SUMMARY

A brief description of each of the muscles of the forearm of *Necturus* is presented. The muscles are named in accordance with the terminology used by Francis (1934) in his descriptions of the muscles of *Salamandra*. Names used by Wilder (1912) in his descriptions of the muscles of *Necturus* are listed as synonyms of the names used by Francis.

The pronator superficialis muscle is described, apparently for the first time.

The flexores breves superficialis, flexores digitorum minimi, interphalangeus digiti III, and interosseus antibrachii, though occurring in *Salamandra*, and previously reported by Wilder in *Necturus*, are not here identified as part of the musculature of *Necturus*.

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The Texas Species of Palafoxia (Compositae)

Lloyd H. Shinners

Taxonomically *Palafoxia* is one of the most perplexing genera of Texas Compositae; phylogenetically and geographically it is one of the most intriguing. It has been discussed by Gray (1884), Bush (1904), Rydberg (1910, 1914), Ammerman (1944), Cory (1946, 1948), and myself (1949), with varying degrees of inadequacy or inaccuracy. Since 1949 I have puzzled over the genus at intervals, working toward a fresh revision of the Texas species. The discovery of part of the vanished type material of *P. riograndensis*, and the accumulation of additional specimens, makes it possible to present as definitive a synopsis as may reasonably be expected from morthodox taxonomic methods, emphasizing morphology and geography. In addition to the collections in the Herbarium of Southern Methodist University (SMU), those in the Tracy Herbarium of Texas A. & M. College (TAM) were used in this study, and selected specimens were examined at the Philadelphia Academy and the Missouri Botanical Garden. In a note following the systematic treatment, some suggestions are ventured regarding phylogeny and geological history.

KEY TO TEXAS SPECIES OF PALAFOXIA

1a. Involucre strigose or glabrate, not glandular-pubescent, 3.5-8 mm. high in flower; pappus 0.1-5 mm. long

2a. Middle and lower stem leaves compound

3a. Pappus 1.2-1.7 mm. long; plant of lower Rio Grande Plain —1a. *P. tripteris* var. *tripteris*
3b. Pappus 0.5-0.8 mm. long; plant of Edwards Plateau —1b. *P. tripteris* var. *brevis*
2b. Middle and lower stem leaves simple
4a. Peduncles 0.5-2.6 cm. long; phyllaries 0.7-1.25 mm. wide; plants of limestone soils, Blackland Prairie southwest to Edwards Plateau
5a. Florets 6-13 per head....................2a. *P. callosa* var. *callosa*
5b. Florets 15-30 per head......................2b. *P. callosa* var. *bella*
4b. Peduncles 1.5-6 cm. long; phyllaries unequal in width, the broader ones 1-1.7 mm. wide; plants of sandy soils, East and South Texas (extending northwest on sandy river terraces into Blackland Prairie)
6a. Leaf blades linear-lanceolate, 1-7 mm. wide, 8-18 times as long as wide; florets 6-22 per head
7a. Pappus 1.3-2.2 mm. long................3a. *P. rosea* var. *rosea*
7b. Pappus 4-5 mm. long..................3b. *P. rosea* var. *papposa*
6b. Leaf blades lanceolate or ovate-lanceolate, 5-15 mm. wide, 3-10 times as long as wide; florets 20-44 per head (as few as 11 on stunted heads of second-growth branchlets late in season)..............................3c. *P. rosea* var. *ambigua*
1b. Involucre both glandular-pubescent and hispid or strigose, 7-16 mm. high in flower; pappus of inner florets 3-10 mm. long
8a. Stem glandular-pubescent throughout with widely spreading hairs
9a. Involucre 10-16 mm. high in flower, at first broadly conical, as wide as or wider than high (15-20 mm. across, as pressed), becoming still broader in fruit; florets 60-90 per head; limb of ray florets 1-2 cm. long —7a. *P. Hookeriana* var. *Hookeriana*
9b. Involucre 7-10 mm. high in flower, at first narrowly conical or conical-cylindric, narrower than high (6-10 mm. across, as pressed), soon becoming broader than high; florets 27-40 per head; limb of ray florets 0.7-1.2 cm. long —7b. *P. Hookeriana* var. *minor*
8b. Stem mostly hispid, strigose, or glabrate: only the upper part, branches, and peduncles with spreading glandular hairs
10a. Phyllaries unequal in width, the broader ones 1.7-2.7 mm. wide, 3-6 times as long as wide, elliptic-oblong or lanceolate-oblong (appearing narrower in age, when inrolled from the sides); stem sparsely to densely hispid-strigose, the trichomes slightly thickened at base, most or all appressed or closely ascending, rather persistent; plants of general distribution
11a. Corolla limb of central florets divided nearly all the way to summit of tube; plants of central and western Texas
12a. Marginal florets not radiate; involucre 7-10 mm. high; pappus scales finely pubescent on back
13a. Pappus scales of inner florets 3-5 mm. long (nearly 6 mm. in a single specimen examined), obtuse to acuminate; plants of Rio Grande Plain, north to Maverick, Uvalde, Medina, Atascosa, and Nueces counties.................................4a. *P. texana* var. *texana*
13b. Pappus scales of inner florets 5-7 mm. long, acuminate or awn-pointed; plants of the Panhandle and South Plains, from Ector and Midland counties northward......................4b. *P. texana* var. *macrolepis*
12b. Marginal florets radiate; involucre 9-12 mm. high; pappus scales either glabrous or pubescent on back —5. *P. sphacelata*

11b. Corolla limb of central florets divided about ⅔-¾; plants of East Texas Pine Belt............................6. *P. Reverchonii*

10b. Phyllaries all very narrow, 1.3-1.7 mm. wide, 6-9 times as long as wide, narrowly oblong-lanceolate or lance-linear; rather densely hispid with appressed or spreading trichomes, mostly with prominent swollen bases, breaking off and leaving the enlarged bases; plants of vicinity of Rio Grande in the Big Bend............................8. *P. riograndensis*

1a. P. TRIPTERIS (DC.) Shinners var. TRIPTERIS. *Florestina tripteris* DC. (Map 1.) Lower Rio Grande Valley, extending north to Frio and San Patricio counties. Corolla usually white or whitish, rarely lavender. Found in flower the year round.

1b. P. TRIPTERIS var. **brevis** Shinners, var. nov. (Map 1.) Pappo abbreviato 0.5-0.8 mm. longo. TYPE: Texas Range Station, about 22½ miles north of Ozona, Crockett Co., Texas, *V. L. Cory 40710,* Oct. 10, 1942 (SMU). Three additional collections have been seen. CROCKETT or VAL VERDE Co.: "Sanderson-Del Rio," *B. C. Tharp,* Oct. 10, 1936 (TAM). SCURRY Co.: 7 miles east of Fluvanna, *R. W. Pohl 4423,* Oct. 13, 1942 (SMU). SUTTON Co.: 24 airline miles south-southeast of Sonora, *Cory 52448,* Oct. 4, 1946 (SMU). Corollas apparently either white or pink. All four collections were made in October.

2a. P. CALLOSA (Nutt.) T.&G. var. CALLOSA *Othake callosum* (Nutt.) Bush. (Map 2.) Eroding or disturbed limestone soils, Black and Grand Prairies and Edwards Plateau, south and west to Travis and Kinney counties. Flowering late July-early November. Possibly found on prairies in Harris County (specimens immature, referred doubtfully to *P. rosea* var. *rosea*).

2b. P. CALLOSA var. **bella** (Cory) Shinners, comb. nov. (Map 2.) *P. bella* Cory, Field & Lab. 16: 62-63. 1948. Limestone soils, Edwards Plateau; known from Bexar, Edwards, Kerr, Llano, Mason, Schleicher, Sterling, Sutton, Terrell, Tom Green, and Val Verde counties; flowering late August-October. Mr. Cory gave counts of number of florets per head on one plant only, and quoted published statements as to the number in *P. callosa* var. *callosa.* Actual count of 8 collections of the former and 16 of the latter gave the totals stated in the key. Corolla color varies greatly in var. *callosa. P. bella* consequently appears to me better treated as a variety of *P. callosa.*

3a. P. ROSEA (Bush) Cory var. ROSEA. *Othake roseum*

Bush. (Map 3.) East Central to South Central Texas; collections examined from Anderson, Brazoria, Brazos, Dallas, Freestone, Galveston, Harris, Leon, Trinity, and Walker counties. June-November. Greatly resembling *P. callosa*, especially when young and with peduncles not fully elongated.

3b. P. ROSEA var. **papposa** Shinners, var. nov. (Map 3.) Pappo elato 4-5 mm. longo. TYPE: Apicultural Laboratory, San Antonio, Bexar Co., Texas, *H. B. Parks*, Aug. 27, 1934 (TAM; fragments, SMU). One additional specimen has been seen, from the same locality, *Parks*, June 29, 1935 (TAM). Except for the conspicuous and striking pappus scales, the plant resembles var. *rosea*.

3c. P. ROSEA var. **ambigua** Shinners, var. nov. (Map 3.) Foliis grandioribus (laminis 5-15 mm. latis, 3-plo ad 6-plo [rarius 10-plo] longioribus), capitulis majusculis 20-44-floris. TYPE: Aransas Pass, San Patricio Co., Texas, *Cory 51241*, Nov. 27, 1945 (SMU). Lower Rio Grande Plain, extending north to Dimmit and San Patricio counties.

The following additional collections may be cited, all from Texas: ARANSAS CO.: Rockport, *Tharp*, July 2, 1939 (SMU, TAM). Goose Island, 8 airline miles north-northeast of Rockport, *Cory 45448*, July 26, 1944 (SMU). CAMERON CO.: 12½ miles southeast of Brownsville, *Cory 36552*, Nov. 15, 1940 (TAM). Port Brownsville, *Cory 51425*, Dec. 1, 1945 (SMU). DIMMIT CO.: 14½ miles south of Catarina, *Cory 35908*, Nov. 8, 1940 (TAM). DUVAL CO.: Ranch of George Frank, *Parks & Cory 14794*, June 8, 1935 (TAM). HIDALGO CO.: Edinburg, *R. G. Burwell*, Sept. 25, 1939 (TAM). JIM HOGG CO.: 12.1 miles southeast of Hebbronville, *Parks & Cory 16941*, Oct. 7, 1935 (TAM). KLEBERG CO.: 5 miles south of Kingsville, *Cory 51299*, Nov. 28, 1945 (SMU). LA SALLE CO.: 14 miles south of Fowlerton, *C. L. & Amelia A. Lundell 14526*, Oct. 16, 1945 (SMU). SAN PATRICIO CO.: 9 miles southwest of Taft, *Fred B. Jones 188*, April 7, 1950 (SMU). 5½ miles southwest of Aransas Pass, *Cory 51246* and *51246a*, Nov. 27, 1945 (SMU). STARR CO.: 6⅓ miles south of Rio Grande City, *Cory 35959*, Nov. 9, 1940 (TAM). WILLACY CO.: near Redfish Bay, *Lundell & Lundell 8774*, May 8, 1940 (SMU).

This has been mistakenly referred to *P. rosea* var. *robusta* (Rydb.) Cory, a quite distinct variety found in southern Tamaulipas. The Mexican variety has the narrow leaf blades of var. *rosea* (8-18 times as long as wide), but larger in all dimensions, and on petioles 10-18 mm. long (in contrast with 3-8 or rarely 10 mm. in var. *rosea*). True var. *robusta* is not known to occur nearer to Texas than the vicinity of Tampico. The plant here named var. *ambigua* has frequently been mistaken for *P. texana* because of the numerous florets and broad leaf blades. The pubescence of the involucre is coarser and denser than in *P. rosea* var. *rosea*.

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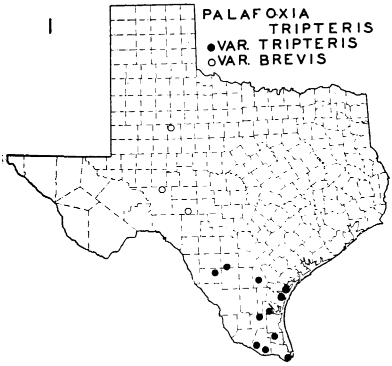
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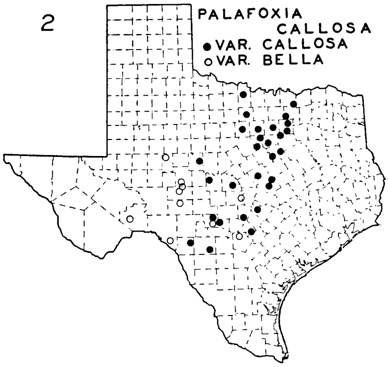
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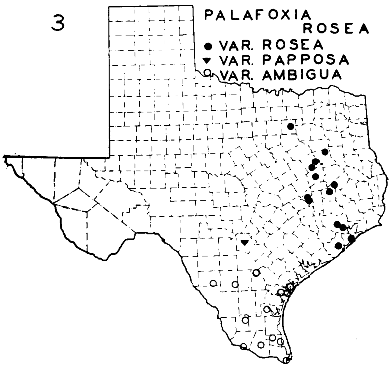
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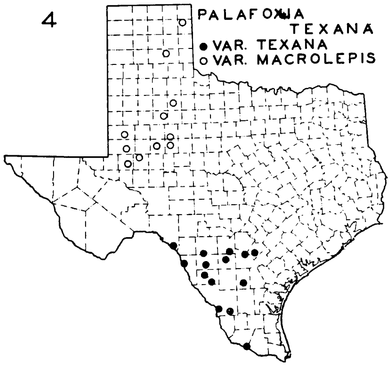
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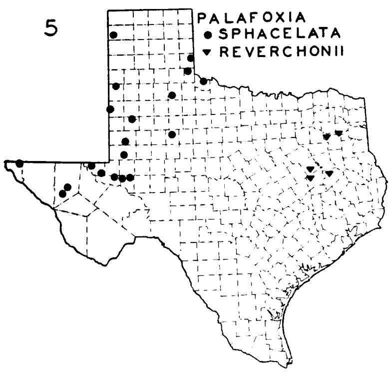
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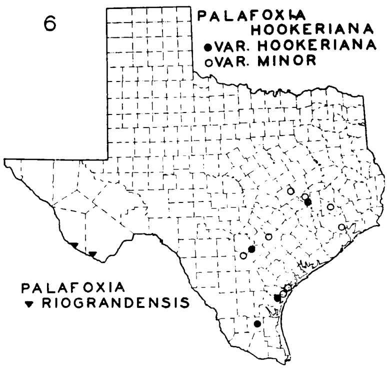
PALAFOXIA
HOOKERIANA
● VAR. HOOKERIANA
○ VAR. MINOR
PALAFOXIA
▾ RIOGRANDENSIS

4a. P. TEXANA DC. var. TEXANA. *Othake texanum* (DC.) Bush. (Map 4.) Central and northern Rio Grande Plain; collections seen from Atascosa (exceptional specimen with pappus nearly 6 mm. long), Dimmit, Duval, Frio, Maverick, Medina, Nueces, Starr, Uvalde, Val Verde, Webb, and Zavala counties. March-October.

4b. P. TEXANA var. **macrolepis** (Rydb.) Shinners, comb. nov. (Map 4.) *Othake macrolepis* Rydb., Bull. Torr. Bot. Club 37: 332. 1910. *Othake texanum* var. *macrolepis* (Rydb.) Ammerman. *Palafoxia macrolepis* (Rydb.) Cory. South Plains and Panhandle, west and northwest to New Mexico, Colorado, and Wyoming. Flowers in Texas May-September. In var. *texana* the pappus is quite variable in size and degree of acumination, but is prevailingly short. In var. *macrolepis* the pappus is always sharply and slenderly pointed, and consistently longer than in var. *texana,* though often not much so. If the species is to be divided into geographic varieties, the break is certainly not between all the Texas plants and those outside, but between the population of the Rio Grande Plain and that found to the north of the Edwards Plateau, which separates the two groups. In treating var. *macrolepis* as a distinct species, Mr. Cory made it plain that he reached that conclusion without examining any specimens of it (1946, p. 85). The Wyoming specimens cited by Miss Ammermann (Herb. Missouri Botanical Garden) do not appear to me to be separable from many Texas collections made in the South Plains and Panhandle areas, nor from collections made in eastern New Mexico. She describes the pappus scales as 6-8 mm. long, but in Rydberg's original description they are stated to be 5-6 mm. long. She described the pappus scales of var. *texana* as 3.5-4.5 mm. long, which is certainly not true of Texas specimens from the area north of the Edwards Plateau, though she treated these as belonging to var. *texana.* On the basis of 47 collections examined, I delimit the varieties as stated in the key.

5. P. SPHACELATA (Nutt.) Cory. *Othake sphacelatum* (Nutt.) Rydb. (Map 5.) Sandy soils, westward and northward from the Edwards Plateau. May-October. Perhaps better regarded as a third variety of *P. texana,* from which it is very difficult to distinguish after the ray florets have fallen.

6. P. REVERCHONII (Bush) Cory. *Othake Reverchonii* Bush. (Map 5.) East Texas Pine Belt; specimens seen from Freestone, Houston, Leon, and Smith counties; type collection made in Upshur County. July-November.

7a. P. HOOKERIANA T.&G. var. HOOKERIANA. *Polypteris maxima* Small. *Othake Hookerianum* (T.&G.) Bush. (Map 6.) Lower Rio Grande Valley, northeastward to Wilson and Brazos counties. July-October. Although no precise measurements are given in the first description of this plant (Hooker, Icones vol. 2 pl. 148, 1837), Torrey & Gray add (Fl. N.A. 2: 368, 1842) "Heads three-fourths of an inch in length; the showy rose-purple rays in Drummond's plant half an inch or more in length, resembling a Gaillardia." These dimensions apply to the plant as here understood.

7b. P. HOOKERIANA var. **minor** Shinners, var. nov. (Map 6.) Capitulis minoribus: involucris 7-10 mm. altis, 27-40-floris; ligularum limbis 0.7-1.2 cm. longis. TYPE: Channelview, Harris Co., Texas, *Geo. L. Fisher 50717,* Oct. 5, 1950 (SMU). Found in the northern part of the range of var. *Hookeriana,* with which it sometimes grows; apparently commoner, and extending farther inland. The characteristic indument of the stem has generally been overlooked, and because of its small size this variety has mistakenly been included in *P. sphacelata,* though the ranges of the two do not meet.

The following additional specimens of *P. Hookeriana* var. *minor* have been examined: ARANSAS CO.: south of Rockport Road, *Parks & Cory 15560-15561,* Sept. 22, 1935 (TAM). ATASCOSA CO.: northeast of Poteet, *Parks & Cory 11757-11758,* Oct. 12, 1934 (TAM). BRAZOS CO.: south from Jones' Bridge, *H. Ness,* Oct. 24, 1927 (TAM). Jones Bridge, *Parks,* Sept. 17, 1946 (TAM); also Oct. 8, 1946 (TAM). GONZALES CO.: Soefje Farm, near Ottine, *Fred A. Barkley 13961,* Oct. 3, 1943 (SMU). MILAM CO.: 5 miles east of Cameron, *Simon E. Wolff, 3655,* Sept. 23, 1932 (TAM). MONTGOMERY CO.: Conroe, *Fisher 51068,* Oct. 2, 1951 (SMU). SAN PATRICIO CO.: 3 miles west of Aransas Pass, *Jones 647,* Oct. 14, 1951 (SMU).

8. P. RIOGRANDENSIS Cory, Rhodora 48: 84. 1946. *P. cyanophylla* Shinners, Field & Lab. 17: 25-27. 1949. (Map 6.) Along the Rio Grande on the western side of the Big Bend, Brewster and Presidio counties; also in southwestern Coahuila, Mexico. Before describing *P. cyanophylla,* I endeavored to obtain specimens of *P. riograndensis,* but none could be found at College Station, nor at the Gray Herbarium where the type was deposited, nor could material answering to Mr. Cory's description (which I had translated into Latin

myself!) be found at the University of Texas nor at the Missouri Botanical Garden. Several points in the description did not fit my Brewster County plant (the type of *P. riograndensis* was from Presidio County), and Mr. Cory on examining it did not think it belonged to his species. Recently Dr. F. W. Gould located two specimens of the type series of *P. riograndensis* (a different number was assigned to every sheet collected by Parks or Cory while at Texas A. & M., so that numerically there are no duplicates). Though quite different in appearance, they indubitably represent small, narrow-leaved individuals of a later, more bushy-branched growth phase of the same species I had mistakenly described as new. *Palafoxia riograndensis* is plainly a close ally of *P. linearis* Cav., with more deeply divided corolla, vitiating the generic distinction between *Palafoxia* and *Othake* emphasized by Miss Ammerman. Old plants of *P. sphacelata* (which also occurs in the Trans-Pecos, though apparently not close to the Rio Grande) are very difficult to distinguish from *P. riograndensis* after the rays have fallen, especially if the phyllaries have become inrolled in drying and appear narrowly linear. At this stage, they can best be distinguished by the finer trichomes of the stem, lacking the greatly swollen bases characteristic in *P. riograndensis*. The following collections (additional to types or material already cited in the original descriptions of the two species) give the known range of *P. riograndensis*.

TEXAS. BREWSTER CO.: along Rio Grande near Santa Helena Canyon, *Omer E. Sperry 1160*, Oct. 19, 1937 (TAM). Santa Helena Canyon, *Parks & Cory 26476-26477*, Oct. 21, 1937 (TAM). PRESIDIO CO.: 3 miles southeast of Presidio, *Parks & Cory 26411*, Oct. 20, 1937 (TAM). 3½ miles southeast of Presidio, *Parks & Cory 31191* (SMU) and *31194* (TAM), Oct. 26, 1938. (These are actually isotypes, though not bearing the type number, *31195*.) MEXICO. COAHUILA: Torreon, *Fisher 44125*, July 10, 1944 (SMU).

Geobotanical Considerations

It is my surmise that the genus *Palafoxia* is ancient, but that the species found in Texas are very young. Support for such a notion is found in the fact that a majority of the genera of the Eocene Wilcox Flora are still represented in the living flora of the Gulf Coastal Plain (Sharp, 1951), that the most distinct species of the genus (all perennials) are rather isolated endemics of Florida and Georgia, and of northwestern Mexico and neighboring portions of the United

States, and that the Texas species (all weedy annuals) differ from each other only in small degrees and in few features. The genus may not be so old as the Eocene; it belongs with the Mexican Plateau flora which developed and spread northward and eastward in the Miocene. Though direct fossil evidence is lacking, the very large number and relationships of the endemic plants of the Edwards Plateau and Trans-Pecos suggest that these were essentially a portion of the region in which the so-called Sierra Madrean Miocene flora arose, and *Palafoxia* is consequently to be considered an autochthonous element of the Texas-North Mexican flora. Support for the belief that the genus is ancient and autochthonous may be found too in the geological record, which shows that there has been dry land in the Texas region almost throughout the history of the flowering plants (cf. Sellards et al., 1932, *passim*). Paleogeographic maps show extensive seas in the Cretaceous, but since Lower Cretaceous deposits in central Texas have dinosaur tracks and fossil cycads, these maps cannot be taken at face value.

With regard to the rate of evolution, we have an example of the development of a whole sequence of species of pine in California from the Pliocene to the present (Mason, 1932), and the family tree of *Homo sapiens* and his near allies goes back no farther than early Pleistocene. From comparison, I should judge that our living species of *Palafoxia* are not older than the Pleistocene, and their weakly differentiated varieties may represent changes that have occurred since the close of that period.

With regard to the mechanics of evolution in *Palafoxia*, there is much room for speculation. An illuminating comparison may be made between the Texas plants of the genus and *Rubus parviflorus*. The population of *Rubus parviflorus* about the upper Great Lakes, which became separated from that of the Rocky Mountains and Pacific Coast area in recent time, includes the same variations of indument found elsewhere, but in different proportions (Fassett, 1941). We have then a picture of a widespread, variable species, within one portion of whose range certain variations are gradually disappearing. Four Texas species of *Palafoxia* show the results to be expected if such a trend as this had continued longer than it has in *Rubus parviflorus*—*P. Hookeriana* (map 6), with two varieties whose ranges overlap so much that they are scarcely geographically distinct; *P. callosa* (map 2), with two varieties whose ranges overlap only in part; *P. texana* (map 4), with two varieties entirely separated geographically, though not morphologically, and not different in habitat preference; and *P. tripteris* (map 1), with two varieties geographically separate, morphologically distinct, and radically different in soil preference. These look very convincingly like the eventual results of differential dying out of portions of a variable population. The contrasting soil preferences of the varieties of *P. tripteris* may have involved a mutation rather than only minor variations in the ancestral population. This would be in accord with the karyotype changes mentioned below.

These suppositions bring up two further topics: kinds of variations, and barriers. As may be seen from the key, the Law of Homologous Variations (Vavilov, 1950) is well illustrated in the genus. But the geographic arrangement of the homologous variations is not always consistent. In *P. Hookeriana* (map 6), few-flowered heads (var. *minor*) occur to the north or northeast, with no great difference in range from many-flowered heads; in *P. callosa* (map 2), the orientation is similar, with only partial overlap in range; in *P. rosea* (map 3), the orientation is again similar, with a gap between the ranges of few-flowered var. *rosea* (northeastern) and many-flowered var. *ambigua* (southern). In *P. tripteris* (map 1), long pappus characterises the southern population (var. *tripteris*), short pappus the northern (var. *brevis*); in *P. texana* (map 4) exactly the opposite is true, the southern race this time being the one with shorter pappus, the northern (var. *macrolepis*) the one with longer; and in *P. rosea* (map 3), the orientation is tilted 90 degrees, so that long pappus (var. *papposa*) occurs to the west, short pappus (var. *rosea*) to the east. (I have purposely disregarded the third variety of *P. rosea*, which I consider to be less closely related to these two than they are to each other.) It would appear from these examples that if there is any survival value in the gene changes which produced the morphological differences, it lies in the physiological changes which accompany them, and not in the obvious morphological changes.

With regard to the breeding barriers or isolating mechanisms which are commonly declared to be necessary prerequisties for the differentiation of populations into distinct taxonomic units, several may have affected *Palafoxia.* All our species are weedy annuals of disturbed soils—*P. tripteris* var. *brevis* and the two varieties of *P. callosa* on limestone, all the others on loose sand. Only in the case of *P. tripteris,* then, does habitat appear to be an isolating factor. In the case of the others, two or more varieties or species may grow together, and presumably could hybridize introgressively. Climatic factors have probably produced the distribution patterns of the varieties of the species, but have not always made sharp boundaries between them. Presumably at least partial breeding barriers exist in these species, but concerning their pollination (cf. Grant, 1949) and cytology we know nothing. The presence of homologous variations does suggest that karyotype changes have been an important factor in the evolution of *Palafoxia,* as Babcock believed to be the case in *Crepis* (1947).

Palafoxia fairly cries out for intensive cytological, genetic, bionomic, and geographic study. Yet it is only one example among many. The whole complex and amazing flora of Texas is like a still closed book of revelation, waiting to be opened and read.

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