* DC., Prodr. 5:659. 1836. TYPE: UNITED STATES. "Georgia" (probably collected in what is now Florida), Baldwin s.n. (Holotype, PH!). *Hymenopappus integrifolium* (Nutt.) Spreng., Syst. 3:449. 1826. *Paleolaria fastigiata* Less., Syn. Comp. 156. 1832. *Palafoxia fastigiata* (Less.) DC., Prodr. 5:125. 1836.

Lomaxeta verrucosa Raf., New Fl. Am. 4:72. 1836. *nom illeg.*

Plants perennial, 50-100 cm tall, stems suffruticose, erect to suberect from woody rootstocks or short rhizomes; usually simple below and divaricately branched above; leaves simple, entire, thick, opposite to sub-opposite below, becoming alternate above, scabrous on both surfaces; mid-

stem leaves 3-7(-9) cm long, 0.5-1.0 cm wide, broadly linear to somewhat lanceolate, with petioles 5-10 mm long; inflorescence corymbiform with 10-40 heads; heads broadly turbinate, 10-15 mm high, 7-10 mm across, 10-12 flowered, on ultimate peduncles 2-6 cm long; involucral bracts rounded at the apex, markedly gradate in 2-3 series, membranous, the outer phyllaries short and spreading or somewhat reflexed; florets regular, white to purplish-white; corolla about 12 mm long, deeply 5 lobed, the lobes 4-5 mm long, throat 1.0-1.5 mm long, tube 5-6 mm long; style branches 3.5-5.0 mm long, 4-sided, somewhat tangentially compressed in peripheral florets, minutely pubescent to nearly glabrate; pappus of 10 lanceolate scales, 6-7 mm long, with conspicuous thickened midribs and membranous margins; chromosome number, $n = 12$.



Fig. 11. *Palafoxia integrifolia*. A. Top of plant, $\times \frac{1}{4}$. B. Head, $\times 1\frac{1}{2}$.

Distribution: Throughout most of Florida, usually in sandy scrubland, or dry pine barrens. Flowering, May-Nov., but most commonly in the late summer and fall. Fig. 5.

REPRESENTATIVE SPECIMENS. UNITED STATES. **Florida:** ALACHUA CO.: Sugarfoot near Gainesville, *Murrill* s.n. (MO); BRADFORD CO.: New River, *Hitchcock* s.n. (F); BREVARD CO.: Indian River region, *Fredholm* 5623 (GH, MO, US); CALHOUN CO.: w/o locality, *Chapman* s.n. (MO); CITRUS CO.: w/o locality, *Hitchcock* s.n. (F); COLUMBIA CO.: Lake City, *Fla. Agric. Col.* 1308 (F); DADE CO.: Miami, *Tracy* 8929 (GH, TEX, US); DUVAL CO.: near Jacksonville, *Curtiss* 1507 (F, GH, MICH, MO, US); GULF CO.: near Apalachicola, 15 Oct. 1890, w/o collector 791a (GH, MO, US); HERNANDO CO.: vicinity of Brooksville, *Jones* 154 (US); HIGHLANDS CO.: Sebring, *Brass* 18146 (GH, US); HILLSBOROUGH CO.: Plant City, *Blanton* 6806 (CAS, TEX); LAKE CO.: vicinity of Eustis, *Nash* 1191 (GH, MICH, MO, UC, US); LEON CO.: 8 miles S of Tallahassee, *Turner* 4657 (TEX); LEE CO.: Fort Myers, *Buswell* 0881 (ARIZ); LIBERTY CO.: between Quincy & Bristol, *Mohr* 1818 (US); MADISON CO.: 9 miles E of Greenville, *Godfrey* 53992 (GH); MANATEE CO.: near Bradenton, *Simpson* 61 (F, MICH, US); MARION CO.: near Ocala, *Palmer* 35186 (GH); ORANGE CO.: S of Orlando, *Bright* 3953 (US); PASCO CO.: New Port Richey, *O'Neill* 1171 (MO); PINELLAS CO.: near St. Petersburg, *Deam* 2826 (MICH, US); POLK CO.: w/o locality, *Ohlinger* 394 (F, MO); PUTNAM CO.: Crescent City, w/o collector (MO); SEMINOLE CO.: Longwood, *Beardslee Jr.* s.n. (UC); VOLUSIA CO.: 2 miles N of Ormond, *Butts* s.n. (GH, UC).

Palafoxia integrifolia was treated as the only species of the genus *Othake* by Baltzer (1944), a treatment also accorded the species by Bush (1904) in his revision of *Othake*. While it is unquestionably the "oddball" of *Palafoxia*, it is, nonetheless, by its floral features and chromosomes, so closely related to *Palafoxia* that little is gained by placing the species in a genus of its own.

6. *Palafoxia linearis* (Cav.) Lag. Elench. Pl. Hort., Matr. 26. 1816. Gen. et Sp. Nov. 26. 1816. TYPE: possible fragments of isotype examined (F). "Ex antiquo herbario generali Herbarium Horti Botanici Matritensis." The plate accompanying the original description matches the material cited (see discussion below).



Fig. 12. *Palafoxia linearis* var. *linearis*. A. Top of plant, $\times \frac{1}{4}$.

6a. *Palafoxia linearis* (Cav.) Lag. var. *linearis*. Fig. 12.

Ageratum lineare Cav., Ic. 3:3. 1794. *Stevia linearis* Cav., Ic. 4:32. *Stevia linearis* (Cav.) Willd., Sp. Pl. 3: 1774. 1804. *Stevia lavandulaefolia* Willd. ex DC., Prodr. 5:125. 1836. As synonym.

Paleolaria carnea Cass., Bull. Soc. Philom. 1818:17. 1818.

Palafoxia leucophylla Gray, Proc. Am. Acad. 8:291. 1870. TYPE: MEXICO. Baja California: Carmen Island, Palmer 2 (Holotype, GH!; isotypes, NY!, US!). *Palafoxia linearis* var. *leucophylla* (Gray) I. M. Johnston, Proc. Calif. Acad. Sci. 12:1202. 1924.

Palafoxia arenaria Brandg., Proc. Calif. Acad. Sci. 2:178. 1889. TYPE: MEXICO. **Baja California:** Boca de Las Animas, *Brandeggee* s.n. (Holotype, UC!; isotypes, GH!, US!).

Plants perennial, 40-80 cm high, up to 150 cm across; stems suffruticose and branched from the base forming conspicuous clumps, rather evenly pubescent with stiff appressed white hairs, glandular, if at all, only in the inflorescence; leaves simple, succulent, alternate; mid-stem leaves lance-linear to nearly obovate, 25-50 mm long, 3-8 mm wide, with petioles 3-8 mm long, blades rather abruptly terminated by an obtuse or rounded apex (very rarely nearly acute), canescent-scabrous on both surfaces; inflorescence a subcorymbose cyme with 3-15(-20) heads; heads subturbinate to nearly cylindric, 5-10 mm across, 20-22 mm high (including the projecting flowers), 10-20 flowered, on ultimate peduncles 1.5-5.0 cm long; principal involucre bracts 8-14, linear, 10-15 mm long, 1-2 mm wide, scabrous-pubescent, especially below (rarely somewhat glandular); florets white with faint tinge of magenta-pink on lobes, regular (outer florets becoming zygomorphic); corolla 7-10 mm long, tube 2-3 mm long, throat cylindric (in outer florets somewhat flaring), 5-7 mm long, the lobes 1-2 mm long; style branches 4-5 mm long, otherwise as described for the genus; achenes 7-11 mm long, linear, 4-sided, densely appressed pubescent; pappus scales 4-8, unequal, with pronounced mid-ribs, the inner florets normally with 4 linear, acute scales, 6-9 mm long on the angles, these alternating with 4 shorter, obtuse or truncate scales of varying lengths (often nearly absent); chromosome number not determined.

Distribution: Dune sand along the eastern sea shore of southern Baja California; also in dunes along the shore of Sonora and Sinaloa. Flowering, Nov.-May, depending on rains. Fig. 13.

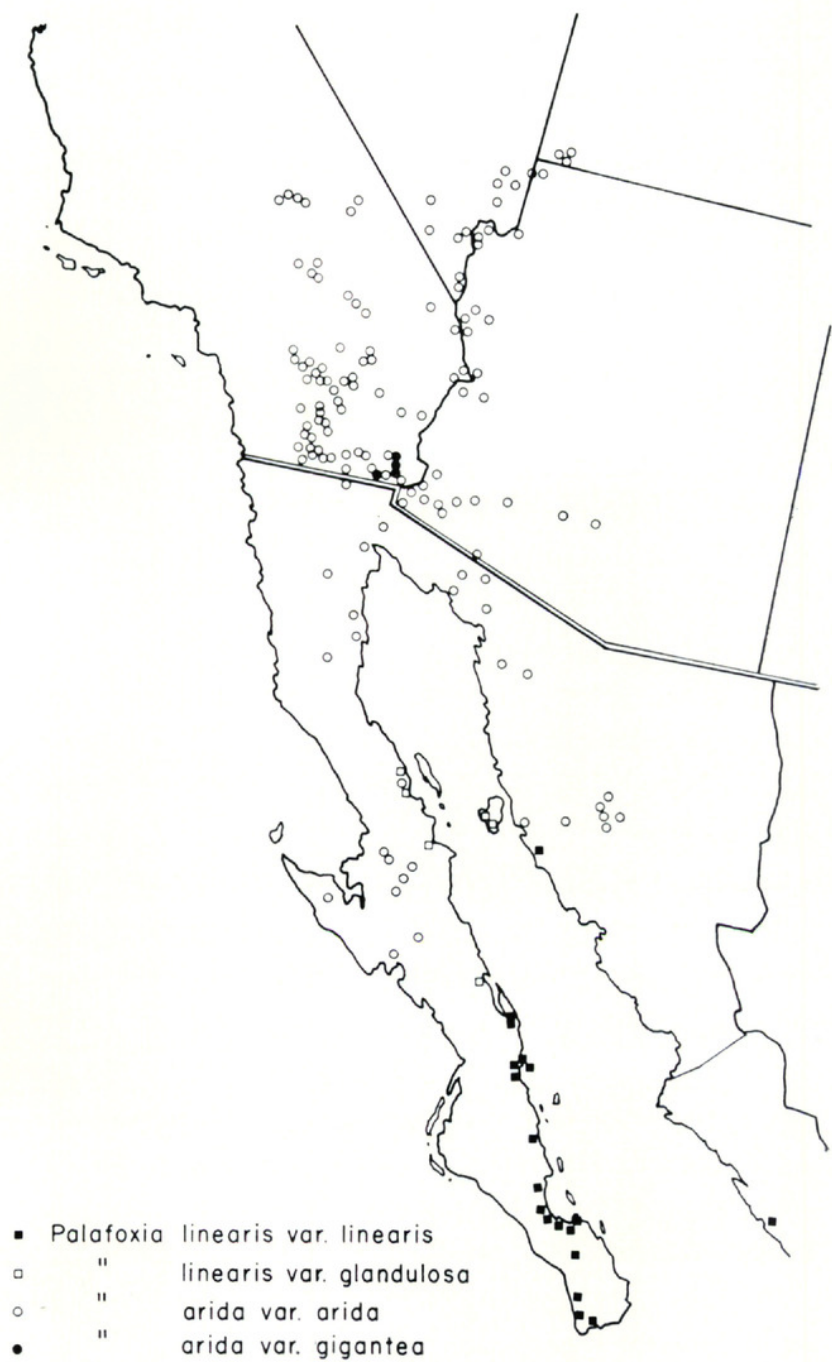


Fig. 13. Distribution of *Palafoxia linearis* var. *linearis*, *P. linearis* var. *glandulosa*, *P. arida* var. *arida*, and *P. arida* var. *gigantea*.

REPRESENTATIVE SPECIMENS. MEXICO. **Baja California:** 18 miles S of Todos Santos, *Carter & Chisaki* 3612 (DS, UC, US); El Mogote, *Carter* 2722 (DS, MO, UC, US); Monserrate Island, *Johnston* 3866 (DS, GH, UC, US); Loreto, *Johnston* 3776 (CAS, GH, MO, UC, US); La Paz, *Jones* 24065 (ARIZ, F, MICH, UC); 17 miles S of Rancho Venancio, *Shreve* 7190 (ARIZ, DS, F, MICH, US); between La Buca and La Ballena, *Wiggins* 5552 (CAS, DS, GH, MICH, UC, US). **Sinaloa:** Altata, *Gentry* 5406 (ARIZ, DS, GH, MICH, MO). **SONORA:** San Pedro Bay, *Johnston* 4322 (CAS).

Palafoxia linearis has long been used for the more northern, Sonoran desert taxon, *P. arida* (Turner & Morris, 1975).

Wiggins (5552, DS) describes the species as "perennial, leaves very fleshy, corolla white with faint tinge of magenta pink." *Palafoxia linearis* is undoubtedly related to the more widespread *P. arida*, presumably having arisen out of that species in the distant past as a strand-line element.

6b. *Palafoxia linearis* var. *glandulosa* B. L. Turner & M. I. Morris, *Madrono* 23(2):79-80. 1975.

TYPE: MEXICO. **Baja California:** mouth of arroyo along beach at Barril, 48 miles E of Pozo Aleman, *Wiggins* 7825 (Holotype, DS!; isotypes, F!, GH!, UC!, US!).

Similar to the var. *linearis* except that the stems and leaves are densely covered with a very rough glandular pubescence; in addition the alternating, abortive pappus scales are shorter (like those of *P. arida* var. *arida*).

Distribution: Coastal dune sands of eastern Baja California from latitude 26° 30' N to 29° 30' N. Flowering, Dec.-May. Fig. 13.

REPRESENTATIVE SPECIMENS. MEXICO. **Baja California:** Freshwater Bay, Tiburon Island, *Johnston* 3264 (CAS, GH, NY, UC, US, in part); Las Animas Bay, *Johnston* 3514 (CAS, GH, UC, US); San Francisquito Bay, *Johnston* 3588 (CAS, US); San Nicholas Bay, *Johnston* 3716 (MO); Los Angeles Bay, *Palmer* 581 (GH).

Wheeler annotated most of the material cited above as intermediate to *Palafoxia linearis* var. *linearis* and *P. arida* var. *arida* (as treated here). *Palafoxia linearis* var. *glandulosa* is closer in total characters to the former taxon and occupies a similar, but more northern habitat. Johnston apparently found both *P. linearis* var. *linearis* and *P. linearis* var. *glandulosa* growing mixed in two of the localities cited above (Johnston 3716; 3264). We could not detect any clear intergradation from specimens collected by Johnston at these localities, although it is suspected that there might be a clinal intergradation from north to south along the shore line.



Fig. 14. *Palafoxia arida* var. *arida*. A. Top of plant, $\times \frac{1}{4}$.

7. *Palafoxia arida* B. L. Turner & M. I. Morris, Madrono 23(2):79-80. 1975. TYPE: UNITED STATES. California: SAN BERNARDINO CO.: The Needles, Jones 3849 (Holotype, US!; isotypes, ARIZ!, CAS!, DS!, F!, NY!, UC!).

- 7a. *Palafoxia arida* B. L. Turner & M. I. Morris var. *arida*. Fig. 14.

Palafoxia linearis var. *linearis* of authors. *Non Palafoxia linearis* (Cav.) Lag.

Plants annual, 10-70 cm tall; stems erect and usually divaricately branched throughout, scabrous and/or with a rough pubescence (rarely nearly glabrous), the upper portions usually with conspicuous glandular trichomes; mid-stem leaves linear to lance-linear, 2-8 mm wide, 20-100 mm long, with petioles 5-20 mm long, blades gradually tapering into an acute apex, canescent-scabrous on both surfaces; inflorescence a subcorymbose cyme with 5-40 heads; heads subturbinate to nearly cylindric, 5-10 mm across, 20-28 mm high (including the projecting flowers), 9-20 flowered, on ultimate peduncles 1-5(-7) cm long; principal involucre bracts (6-)7-15, linear 10-20 mm long, 1-2 mm wide, scabrous to densely glandular, often somewhat keeled on the back; florets pinkish-white to pink, the inner ones regular, the corolla 9-11 mm long, the tube 2-4 mm long, the throat cylindric 6-8 mm long, the lobes 1-2 mm long; style branches 4-5 mm long; achenes 10-15 mm long, linear, 4-sided, densely to sparsely appressed pubescent; pappus scales 4-8 unequal, with pronounced mid-ribs, the innermost achenes normally with 4 linear, acute scales on the angles, 8-12 mm long, these alternating with 4, much shorter, abortive scales; outermost achenes with 3-8 separate scales of varying lengths (often completely absent); chromosome number, $n = 12$.

Distribution: Mojave, Colorado and Sonoran deserts of the southwestern United States and Mexico, usually in sandy soils at low elevations. Flowering, Feb.-May (rarely later with rains). Fig. 13.

REPRESENTATIVE SPECIMENS. UNITED STATES. **Arizona:** MARICOPA CO.: Sentinel, *Harrison & Belden* 3556 (ARIZ); MOHAVE CO.: Willow Beach, *Clokey* 5957 (DS, MO, TEX, UC); PINAL CO.: 10 miles W of Casa Grande, *Parker* 8259 (ARIZ); YUMA CO.: 14 miles E of Yuma, *Wolf* 2286 (CAS, DS, GH). **California:** IMPERIAL CO.: near Fish Springs, *Nelson & Nelson* 3293 (DS, GH, MO, UC, US); RIVERSIDE CO.: ca. 12 miles E of Indio, *Hitchcock* 5848 (DS, GH, MO, UC); SAN BERNARDINO CO.: Slate Mountains, *Epling, Ellison & Anderson* s.n. (MICH, MO, US); 5 miles SW of Trona, *Gould* 986 (ARIZ, GH, MO); SAN DIEGO CO.: Coyote Canyon, *Hall* 2768 (DS, MO, UC, US). **Nevada:** CLARK CO.: Logan, *Kennedy* s.n. (CAS, DS, GH, UC, US). **Utah:** WASHINGTON CO.: Red Hill N of St. George, *Hall* 514 (US); Leeds, *Cottam* 5389 (TEX).

MEXICO. Baja California: Calamilli, *Brandegge* s.n. (UC); 15.5 km NW of El Arco, *Carter et al.* 1907 (DS, UC, US); 59 km SW of San Ignacio, *Carter et al.* 2514 (DS, MO, UC, US); sand hills of the Viscaino Depression, south and west of Scammon's Lagoon, *Gentry* 7524 (ARIZ, DS, UC); 32 miles S of Pozo Aleman, *Shreve* 7008 (ARIZ, F, GH, MICH, MO); southern part of the Sierra San Pedro Martir, *Wiggins* 9915 (DS, US); 27.4 miles S of Pozo Aleman, *Wiggins* 7863 (DS, F, GH, MICH, UC, US). **Sonora:** Rocky Point, *Clark* 11213 (GH); along Rio de Sonora, Hermosillo, *Drouet & Richards* 3480 (F); 6 km N of Hermosillo, *Drouet & Richards* 3758 (F); E of Villa de Seris along Rio de Sonora, *Drouet, Richards & Alvarado* 3395 (F); Hermosillo, *Eisen* s.n. (US); 173 miles S of Nogales, *Frye & Frye* 2288 (ARIZ, DS, GH, UC); S side of Punta Penasco, *Hammerly* 16 (DS, TEX, UC); 2 miles W of Cabarco, *Keck* 4021 (CAS); 22 miles S of Sonoyta, *Keck* 4161 (DS, US); Cabarco, *Long* 74 (US); Papago Tanks, *MacDougal* 35 (US); Hermosillo, *Maltby* 208 (US); Colorado River at Colonia Diaz, *Mearns* 2831 (DS, US); Lerdo, *Palmer* 940 (GH, UC); 20 miles N of Hermosillo *Parker* 8224 (ARIZ, UC); 4 miles NW of Caborca, *Wiggins* 8231 (DS, GH, MICH, UC, US); 2 miles N of the fishing village on Kino Bay, *Wiggins & Rollins* 167 (ARIZ, DS, GH, MICH, MO).

This relatively common, widespread species has heretofore been called *Palafoxia linearis* by nearly all recent taxonomists working in the desert Southwest. This name, however, applies to a well-marked, related taxon which occurs in southern Baja California, the type apparently having been collected near La Paz. Wheeler, by annotation only, also recognized the two taxa as specifically distinct, correctly restricting the name, *P. linearis*, to the populations from southern-most Baja California. Gray also recog-

nized the taxa as specifically distinct, but contrary to the present Code, proposed the name *P. leucophylla* for the more southern element. Johnston, apparently accepting Gray's nomenclature but not his hierarchial ranking, reduced Gray's synonym to varietal status.

In our opinion, *Palafoxia arida* and *P. linearis* are relatively "clean" species in that they are readily distinguished morphologically, have different, essentially allopatric distributions, and grow under different climatic regimes. At least the two taxa are more distantly related than are certain other allopatric taxa regarded as species by previous workers, as well as by us (e.g., the three closely related species, *P. hookeriana*, *P. sphacelata* and *P. reverchonii*).

7b. *Palafoxia arida* var. *gigantea* (M. E. Jones) B. L. Turner & M. I. Morris, *Madrono* 23(2):79-80. 1975.

Palafoxia linearis var. *gigantea* M. E. Jones, *Contrib. West. Bot.* 18:79. 1933. TYPE: UNITED STATES. **California:** W of Yuma, sand dunes, *Jones* 28599 (Holotype, POM!; isotypes, MO!, UC!).

Palafoxia linearis var. *arenicola* Nels., *Am. Jour. Bot.* 23:265-66. 1936. TYPE: UNITED STATES. **California:** in the sand dunes, Calif., W of Yuma, Arizona, *Nelson* 11161 (Holotype, RM!; isotypes, DS!, MO!).

Plants apparently annual or short lived perennials (described by some collectors as a succulent perennial), 80-200 cm tall; stems erect, branched from the base, the larger branches 0.5-1.0 cm in diameter, glabrous or nearly so; leaves simple, alternate, mid-stem ones lance-linear, 6-12 cm long, 0.7-1.5 cm wide, with petioles 1.0-1.5 cm long, the blades tapering into an acute apex, scabrous on both surfaces; inflorescence a subcorymbose cyme with 10-20 heads; heads subturbinate, 10-20 mm across, 28-35 mm high (including the projecting flowers), 18-40 flowered, on ultimate peduncles 2-7 cm long; principal involucre bracts 10-16, linear, 16-25 mm long, 1.0-2.5 mm wide, scabrous, often somewhat keeled on the back; florets "lavender-white," regular, the corolla 10-13 mm long, the tube 3.0-4.5 mm

long, the throat cylindric, 7-9 mm long, the lobes 1-2 mm long; style branches 4-6 mm long, otherwise as described for the genus; achenes 12-16 mm long, linear, somewhat 4-sided to nearly cylindric, densely short pubescent with closely ascending hairs; pappus scales 4-8, unequal, with pronounced midribs, the innermost achenes normally with 4 linear, acute scales 9-12 mm long, these alternating with 4 much shorter scales, 2-5 mm long; outermost achenes with 3-8 scales of varying lengths; chromosome number, $n = 12$.

Distribution: Restricted to the actively blowing sand hills just west of Yuma, Arizona. Flowering, Feb.-May (often later with rains). Fig. 13.

REPRESENTATIVE SPECIMENS. UNITED STATES. California: IMPERIAL CO.: 6 miles W of Winterhaven, *Alexander & Kellogg* 1889 (DS, GH, TEX, UC); sand dunes W of Yuma, *Alexander & Kellogg* 1936 (ARIZ, CAS, DS, GH, MO, TEX, UC); 25 miles W of Yuma, *Munz* 11968 (UC); Holtville, *Munz & Hitchcock* 12131 (DS, F, MO, UC); 16 miles E of Brawly, *Turner* 4759 (TEX); 22 miles W of Yuma, *Wiggins* 8920 (CAS, DS); 2 miles E of Gray's Well on road from Yuma to Holtville, *Wolf* 1888 (DS).

The variety *gigantea* is undoubtedly closely related to *Palafoxia arida* var. *arida* presumably having arisen relatively recently from that taxon (within the time of the formation of the large northwest-southeast trending dune sands in the southern portion of the Coachella Valley, probably about 5000 years ago or less). It is distinguished almost solely by its more robust habit and larger heads. After a visit by the senior author to the type locality, he was reasonably convinced that the variety was a good taxon, primarily because the smaller-headed var. *arida* grows adjacent to, and often upon, some of the lesser dunes in the area, while the larger-headed forms were restricted almost entirely to the dune sands. This is true even in depauperate (less than 0.9 m tall) forms of var. *gigantea*. Blake (1945) also recognized the variety as did Nelson (1936), who presumably was unaware of Jones' (1933) earlier varietal epithet.



Fig. 15. *Palafoxia riograndensis*. A. Whole plant, $\times \frac{1}{3}$. B. Head. $\times 2$.

8. *Palafoxia riograndensis* Cory, Rhodora 48:84. 1946. Fig. 15. TYPE: UNITED STATES. Texas: PRESIDIO CO.: 3½ miles SE of Presidio, Cory 31195 (Holotype, GH!; isotype, US!).

Palafoxia cyanophylla Shinnery, Field & Lab. 17:23-30. 1949. TYPE: UNITED STATES. Texas: BREWSTER CO.: in bare sand, mouth of Santa Elena Canyon, Big Bend National Park, Shinnery 8792 (Holotype, SMU!).

Plants annual, 30-60 cm tall; stems erect, usually branched from the base, pubescent with stiff white hairs and generally scabrous; leaves simple, alternate, the mid-stem ones linear-lanceolate, 3-7 cm long, 2-8 mm wide, with petioles 5-15 mm long, the blades gradually tapering into an acute apex, white scabrous pubescent on both surfaces; inflorescence a subcorymbose cyme with 5-numerous heads; heads cylindrical-turbinate, 15-25 mm high (including the exerted florets), 4-10 mm wide, 8-25 flowered, on ultimate glandular-pubescent (viscous) peduncles 1.5-6.0 cm long; principal involucre bracts 7-10, narrowly lance-oblong, 10-15 mm long, 1.2-2.0 mm wide, scabrous or hispid on the back; florets "pale pinkish purple" to "purple," outer florets distinctly zygomorphic (but not ligulate), the inner florets nearly regular; corolla 6-9 mm long, tube cylindric, 2.3-4.0 mm long, throat conspicuously pubescent, narrowly funnel-form, 1.5-3.0 mm long, the lobes lanceolate-oblong, 1.8-3.0 mm long; style branches 3-4 mm long, otherwise as described for the genus; achenes linear, 4-sided, obpyramidal, 7-12 mm long, variously hispid, but especially so on the angles; pappus of inner florets composed of 4 lanceolate scales, 5-8 mm long (these often alternating with much smaller, obtuse scales), outer-most florets with abortive pappus scales, these usually fused into an irregular crown; chromosome number, $n = 12$.

Distribution: Dune sand and silty-sandy soils along stream beds of the Chihuahuan desert in north-central Mexico, entering the United States only along the Rio Grande River in Texas. Flowering, Apr.-Nov., depending on rains, but usually in the late summer and fall. Fig. 16.

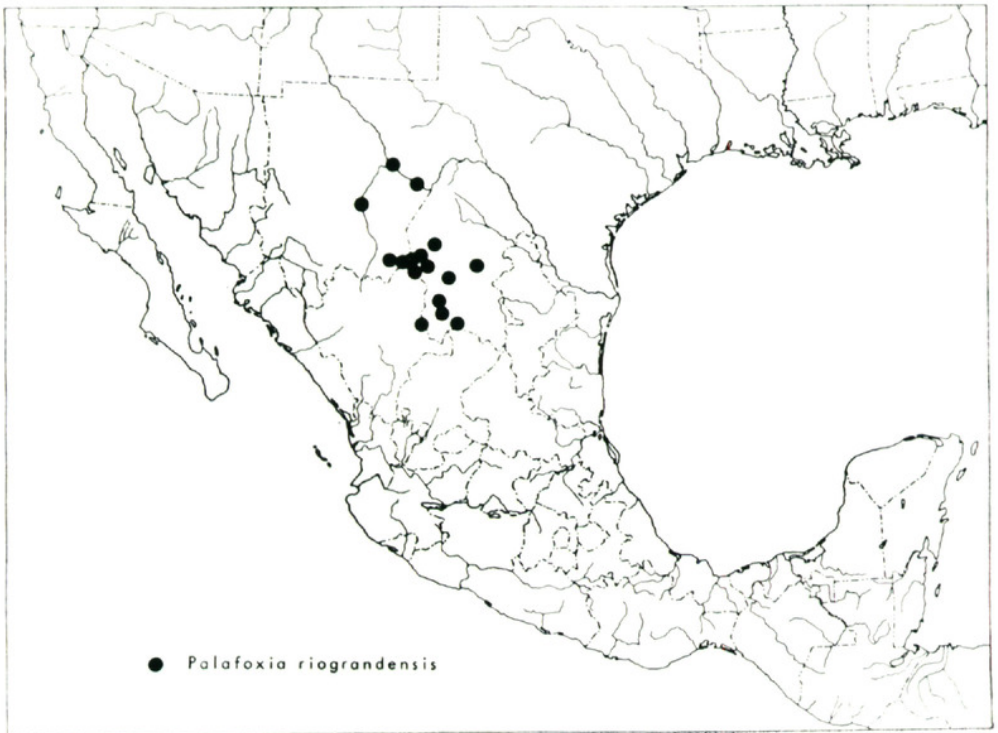


Fig. 16. Distribution of *Palafoxia riograndensis*.

REPRESENTATIVE SPECIMENS. UNITED STATES. **Texas:** BREWSTER CO.: entrance to Santa Elena Canyon, *Warnock* 1160 (GH); near entrance to Santa Elena Canyon, *Sperry* 1160 (US); mouth of Santa Elena Canyon, *McVaugh* 12708 (MICH); PRESIDIO CO.: 2-3 miles E of Presidio, *Hinckley* 3235 (GH, US); 3½ miles SE of Presidio, *Cory* 31195 (US).

MEXICO. Chihuahua: 5 miles NE of Laguna Palomas, *Johnston* 7826 (GH); 6 miles NE of Carillo, *Shreve* 8848 (ARIZ, MICH, US). **Coahuila:** 3 miles SW of Torreon on Nazas River, *Fisher* 44125 (GH, MO, NY); Tanque Colorado, road from Zacatosa, SE to Puerto Colorado, *Johnston* 8666 (GH, TEX); Torreon and vicinity, *Palmer* 486 (F, GH, MO, UC, US); Monclova, *Palmer* 643 (F, GH, NY, US); Movano, *Purpus* 4473 (UC); SW end of Laguna del Rey, *Stewart* 3022 (GH); 5 km NE of Las Delicias, *Stewart* 2840 (GH); 1 km SE Las Margaritas, *Stewart* 2946 (GH); 21 miles W of El Oro, *White* 2011 (MICH).

As indicated by Shinnars (1952), *Palafoxia cyanophylla* is clearly synonymous with the earlier *P. riograndensis*, although he failed to find that Baltzer (1944) cited a specimen of this taxon (*Palmer* 486, MO) as belonging to *P. linearis* var. *leucophylla*. While *P. riograndensis* is super-

ficially similar to *P. linearis* (as indicated by Shinnars), it is clearly distinct. It has the habit of *P. arida*, but possesses quite different floral features (corolla lobes longer than the throat and irregular florets along the periphery of the head).

Palafoxia riograndensis is apparently introduced periodically into Texas along the Rio Grande where it occurs in small populations on sand banks along the river. It presumably washes into the Rio Grande from streams feeding from the more southern sandy areas of the Chihuahuan desert.

9. *Palafoxia lindenii* Gray, Pl. Wright. 1:120. 1850. Fig. 17. TYPE: MEXICO. Veracruz: on sandhills near the sea, Galeotti 2627 (Holotype, K!; fragment of holotype, GH!).

Polypteris lindenii (Gray) Gray, Proc. Am. Acad. 19:30. 1883. *Othake lindenii* (Gray) Bush, Trans. Acad. Sci. St. Louis 14:173. 1904.

Plants annual, 50-100 cm tall or sometimes appearing perennial and rhizomatous when rooting at the nodes in blown dune sand; stems suffruticose, sparsely branched, suberect to erect, strigillose throughout; leaves entire, simple and opposite at first, becoming alternate above, the mid-stem ones oblong-lanceolate to narrowly elliptic, 4-6 cm long, 5-8 mm wide, thick, puberulent on both surfaces, acute to rounded at the apex, petioles 7-10 mm long; inflorescence corymbose with 3-10 heads; heads turbinate, 1-1.5 cm wide, 1.5-2 cm high (including the extended florets), 18-30 flowered, on ultimate thickened, densely glandular-pubescent peduncles 1.5-6 cm long; involucre bracts 10-15, linear, 8-10 mm long, 1.0-2.5 mm wide, thickened on the back, somewhat scarious along the margins; florets apparently whitish, regular; corolla about 10 mm long, tube glandular-pubescent almost 3 mm long, throat cylindric, 1.5-2.0 mm long, lobes linear, 4-5 mm long; anthers 4 mm long; style branches 3-4 mm long, otherwise as described for the genus; achenes obpyramidal, 5-6 (-7)



Fig. 17. *Palafoxia lindenii*. A. Top of plant, $\times \frac{1}{4}$. B. Floret, $\times 3$.

mm long, glabrous or nearly so; pappus of 12 lanceolate scales, 4-5 mm long, acute at the apex, without an extended awn or mucro; chromosome number, $n = 11$.

Distribution: Known from only a few collections about Veracruz, Mexico, where it is apparently confined to dune sands. Flowering, Aug.-Jan., and probably later. Fig. 18.

REPRESENTATIVE SPECIMENS. MEXICO. Veracruz: at Veracruz, Fisher 122 (CAS, DS, MICH, TEX); Nautla, "vegetacion litoral," Gold 121 (NY); near shore, N of Veracruz, Greenman 95 (F, GH, NY); Veracruz, Medanos de Perro, Juzepczuk 1147 (US); Gulf Coast, Purpus 6025 (F, GH, MO, NY, UC, US); shore of Gulf of Mexico near San Carlos, Purpus 14168 (F, GH, UC).

The species is undoubtedly related to *Palafoxia texana*, presumably derived out of that species relatively recently through an insular-type adaptation to the dune sands in and about Veracruz, Mexico. Both species are diploid with $n = 11$ and both possess similar head and floral features.

10. *Palafoxia callosa* (Nutt.) T. & G., Fl. N. Am. 2:369. 1842. Fig. 19.

Stevia callosa Nutt., Jour. Acad. Phila. 2:121. 1821. TYPE: UNITED STATES: on the gravelly banks of the Arkansas, rare, Nuttall s.n., (Probable holotype, PH!). *Florestina callosa* (Nutt.) DC., Prodr. 5:655. 1836. *Othake tenuifolium* Raf., New Fl. 4:74. 1838. *Polypteris callosa* (Nutt.) Gray, Proc. Am. Acad. 19:30. 1883. *Othake callosum* (Nutt.) Bush, Trans. Acad. Sci. St. Louis 14:174. 1904.

Palafoxia bella Cory, Field & Lab. 16:62. 1948. TYPE: UNITED STATES. Texas: TOM GREEN CO.: 3 miles S of Christoval, Cory 50467. (Holotype, SMU!). *Palafoxia callosa* var. *bella* (Cory) Shinnars, Field & Lab. 20:94. 1952.

Plants annual, 20-60 cm tall; stems brittle, slender, or less often, stout and diffusely branched; leaves sessile or shortly petioled, linear, 1-4 mm wide, 20-70 mm long, 1-nerved, strigose-hispidulous on both surfaces; inflorescence corymbose with several to numerous heads, the branches

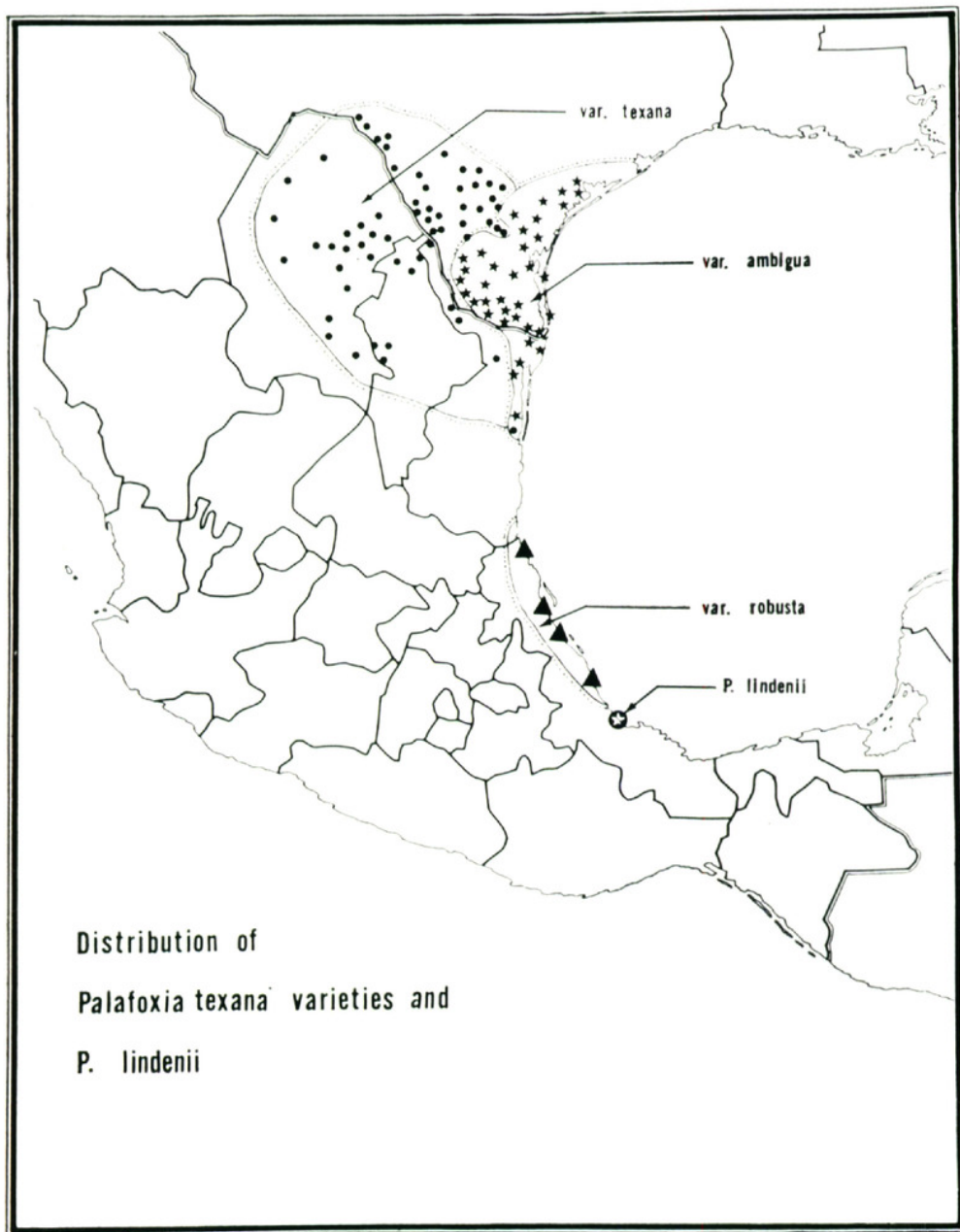


Fig. 18. Distribution of *Palafoxia lindenii*, *P. texana* var. *texana*, *P. texana* var. *ambigua*, and *P. texana* var. *robusta*.

densely black-granular; heads turbinate, 3-6 mm high, 3-5 mm broad, 5-30 flowered, on ultimate peduncles 1-4 cm long; involucral bracts 10-12, linear-oblongate, strigose, 3-5 mm long, ca. 1 mm wide; florets lavender, pale-violet (pink) to white, regular, 5-6 mm long, tube 1-2 mm long, the lobes linear, 4-5 mm long; achenes mostly 3-5 mm long, obpyramidal, hirsutulous; pappus scales 8, obovate, 0.3-1.0 mm long; chromosome number, $n = 10$.

Distribution: Calcareous, usually rocky limestone soils from southern Missouri to northeastern Mexico, mostly in juniper glades or in disturbed grasslands. Flowering, Jun.-Nov. Fig. 10.

REPRESENTATIVE SPECIMENS. UNITED STATES. **Arkansas:** BAXTER CO.: Henderson, *Demaree* 28526 (TEX); BENTON CO.: w/o locality, *Bush* 15752 (MO); CARROLL CO.: Beaver, *Palmer* 4492 (MO, US); IZARD CO.: Guion, *Demaree* 23758 (MO, UC); MARION CO.: Bull Shoals Dam Reservoir, *Demaree* 29971 (TEX); RANDOLPH CO.: Noland, *Demaree* 53-790 (TEX); SEARCY CO.: Gilbert, *Emig* 43 (MO). **Missouri:** BARRY CO.: Eagle Rock, *Mackenzie* s.n. (MICH, MO); DOUGLAS CO.: Richville, *Steyermark* 14657 (MO); GREENE CO.: w/o locality, *Bush* 203 (F, GH, MO, UC, US); McDONALD CO.: Butler Creek, Noel, *Palmer* 4078 (MO, US); OZARK CO.: Tecumseh, *Palmer* 33012 (MO); STONE CO.: Gelena, *Palmer* 4633 (MO, US); TANEY CO.: Swan, *Bush* 476 (GH, MO, UC, US). **Oklahoma:** ADAIR CO.: Westville, *Moore* s.n. (TEX); BECKHAM CO.: 6 miles S of Elk City, *Eskeu* 1502 (GH, MO). **Texas:** BANDERA CO.: 4 miles S Pipecreek, *Turner* 3840 (TEX); BASTROP CO.: w/o locality, *Duval* s.n. (TEX); BLANCO CO.: gravel bars of river, *Palmer* 12856 (GH, MO, UC, US); BRAZOS CO.: w/o locality, *Palmer* 10732 (DS); BROWN CO.: near Brownwood, *Palmer* 26816 (GH); BURNET CO.: near Buchanan Dam, *Gentry* 15 (TEX); CHEROKEE CO.: dry hills N of Jacksonville, *Eggert* s.n. (MO); COLEMAN CO.: 1 mile SE of Goldsboro, *Turner* 4860 (TEX); COMAL CO.: New Braunfels, *Lindheimer* 956 (ARIZ, F, GH, MO, TEX, UC, US); CORYELL CO.: near highway along Camp Hood, *Gould* 5371 (TEX); DALLAS CO.: limestone prairies, *Reverchon* 3288 (GH, MO, US); EASTLAND CO.: Ranger, *Robinson* s.n. (TEX); FANNIN CO.: 2 miles SE of White-wright, *Turner & Tharp* 3131 (TEX); FAYETTE CO.: 4 miles E of La Grange, *Turner* 4452 (TEX); FREESTONE CO.: 12.5 miles ESE of Fairfield, *Shinners* 9633 (TEX); GILLESPIE CO.: Willow Cr., *Jermey* 804 (MO, US); GRAYSON CO.: Denison, *Letterman* s.n. (MO, US); HAYS CO.: near Wimberley, *Warnock* W900 (GH, TEX); HOOD CO.: Comanche Peak near Grabury, *Palmer* 6443 (MO, US); KENDALL CO.:



Fig. 19. *Palafoxia callosa*. A. Whole plant, $\times \frac{1}{4}$. B. Head, $\times 3$.

Spanish Pass, *Clemens & Clemens* 1029 (DS, MO); KERR CO.: Turtle Creek, 13.75 miles W of Kerrville, *Cory* 52417 (DS, UC, US); LAMPASAS CO.: 2 miles S of Lampasas, *Turner* 4587 (TEX); LLANO CO.: 17.6 miles E of Llano, *Turner & Johnston* 2484 (TEX); MCLENNAN CO.: Waco, *Bodin* s.n. (F, UC); PALO PINTO CO.: 9 miles W of Mineral Wells, *Whitehouse* 19242 (MICH, UC, US); PARKER CO.: Weatherford, *Tracy* 8142 (F, GH, MO, TEX, US). PECOS CO.: between Sheffield & Pecos River, *Ferris & Duncan* 2915 (CAS, DS, MO); REAL CO.: along Pulliam Creek near Camp Wood, *Correll* 15203 (US); SCHLEICHER CO.: 9.5 miles N of Eldorado, *Cory* 52513 (DS, UC, US); SOMERVELL CO.: Paluxy Creek, 2 miles above Glen Rose, *Ward* s.n. (US); STERLING CO.: 11 miles NW of Sterling City, *Cory* 50465 (DS, GH, TEX, UC, US); SUTTON CO.: Schoolhouse Hill, Sonora, *Cory* 40835 (TEX); TARRANT CO.: w/o locality, *Ruth* 738 (DS, US); TAYLOR CO.: Abilene State Park, *Tolstead* 7610 (MICH, MO, UC); TOM GREENE CO.: South Concho River, 1.5 miles N of Christoval, *Cory* 52517 (DS, US); TRAVIS CO.: 3 miles NW of Austin, *Warnock* 45-67 (DS, MO, TEX, UC); UVALDE CO.: 2 miles S of Blewett, *Turner* 3866 (TEX); VAL VERDE CO.: 9¼ miles N of Del Rio, *Cory* 20867 (GH); WILLIAMSON CO.: 7 miles W of Round Rock, *York* 46314 (F, MO, TEX, UC).

MEXICO. Coahuila: Muzquiz, Santa Anna Canyon, *Marsh* 540 (TEX); 65 miles NW Sabinas, *Gould* 10676 (TEX); 17 miles W of Ciudad Acuna, *Powell et al.* 1411 (TEX); 43 miles NW of Muzquiz, *Powell et al.* 1587 (TEX).

Palafoxia callosa is easily recognized by its linear leaves and narrow turbinate involucre. Some of the larger-headed (i.e., with more numerous florets), paler-flowered, more western populations were recognized as a species, *P. bella*, by Cory but these seem hardly worthy of the varietal recognition accorded the populations by Shinnars.

Palafoxia callosa seems closest to *P. rosea*. Both species are diploid with $n = 10$ and while they are partially sympatric in a geographic sense, the former occurs predominantly, or only, on calcareous soils, the latter on siliceous, sandy soils. Synthetic hybrids between the species are easily made, but hybrids or their derivatives have not been observed in the field.

11. *Palafoxia rosea* (Bush) Cory, *Rhodora* 48:86. 1946. TYPE: UNITED STATES. Texas: HARRIS CO.: Sheldon, 18 miles E of Houston, *Reverchon* 3656 (Holotype, MO!; isotypes, GH!, NY!).

11a. *Palafoxia rosea* (Bush) Cory var. *rosea*. Fig. 20.

Othake roseum Bush, Trans. Acad. Sci. St. Louis 14:175. 1904. *Polypteris rosea* (Bush) Small, Fl. S. E. U. S., ed. 2, 1372. 1913.

Annual herbs, 10-50 cm tall; stems brittle, scabrous; leaves simple, opposite at first but soon becoming alternate, the mid-stem ones linear-lanceolate, 2-10 mm wide, 3-6 cm long, petioles 3-15 mm long, blades inconspicuously 3-nerved, scabrous on both surfaces; inflorescence corymbose with mostly 3-10 heads; heads narrowly to broadly turbinate, 6-12 mm across, 10-16 mm high (including disc florets), 10-30 flowered, on ultimate peduncles 1-5 cm long; principal involucre bracts 8-12, oblanceolate, 5-7 mm long, 1.2-3.0 mm wide, often purplish tinged, pubescent with short rough hairs interspersed with glandular capitate trichomes (the latter sometimes absent or nearly so); florets pale-violet, regular 7-10 mm long, the throat 4-5 mm long slit to the base or nearly so, the lobes linear, 4-5 mm long; achenes mostly 5-8 mm long, densely short, appressed pubescent; pappus scales usually 8, 1-3 mm long, scarious except for the prominent midrib, obtuse to acute at the apex; chromosome number, $n = 10$.

Distribution: Sandy soils in eastern Texas. Flowering, May-Nov. Fig. 21.

REPRESENTATIVE SPECIMENS. UNITED STATES. Oklahoma: CADDOK CO.: 4 miles W of Anadarko, *Hopkins & Nelson* 881 (DS, TEX, UC); COMANCHE CO.: State Fish Hatchery, *Robertson* 106 (TEX); SWANSON CO.: near Mountain Park, *Stevens* 1278 (DS, US). Texas: AUSTIN CO.: Industry, *Wurzlöw* 35 (US); BRAZORIA CO.: Substation no. 3, Angleton, *Cory* 51081 (DS, GH, UC, US); BRAZOS CO.: 2 miles S of College Station, *Ammerman* 7 (MO, UC); BURLESON CO.: Lyons, *Maite* 6536 (TEX); COLORADO CO.: Eagle Lake, *Biology Class* 41 (TEX); DALLAS CO.: N of Dallas, *Eggert* s.n. (MO); FAYETTE CO.: Muldoon, *Ripple* 51-743 (TEX); FREESTONE CO.: 11.5 miles ESE Fairfield, *Turner* 4447 (TEX); GALVESTON CO.: Moses Lake, 3 miles NW of Texas City, *Turner* 3070 (TEX); HARRIS CO.: 5 miles SE of Genoa, *Cory* 50695 (DS, GH, UC, US); LEE CO.: 1½ miles SW of Giddings, *Cory* 55758 (US); MONTGOMERY CO.: pine woods, *Dixon* 478 (F); SAN JACINTO CO.: Evergreen, *Joor* s.n. (MO); SAN JACINTO CO.: S of Mathis, *Rose*



Fig. 20. *Palafoxia rosea* var. *rosea*, A & B. *P. rosea* var. *macrolepis*, C. A. Top of plant, $\times \frac{1}{4}$. B. Achene and pappus, $\times 3$. C. Achene and pappus, $\times 3$.

& Russell 24159 (GH); SAN SABA CO.: Cherokee, Joor s.n. (MO); TRAVIS CO.: Austin, *Tharp* 189 (GH, TEX); VICTORIA CO.: 10 miles SW of Victoria, *McVaugh* 12412 (MICH, US); WALKER CO.: SW of Huntsville, *Cory* 50669 (GH); WILBARGER CO.: *Ball* 1230 (F).

This variety is mostly confined to forest areas of eastern Texas and is best distinguished by its smaller heads, with smaller florets and pappus. In central Texas it appears to intergrade with the western populations, which are designated below as var. *macrolepis*. In Llano Co., for example, short and long pappus forms are found in the same population (*Turner & Johnston* 2512, TEX) although the plants possess the larger heads of var. *macrolepis*.

11b. *Palafoxia rosea* var. *macrolepis* (Rydb.) B. L. Turner & M. I. Morris, comb. nov. Fig. 20.

Othake macrolepis Rydb., Bull. Torr. Bot. Club 37:332. 1910. TYPE: UNITED STATES. **Colorado:** BENT CO.: Rule Creek, *Osterhout* 4097 (Holotype, NY!). *Polypteris macrolepis* (Rydb.) Cory, Rhodora 38:408. 1936. *Othake texanum* var. *macrolepis* (Rydb.) Baltzer. Ann. Mo. Bot. Gard. 31:258. 1944. *Palafoxia texana* var. *macrolepis* (Rydb.) Shinnery, Field & Lab. 20:97. 1952.

Palafoxia rosea var. *papposa* Shinnery, Field & Lab. 20:95. 1952. TYPE: UNITED STATES. **Texas:** BEXAR CO.: San Antonio, Apicultural Laboratory, *Parks* s.n. (Holotype, TAM!; isotypes, SMU!).

Similar to var. *rosea*, but possessing larger heads and longer pappus.

Distribution: Sandy soils in plains country of south Texas NW to Wyoming. Flowering, May-Sept. Fig. 21.

REPRESENTATIVE SPECIMENS. UNITED STATES: **Colorado:** LAS ANIMAS CO.: 3 miles SW of Tobe, *Rogers* 6128 (TEX). **Kansas:** SUMNER CO.: Caldwell, *Carleton* 340 (US). **New Mexico:** LEA CO.: 21 miles W of Hobbs, *Waterfall* 7837 (GH); QUAY CO.: Tucumcari Field Station, *Burnham* s.n. (US); ROOSEVELT CO.: 2 miles S of Portales, *Turner* 4720 (TEX). **Oklahoma:** CADDO CO.: 4 miles W of Anadarko, Hopkins, *Nelson & Nelson* 881 (MO); MC CLAIN CO.: Johnson's pasture, *Barkley* 1499 (MO). **Wyoming:** CONVERSE CO.: T. 38

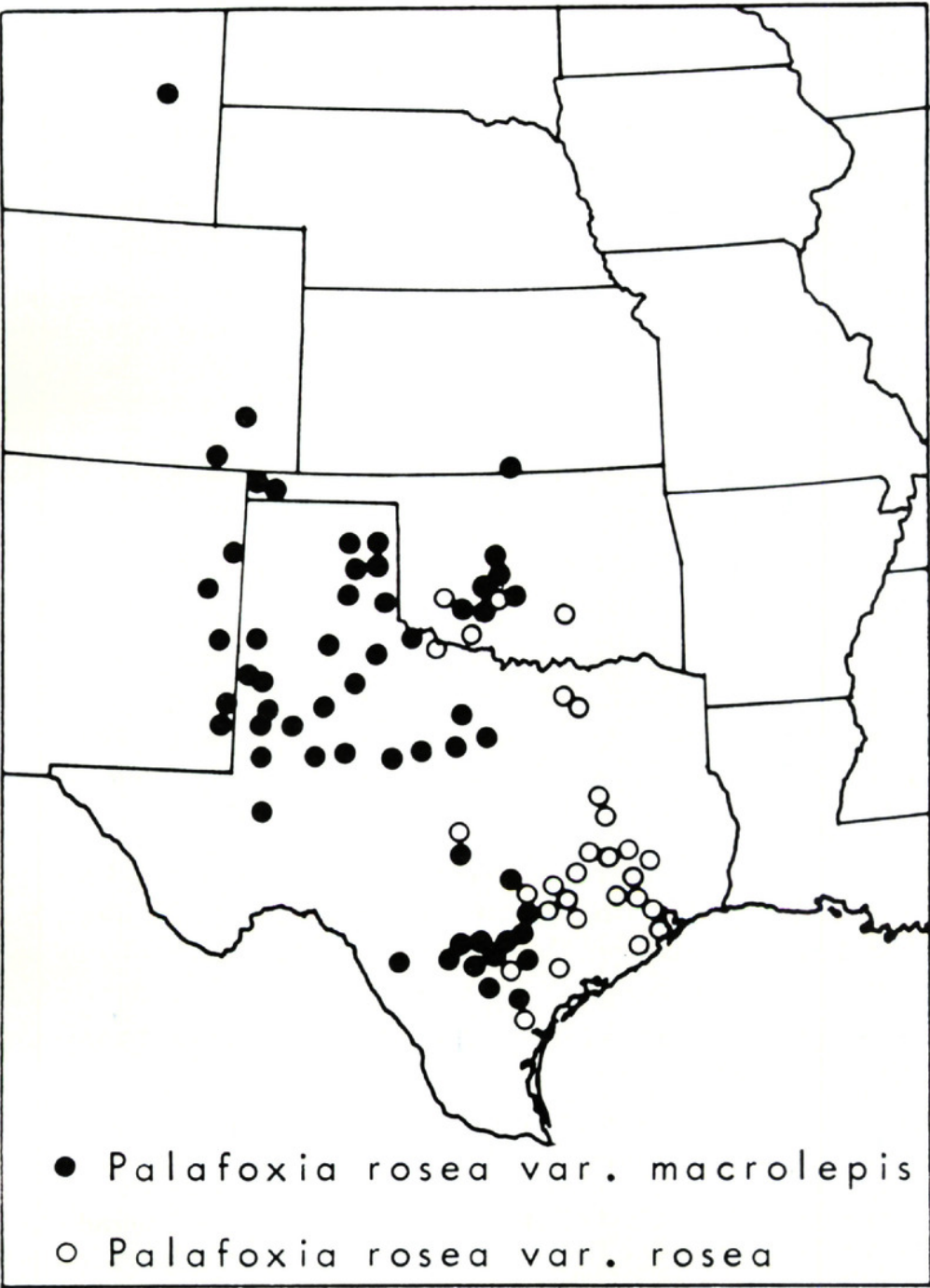


Fig. 21. Distribution of *Palafoxia rosea* var. *rosea* and *P. rosea* var. *macrolepis*.

N., R. 67 W., *Ownbey* 1051 (GH, MO, NY, UC). Texas: ANDREWS CO.: 1 mile S of Andrews, *Gentry* 1919 (ARIZ); ATASCOSA CO.: Pleasanton, *Palmer* 9757 (DS, US); BEE CO.: Papalote, *Albers* 46338 (TEX); BEXAR CO.: S of San Antonio, *Ammerman* 97 (MO, UC); CALLAHAN CO.: Clyde, *Palmer* 13818 (US); COCHRAN CO.: Whiteface, *Turner* 4718 (TEX); CRANE CO.: 4 miles S of Crane, *Tharp* s.n. (GH, TEX); DAWSON CO.: 8 miles N of Lamesa, *Rose-Innes & Moon* 1062 (TEX); DEWITT CO.: western part of county, *Riedel* s.n. (TEX); DICKENS CO.: Spur, *Reed* 3240 (US); DONLEY CO.: 10 miles NW of Clarendon, *Rose-Innes & Moon* 1022 (TEX); EASTLAND CO.: Ranger, *Hodge Oak School* s.n. (UC); ECTOR CO.: 8 miles S of Odessa, *Tharp* s.n. (TEX, US); FLOYD CO.: escarpment of Staked Plains, *Ferris & Duncan* 3375 (CAS, DS, MO); GARZA CO.: 10 miles from Post City, *Ruth* 1246 (MICH); GONZALES CO.: *Whitehouse* s.n. (MICH, TEX); HARDEMAN CO.: Chillicothe, *Ball* 979 (US); HOWARD CO.: Big Springs, *Tracy* 7882 (F, GH, TEX, US); KARNES CO.: Karnes City, *Johnson* 827 (TEX); LIVE OAK CO.: 11 miles N of Three Rivers, *Thompson & Turner* 12 (TEX); LLANO CO.: Field Creek, *Turner & Johnston* 2512 (TEX); MITCHELL CO.: Colorado City, *Oyster* s.n. (CAS, MICH); HEMPHILL CO.: 2 miles NE of Canadian, *Cory* 16272 (GH); TERRY CO.: Wellman, *Reed* 3788 (TEX, US); TRAVIS CO.: Austin, *Tharp* 189 (MO, TEX); WILSON CO.: 10 miles SW of Floresville, *Sullivan & Turner* 1 (TEX).

Baltzer (1944) recognized this taxon as a variety of *Palafoxia texana* as did Shinnars (1952), although the former worker restricted the name to plants from Colorado and Wyoming, designating the Texas and Oklahoma material as variety *texana*. We agree with Shinnars that the Texas populations belong with var. *macrolepis*, but differ with his placement of the variety in *P. texana*. Rydberg (1910) also suggested that the relationship of var. *macrolepis* is with *P. rosea* but preferred to confer specific status.

The two varieties of *Palafoxia rosea*, as treated here, both having chromosome numbers of $n = 10$, intergrade over a broad region from east to west, and occupy sandy soils. After years of observations on numerous populations, we conclude that they are indeed more closely related to each other than either is to any other taxon. *Palafoxia texana* is composed of 3 varieties, all diploid with $n = 11$; these taxa replace each other geographically and intergrade peripherally. To the north *P. texana* is replaced by the contiguous *P. rosea*.

12. *Palafoxia texana* DC. Prodr. 5:125. 1836. TYPE: UNITED STATES. Texas: Berlandier pl. exs. 2014 (Photograph of holotype, G-DC!; isotypes, GH!, MO!).

12a. *Palafoxia texana* DC. var. *texana*. Fig. 22.

Polypteris texana (DC) Gray, Proc. Am. Acad. 19:30. 1883. *Othake texanum* (DC.) Bush, Trans. Acad. Sci. St. Louis 14:176. 1904.

Othake canescens Rydb., N. Am. Fl. 34:60. 1914. TYPE: MEXICO. Nuevo Leon: Monterey, Pringle 1919 (Holotype, NY!; isotypes, F!, MICH!, UC!, US!).

Plants annual, 20-80 cm tall; stems erect, usually several from a suffruticose base (often appearing perennial), densely pubescent with white, scabrous, appressed hairs, capitate glandular only in the inflorescence; mid-stem leaves linear-lanceolate to ovate-lanceolate, 3-nerved, 0.5-2.0 cm wide, 3-8 cm long, with petioles 1-3 cm long; principal involucral bracts 12-15, linear-ob lanceolate, acute to obtuse, densely strigose, not or rarely glandular; florets pinkish-white to pink, regular; corolla 8-10 mm long, tube slender, 3.5-5.0 mm long, throat campanulate, 0.4-0.6 mm long, lobes linear, 3-4 mm long; style branches 3-5 mm long; achenes 4-6 mm long, obpyramidal, 4-sided, rather evenly pubescent with short, silky, ascending hairs; pappus scales 8, 2.5-5.0 (-6) mm long (the outermost achenes with the shorter scales); chromosome number, $n = 11$.

Distribution: Southern Texas and adjacent Mexico, mostly in rocky or gravelly calcareous soils. Flowering, Mar.-Nov. depending on rains. Fig. 18.

REPRESENTATIVE SPECIMENS. UNITED STATES. Texas: DIMMIT CO.: Carrizo Springs, Palmer 33725 (MO, US); DUVAL CO.: 9 miles N of Freer, Thompson & Turner 35 (TEX); FRIO CO.: Melon, Muller 2608 (MICH, UC); HIDALGO CO.: 1 mile N of Tabasco, Clover 93 (ARIZ); KINNEY CO.: "river highway" 1 mile N of Maverick County line, Johnston 3879 (TEX); LA SALLE CO.: 1 mile E of Cotulla, Ferris & Duncan 3041 (CAS, DS, MO); MC MULLEN CO.: 2.5 miles S of Tilden, Tharp & Johnston 541776 (TEX); MAVERICK CO.: 6 miles N of



Fig. 22. *Palafoxia texana* var. *texana*. A. Whole plant, $\times \frac{1}{4}$. B. Head, $\times 2\frac{1}{2}$.

Quemado, *Johnston* 3861 (TEX); MEDINA CO.: 2 miles SW of Devine, *Turner* 4561 (TEX); STARR CO.: about 5 miles SE of Rio Grande City, *Correll* 14894 (US); UVALDE CO.: 7 miles SW of Uvalde, *Shinners* 7371 (GH, UC); VAL VERDE CO.: Del Rio, *Jones* 26398 (DS, MO, US); WEBB CO.: near Laredo, *Mackenzie* 7 (ARIZ, MICH, MO); ZAPATA CO.: Highway 83, *Parks* RX 2884 (MO).

MEXICO. Coahuila: between Hipolito and Sacramento in El Desierto de la Playa, *Wynd & Mueller* 83 (ARIZ, GH, US); San Lazaro near the northern entrance of El Puerto de San Lazaro, *Wynd & Muller* 120 (ARIZ, GH, US); 23 miles SW of Monterey, *Warnock & Barkley* 14878M (F, TEX); 90 miles N of Saltillo, *Turner*

3981 (TEX); 20 miles N of Monclova, *Turner* 3984 (TEX); 8 miles SW of Saltillo, *Shreve* 8730, (ARIZ, MICH, US); La Rosa, W of Saltillo, *Shreve & Tinkham* 9589 (GH, MICH, UC); La Fariba cerra de Nuevo Laredo, *Selar* 1031 (GH); about 30 km ESE of Cuatro Cienegas, *Schroeder* 164 (GH); Soledad, Sabinas, *Nelson* 6772 (US); Muzquiz, *Marsh* 1124 (F, GH, TEX); Hermanas, about 40 km north-easterly from Monclova, *Marsh* 1616 (F, GH, TEX); Monclova, *Marsh* 1730 (F, GH, TEX); 15 miles SE of Sabinas on the road to Don Martin, *Johnston* 4335 (TEX); 8 miles W of Saltillo, *Johnston* 7665 (GH); Canon de la Charretera, Sierra de la Madera, *Johnston* 9171 (GH); 6 km E of Saltillo, *Hinton* 16873 (GH). **Nuevo Leon:** 14 km S of Nuevo Laredo, *Frye & Frye* 2385 (DS, GH, MO, UC, US); 12 miles N of Sabinas Hidalgo, *Heard & Barkley* 14546 (GH, TEX, US); 16 miles SW of Villa Santa Catarina, *Hernandez, Roswell, Jr. & Barkley* 16M514 (TEX); 27 miles W of Monterey, *Johnston & Graham* 4318 (TEX); Monterey, *Pringle* 1919 (F, MICH, UC). **Puebla:** w/o locality, *Nicolas* s.n. (F). **Tamaulipas:** 10 miles S of Nuevo Laredo, *Heard & Barkley* 14583 (TEX, US); near Dolores (24° 00' × 97° 55'), *Crutchfield & Johnston* 5048 (TEX); 3 miles W of Morales, *Crutchfield & Johnston* 5351 (TEX).

Palafoxia texana var. *texana* apparently grades into var. *ambigua* along the eastern portion of its range (*Tharp & Johnston* 541776, TEX; *Thompson & Turner* 35, TEX; *Graham & Johnston* 4367, TEX).

Shinners (1952) treated the *macrolepis* segregate as a variety of this species but on cytological, morphological and geographical grounds the former appears to be better treated as a variety of *Palafoxia rosea*. For the same reasons *P. rosea* var. *ambigua* of Shinners appears to be best treated as a variety of *P. texana*.

12b. *Palafoxia texana* var. *ambigua* (Shinners) B. L. Turner & M. I. Morris, comb. nov. Fig. 23.

Palafoxia rosea var. *ambigua* Shinners, Field & Lab. 20: 95. 1952. TYPE: UNITED STATES. **Texas:** SAN PATRICIO CO.: Aransas Pass, *Cory* 51241 (Holotype, SMU!; isotypes, DS!, GH!).

Resembling var. *texana* except in being less branched at the base, and possessing longer leaves, shorter pappus scales, narrower and mostly eglandular involucre bracts; chromosome number, $n = 11$.

Distribution: Southernmost Texas and adjacent Mexico, mostly in sandy or silty-sandy soils. Flowering, Feb.-Nov., depending on rains. Fig. 18.

REPRESENTATIVE SPECIMENS. UNITED STATES. Texas: ARANSAS CO.: Rockport, *Fisher* 39091 (ARIZ, CAS, TEX, US); BEE CO.: Highway 181, *Parks* s.n. (MO); BEXAR CO.: Highway 181, *Parks* s.n. (MO); BROOKS CO.: 12.1 miles SE of Hebbronville, *Cory* 16943 (GH); CAMERON CO.: Rio Hondo, *Chandler* 7035 (GH, UC, US); CALHOUN CO.: Magnolia Beach, *Turner* 4332 (TEX); DUVAL CO.: 17¾ miles N of Freer, *Cory* 55315 (US); HIDALGO CO.: Edinburg, *Fisher* 41060 (CAS, US); JACKSON CO.: S of Vanderbilt, *Tharp & Barkley* 13A156 (DS, TEX); JIM HOGG CO.: Peira Station, *Harvard* s.n. (US); JIM WELLS CO.: 2 miles S of Premont, *Ferris & Duncan* 3246 (CAS, DS); KARNES CO.: 2.4 miles NNE of Runge, *Johnston* 971 (TEX); KENEDY CO.: El Toro Island, *Tharp* 49120 (TEX, US); KLEBERG CO.: Riviera, *Tharp* 3876 (TEX, US); MC MULLEN CO.: 15 miles N of Freer, *Thompson & Graham* 78 (TEX); NUECES CO.: Corpus Christi Bay, *Heller* 1562 (ARIZ, GH, MICH, MO, UC, US); REFUGIO CO.: Highway 35, *Parks* s.n. (MO); SAN PATRICIO CO.: Aransas Pass, *Cory* 51241 (DS, GH); STARR CO.: 3 miles W of Sullivan City, *Lundell & Lundell* 9884 (ARIZ, DS, MICH, US); VICTORIA CO.: Highway 77, *Parks* s.n. (MO); WILLACY CO.: near Redfish Bay, *Lundell & Lundell* 8774 (GH, MICH); WILSON CO.: w/o locality, *Parks* s.n. (MO); ZAPATA CO.: San Ygnacio, *Tharp* 3880 (TEX, UC).

MEXICO. Tamaulipas: de Matamoras a San Fernando, *Berlandier* 3027 (GH, MO); 34 miles S of Matamoras, *Crutchfield & Johnston* 5484 (TEX); south of Rio Tigre crossing, *LeSueur* 482 (F, TEX); Morales, *LeSueur* 483 (ARIZ, F, TEX).

Shinners (1952) treated this taxon as a variety of *Palafoxia rosea* apparently because it usually possesses eglandular involucre bracts, a technical feature which he used to distinguish between the species *P. rosea* and *P. texana*. Occasional specimens of *P. texana* var. *ambigua* are found with conspicuous glandular bracts (e.g. *Warnock* 21002, TEX) and many specimens may be found with only a few scattered glandular trichomes. Likewise, specimens similar to var. *texana* are often found with eglandular bracts. On total morphological grounds, chromosome number, distribution, and because it grades into *P. texana* to the west, we have treated the taxon as a variety of that species.



Fig. 23. *Palafoxia texana* var. *ambigua*, A & B. *P. texana* var. *robusta*, C & D. A. Head, $\times 2\frac{1}{2}$. B. Floret, $\times 3$. C. Head, $\times 2\frac{1}{2}$. D. Floret, $\times 4$.

- 12c. *Palafoxia texana* var. *robusta* (Rydb.) B. L. Turner & M. I. Morris, comb. nov. Fig. 23.

Othake robustum Rydb., N. Am. Fl. 34:60. 1914. TYPE: MEXICO. **Tamaulipas:** sand dunes of Gulf Coast, Tampico, *Pringle* 6354 (Holotype, NY!; isotypes, CAS!, F!, MO!, UC!). *Polypteris robustum* (Rydb.) Cory, Rhodora 38:408. 1936. *Othake roseum* var. *robustum* (Rydb.) Ammerman, Ann. Mo. Bot. Gard. 31:257. 1944.

Much resembling *P. texana* var. *ambigua* but differing from that taxon in being much more robust (mostly 0.9-2.1 m tall), with larger heads and longer achenes (6-7 mm); chromosome number not determined.

Distribution: Dune sands along the Gulf Coast from northernmost Veracruz to central Tamaulipas. Flowering, Jul.-Nov. or later, depending on rains. Fig. 18.

REPRESENTATIVE SPECIMENS. MEXICO. **Tamaulipas:** Tampico, *Fisher* 46177 (CAS, US); Tampico, *Kenoyer* 728 (F, MO); 1 mile N of Ciudad Madero, *King* 4003 (TEX); 2 miles NE of Altamira, *King* 4030 (TEX); Tampico, Miramar, *Mell* s.n. (NY); vicinity of Tampico, *Palmer* 38 (CAS, F, GH, MO, NY, US); 8 miles NE of Tampico, *Waterfall & Wallis* 14642 (F). **Veracruz:** 1 miles N of Las Casitas (across the river from Nautla), *Graham & Johnston* 4803 (TEX); 2 kilometers out of Tampico on road to Valles, *Johnston* 4055A (TEX); La Guadalupe (20° 25' N.L.), ca. 15 kilometers S of Rio Tecolutla mouth, *Sauer & Gade* 3022 (WIS).

EXCLUDED NAMES

Palafoxia pedata (Cav.) Shinnery, Field & Lab. 17:25. 1949. This name refers to *Florestina pedata* (Cav.) Cass. Dict. Sci. Nat. 17:155. 1820.

Palafoxia liebmanni (Schz. Bip. ex Greenm.) Shinnery, Field & Lab. 17:25. 1949. This name refers to *Florestina liebmanni* Schz. Bip. ex Greenm. Field Mus. Publ. Bot. 2: 272. 1907.

Palafoxia tripteris (DC.) Shinnery, Field & Lab. 17:24. 1949. This name refers to *Florestina tripteris* DC. Prod. 5:655. 1836.

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