A BIOSYSTEMATIC STUDY OF THE GENUS PENSTEMON (SCROPHULARIACEAE) IN THE GREAT PLAINS

by

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B.S., Wartburg College, 1978

A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Division of Biology

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1981

Approved by:

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ACKNOWLEDGEMENTS

I am particularly grateful to Dr. T.M. Barkley for suggesting this problem and for his guidance and support throughout the study. Thanks also go to Dr. A.S. Tomb for his support and assistance, particularly with many of the technical aspects of the study. I wish also to acknowledge my wife, Jane, for her unending encouragement and support throughout the undertaking, her company on several of the collecting trips, and her help in typing and proofreading of the manuscript.

Special thanks also go to Mark Wetter for his assistance and companionship on several of the collecting trips.

Drs. L.C. Hulbert and P.C. Twiss are also acknowledged for their reading the manuscript and helpful suggestions.

I wish to thank the members of the Frazier Botanical Fund Committee for their award of the John C. Frazier Memorial Fund in 1980 and 1981, funds from which helped support some of the fieldwork and purchase laboratory supplies. Additional support for fieldwork as well as scanning electron microscope time was provided by the Kansas Agricultural Experiment Station.

Acknowledgement is made to the curators and staffs of the following herbaria for providing loan material for examination or in which, specimens were examined. Acronyms are those of Holmgren and Keuken (1974), with the exception of Kearney State College Herbarium, the acronym for which has been provided by the author.

CS Colorado State University Herbarium, Ft. Collins, CO.

FHKSC Elam Bartholomew Herbarium of Fort Hays State College, Ft. Hays, KS.

IND Indiana University Herbarium, Bloomington, IN.

KANU University of Kansas Herbarium, Lawrence, KS.

*KNSC	Kearney State College Herbarium, Kearney, NE.
KSC	Kansas State University Herbarium, Manhattan, KS.
KSP	Pittsburg State University Herbarium, Pittsburg, KS.
MO	Missouri Botanical Garden Herbarium, St. Louis, MO.
NEB	University of Nebraska at Lincoln Herbarium, Lincoln, NE.
NDA	North Dakota State University Herbarium, Fargo, ND.
NY	New York Botanical Garden Herbarium, New York, NY.
OKL	Bebb Herbarium of the University of Oklahoma, Norman, OK.
OKLA	Oklahoma State University Herbarium, Stillwater, OK.
RM	Rocky Mountain Herbarium of the University of Wyoming, Laramie, WY.
SDC	South Dakota State University Herbarium, Brookings, SD.
SDU	University of South Dakota Herbarium, Vermillion, SD.
TTC	E.L. Reed Herbarium of Texas Tech University, Lubbock, TX.
WET	Wartburg College Herbarium, Waverly, IA.

INTRODUCTION

Penstemon (Scrophulariaceae: Cheloneae) is a large North American genus of about 280 species distributed from Alaska to Guatemala. The major center of distribution is in the Intermountain Region of the western United States where the state of Utah boasts 68 species (Holmgren, 1979b). A tally of species in states to the east of Utah reveals a rather dramatic decrease in numbers until one reaches the New England states where only 5 species are found. In the Great Plains, 22 species of Penstemon are known to occur. Species numbers in states entirely within the boundaries of the study area include Kansas with 11, Nebraska with 10, South Dakota with 8, and North Dakota with 8. Members of the genus are found in a wide variety of communities and often in disturbed or unstable habitats (Straw, 1966). In the Great Plains, some species, such as Penstemon albidus Nutt., are widely distributed and found throughout most of the region, while others like Penstemon haydeni S. Wats. have quite restricted ranges and more strictly defined ecological tolerances.

Penstemons are known colloquially as beardtongues, an allusion to the pubescent staminode found in many species. The genus is of economic importance only as an ornamental cultivar.

Penstemon is a well-defined natural group, characterized within the Cheloneae by having flowers with a single staminode that is normally well-developed and usually pubescent, epistaminal nectaries of glandular hairs, the inflorescence racemose to cymose, the seeds unwinged, and a base chromosome number of $x = 8$. Recent studies have resulted in the recognition of a number of generic segregates based on floral anatomy, gross morphology, and cytology. These segregates include Keckiella (Straw, 1966, 1967), Nothochelone (Straw, 1966), and Pennellianthus (Crosswhite &

Kawano, 1970). An excellent comparative study of the North American and east Asian genera of Tribe Cheloneae is provided by Straw (1966).

For the past half-century, students of Penstemon have examined the genus in a fragmentary fashion, studying sections, subsections, series, and alliances (Holmgren, 1979b). Revisionary studies include those of Keck (1932, 1936a, 1936b, 1937a, 1937b, 1938, 1940, 1945), Keck & Cronquist (1957), Straw (1959, 1962, 1963), and Crosswhite (1965a, 1965b, 1965c, 1966, 1967a, 1967b, 1967c, 1970a). Additionally, floristic studies of the genus by Pennell (1920, 1922, 1935, 1941), Keck (1951a, 1951b, 1952, 1959), Penland (1954), Cronquist (1959), Nisbet & Jackson (1960), and Crosswhite (1970b), to name but a few, have compiled and contributed valuable information, and Bennett (1959, 1960, 1963a, 1966) has compiled a number of useful nomenclatural lists. Recent studies in the Intermountain Region by Holmgren have resulted in the naming of a number of new species and nomenclatural changes in preparation of a taxonomic treatment of the genus for the Intermountain Flora (Holmgren, 1971, 1978a, 1978b, 1979a, 1979b, 1979c, 1980).

Nearly all revisionary studies have been based exclusively on morphological features, particularly floral characters. However, some studies exist that have explored other data sources, including cytology (Clausen, 1933; Clausen, Keck, & Hiesy, 1940; Keck, 1945; Crosswhite, 1965d; Crosswhite & Kawano, 1965; Nisbet & Jackson, 1960), floral morphology and ecology (Straw, 1955, 1956a, 1956b), pollination (Crosswhite & Crosswhite, 1966; Schmid, 1976), and biochemistry (Wang, Schermeister, & Khalil, 1976).

In the Great Plains, the genus displays an interesting and complex array of sectional and subsectional diversity as species representative of eastern, southwestern, and Rocky Mountain floras are found along with Plains

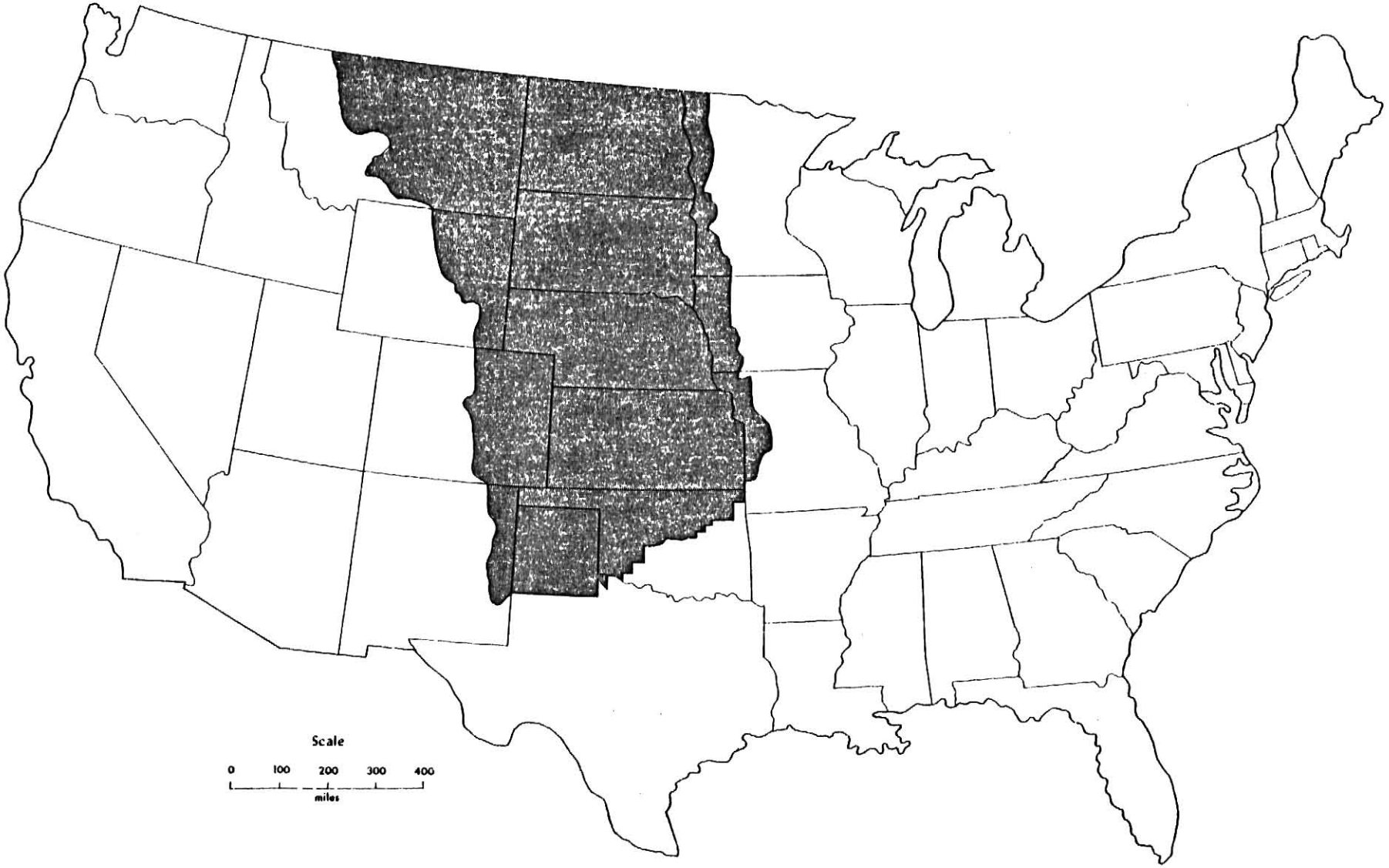
endemics. Such diverse phylogenetic and floristic affinities have caused taxonomic problems for Plains botanists. Many early Great Plains floristic studies relied heavily on peripheral floristic studies for taxonomic determinations and as a result, much erroneous information found its way into the literature. In the past half-century, however, much of this misinformation has been corrected as a result of revisionary studies.

For the purposes of this study, the Great Plains is delimited to coincide with the area to be covered in the incipient Flora of the Great Plains. This area is bounded by Canada to the north and extends south through the Texas panhandle. The western boundary is the eastern base of the Rocky Mountain uplift (excluding the isolated ranges of central Montana but including the Black Hills of South Dakota and Wyoming) while the eastern boundary is placed where at present there is continuous deciduous woodlands on non-agricultural land (Figure 1). The area includes the entire states of Kansas, Nebraska, South Dakota, and North Dakota, plus the western quarters of Minnesota and Iowa, northwestern eighth of Missouri, northwestern half of Oklahoma, the Texas panhandle, northeastern eighth of New Mexico, and those portions of Colorado, Wyoming, and Montana east of the Rocky Mountain uplift. The Great Plains are floristically and geographically coherent (Great Plains Flora Association, 1977) and dominated primarily by prairie grasslands with interfingering deciduous woodlands on the east.

This study was undertaken with two primary objectives in mind, 1) to yield a taxonomic treatment of the genus for the Flora of the Great Plains, and 2) to examine the Great Plains members of the genus Penstemon utilizing modern morphological, cytological, palynological, and chromatographic techniques to determine the potential utility of each technique in future revisionary studies of the genus.

Figure 1

Area treated in the Flora of the Great Plains.



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TAXONOMIC HISTORY

The genus Penstemon has a rich taxonomic history, however, little effort has been directed here towards a comprehensive recounting of this history because of the floristic nature of this study and the fact that others have covered the subject. Rather, the reader is referred to studies by Pennell (1935) and Holmgren (1979c), as well as those revisionary studies cited in the introduction, for discussions at the sectional and infrasectional levels. The nomenclature associated with the genus is replete with synonomy, particularly at the infrageneric levels. In addition, the genus name was subjected to a rash of orthographic manipulation in the late 18th and early 19th century. Again, much information concerning this subject may be found in the previously mentioned works. A useful discussion of the orthographic variants of Penstemon can be found in a paper by Crosswhite (1967d).

The genus Penstemon was erected in 1741 by a British physician, John Mitchell, who resided in Virginia. Mitchell's Penstemon appeared in his paper, "Plantarum quaedam Genera recens condita et in Virginia observata", along with 20 additional new genera (Pennell, 1951). However, it was not until 1748 that the genus was published with a description in England, appearing in "Acta physico-medica academiae caesareae leopoldino-franciscanae naturae curiosorum exhibentia ephemerides sive observationes historias et experimentat". This paper was reprinted verbatim in Nova Genera Plantarum Virginiensium 36, in 1769 (Pennell, 1951).

Linneaus (1753), in his Species Plantarum, did not recognize Mitchell's genus Penstemon. Instead he used the name as a specific epithet in the genus Chelone. Linneaus modified the orthography by adding a "t" after the first syllable "Pen-", and it is this orthographic variant that was extensively utilized in many American floras until Pennell (1935) argued that the

original spelling, though not etymologically correct, was chosen deliberately by Mitchell and was therefore appropriate. Pennell suggested Mitchell's name was derived from the Greek "penta", five, and "stemon", stamen; an apparent allusion to the staminode as a fifth stamen. Straw (1966) offered an alternate interpretation, suggesting the prefix "paene", meaning almost, might have been intended by Mitchell and that subsequent "corrections" were based on etymological misinterpretations.

In 1763, Schmidel carefully described the genus Penstemon on page 2 of the introduction to his Icones Plantarum. His description was that of Penstemon laevigatus Solander (Chelone pentstemon L.).

In the beginning of the 19th century, most botanists working in North America recognized Penstemon and Chelone as distinct genera, as was the case in Michaux's Flora Boreali-Americana (1803). Pursh, in his Flora Americae Septentrionalis (1814), included 7 species in Penstemon, 4 of them from the Missouri River valley and collected by Bradbury on his trip up the river in 1811 with Thomas Nuttall. In 1818, Nuttall published The Genera of North American Plants in which he recognized 9 species of Penstemon, 6 from his 1811 trip up the Missouri River.

Between 1820 and 1870, numerous botanical expeditions into the western United States resulted in the discovery and naming of a great number of new species of Penstemon. Bentham included a number of these in his treatment of the genus in DeCandolle's Prodromus Systematis Naturalis Regni Vegetabilis (1846). In this work, he listed 54 species.

In 1878, Asa Gray published his Synoptical Flora of North America in which he listed 71 species and numerous varieties of Penstemon. This number was increased to 82 species and 30 varieties with his second edition published in 1886. Most of these species were from the western United States.

The last comprehensive treatment of the genus was carried out by Krautter (1908). This treatment included 148 species and 35 varieties.

Since Krautter's study, Penstemon has been studied by a great many individuals, the most productive of whom are listed in the introduction. A tally by Holmgren (1979b) indicates that the genus consists of some 280 species, with undoubtedly more to be discovered. Additionally, much of the genus has never been critically examined, such as the particularly enigmatic Section Coerulei. And still the most monumentous task of all, a comprehensive treatment of the genus, awaits some ambitious soul.

CHROMOSOMAL STUDIES

Introduction. The first chromosome counts for Penstemon were reported by Winge (1925) and included 8 species. Since these initial counts, sporadic reports of chromosome numbers for Penstemon species have been the rule, typically found as inclusions in cytological studies of various floras. There have been, however, a handful of cytological studies dealing exclusively with the genus (e.g. Clausen et al., 1940; Keck, 1945; Nisbet & Jackson, 1960; and Crosswhite & Kawano, 1965). These studies have made important contributions to the knowledge of chromosome numbers of numerous species, yet relatively little insight has been gained into the cytological relationships of species or higher taxonomic groups in the genus as a whole.

Put mildly, the genus Penstemon lacks the cytological flair exhibited by many other genera, especially when one considers its size. Penstemon has a base number $x = 8$. Polyploidy is relatively uncommon and restricted to three sections of the genus. Counts for about one-half of the species in the genus have been reported.

Materials and Methods. Bud material for meiotic counts was collected in the field, fixed in modified Carnoy's solution (4 parts chloroform: 3 parts absolute ethanol: 1 part glacial acetic acid, v/v/v) and subsequently refrigerated in the fixative until used. Counts were made from microsporocytes using the aceto-carmine squash technique (Turner & Johnston, 1962). Semi-permanent slides were made by applying Krönig cement to the periphery of the cover slips.

Mitotic counts were also obtained for a number of populations. Seeds were collected in the field or taken from herbarium specimens and placed on moist filter paper in petri dishes at room temperature. At the outset, it was found that germination success was exceedingly low for most taxa and

thus another method was developed. This involved placing seeds on moist filter paper in petri dishes for 1 to 4 days, after which time embryos of selected seeds were removed from the seeds and replaced on the moist filter paper. Elongation of root tips generally followed in 1 to 2 days and was allowed to proceed until the tips attained a length of 2 to 4 mm, whereupon the seedlings were submerged in a saturated aqueous solution of paradichlorobenzene (PDB) for 90 minutes at room temperature. The root tips were subsequently excised from the seedlings and placed in a watch glass containing 9 drops of 2% aceto-orcein and 1 drop of 1N HCl (Tijo & Levan, 1950). The watch glass was then heated over a steam bath until a puff of vapor was seen to rise from the stain (ca 4 seconds). Root tips were then placed on a slide and cover-slipped. Initially, a slight amount of pressure was applied by tapping the cover slip to facilitate spreading of root tip cells, followed by firm pressure to squash the material. Semi-permanent slides were made using the same procedure outlined for meiotic preparations.

Camera lucida drawings were made of all meiotic and mitotic counts (Figures 2-23) using a Zeiss Universal microscope at a magnification of 2000x. Voucher specimens have been deposited in the Kansas State University Herbarium, or in the case of some herbarium specimens used as seed sources for mitotic counts, at the designated herbaria.

Results. Seventy-four populations of Penstemon were examined for chromosome number (Table 1). Counts obtained were from 20 species and include the first known counts for the following taxa: P. albidus, P. angustifolius var. angustifolius, P. auriberbis, P. buckleyi, P. cobaea var. purpureus, P. fendleri, P. haydeni, and P. oklahomensis. All new counts are $n = 8$ or $2n = 16$ and counts for the additional species are consistent with previously reported counts for Great Plains taxa given in Table 2.

Discussion. Initially, it was hoped that a cytotaxanomic study of the Great Plains species of Penstemon might help elucidate the relationships between the various taxa of the region. Even though some contributions were made and a few insights gained, no great revelations resulted from the study.

Chromosome numbers proved to be of little assistance in understanding the relationships of most Great Plains Penstemons. A case in point is Section Coerulei, particularly Penstemon angustifolius var. angustifolius, Penstemon angustifolius var. caudatus, Penstemon buckleyi, and Penstemon nitidus var. nitidus. The relationship of these taxa has long been something of an enigma to taxonomists and chromosome counts merely confirm that they may be closely related, for all have haploid numbers of 8.

Cytological data have, on the other hand, provided some insight into the relationship of certain members of Section Penstemon. Winge (1925) was the first to report the chromosome number of the dodecaploid Penstemon digitalis ($2n = 96$) and was somewhat astonished by the level of polyploidy exhibited by this species. La Cour (1931) later reported Penstemon laevigatus also to be a dodecaploid. Pennell (1935), in his treatise on the eastern temperate North American Scrophulariaceae, considered Penstemon tubaeflorus to be closely allied and derived from the open-flowered species of Penstemon from the eastern United States, Series Penstemon of Crosswhite (1965c), which included Penstemon digitalis, P. tenuis, P. calycosus, P. alluviorum, P. laevigatus, and P. deamii. Keck (1945) also found the dodecaploid nature of Penstemon digitalis to be remarkable and alluded to the possible amphiploid origin of the species. Subsequently, Crosswhite and Kawano (1965) reported an additional dodecaploid, Penstemon calycosus, and in the same paper, reported the first counts for Penstemon tubaeflorus, finding it to be a tetraploid ($2n = 32$).

In light of this information, Pennell's contention that Penstemon tubaeflorus was derived from the open-flowered Penstemons seems highly unlikely. Rather, chromosomal data suggest Penstemon digitalis, P. calycosus, and P. laevigatus to be more advanced than P. tubaeflorus. While chromosome counts have not been reported for Pennell's other three open-flowered species (i.e. Penstemon deamii, P. alluviorum, and P. tenuis), several scenarios might be proposed to explain the evolution of the dodecaploid species.

First, species of Series Penstemon may be viewed as a complex having evolved from a common dodecaploid ancestor. Such an ancestral species might have, for example, arisen if Penstemon tubaeflorus ($2n = 32$) hybridized with a diploid species ($2n = 16$) to produce a triploid F_1. If chromosome doubling followed, a hexaploid species could have resulted. An additional doubling event could have yielded a dodecaploid. Such a scenario would lend credence to Bennett's (1963b) treatment of these open-flowered species as subspecies of Penstemon laevigatus. Secondly, these open-flowered species might have arisen independently but by means similar to that outlined in the first scenario.

Whatever the evolutionary pathway by which the dodecaploid species of Series Penstemon arose, multivalent associations in metaphase I reported by Winge (1925) and Keck (1945) suggest, in Keck's words, "considerable cytological relationship between the parental chromosomes". Such mutivalent associations have also been reported as common in polyploids of Subsection Proceri by Keck (1945).

A perusal of the reported chromosome numbers in Penstemon draws immediate attention to the cytological conservativeness exhibited by the genus. Keck (1945) was the first to point out this fact, noting the restriction of polyploidy to three sections. A tabulation of existing data shows polyploidy is encountered only in Sections Penstemon (in Subsections Penstemon,

Porceri, and Humiles), Saccanthera (in Subsection Saccanthera), and Bridgesiani. One polyploid count is reported in Section Cristati for Penstemon cobaea (2n = 64; Piotrowska, 1934), however this count is questionable. All subsequent counts indicate this species to be a normal diploid. Keck (1945) was of the opinion that the conservative chromosomal trend exhibited by Penstemon was indicative of the genus being genetically young. He also contended the genus was in the initial phases of species building through the process of amphiploidy, however, this has not yet been demonstrated.

To this point in time, cytological studies in the genus have been most productive at the generic level. Chromosome counts, in combination with careful studies of floral anatomy and gross morphology, have led to the recognition of three generic segregates. These segregates include Keckiella (Straw, 1966, 1967) with 7 species and n = 8, Nothochelone (Straw, 1966) with one species and n = 15, and Pennellianthus (Crosswhite & Kawano, 1970) with one species and n = 20.

Future cytotaxonomic studies of Penstemon have several potentially useful and virtually untapped sources from which phylogenetic information might be drawn. These sources include karyotypic and hybridization studies. It was noted in this study that the chromosomes of Penstemon are usually metacentric to submetacentric in morphology, however, noticeable differences exist in the average size of chromosomes from one karyotype to another (e.g. Fig. 10 and Fig. 11). These size differences were not found to be associated with sectional trends, but more refined studies might reveal such trends. Hybridization studies would appear to offer much in the elucidation of phylogenetic relationships in the genus. Limited studies of hybridization in the genus suggest that internal isolation mechanisms among species are possibly uncommon. The examination of hybrid meiotic figures could shed much light on phylogenetic relationships in the genus.

Table 1

CHROMOSOME COUNTS FOR GREAT PLAINS SPECIES OF *PENSTEMON*

Taxon	Locality & Voucher	n	2n
*Penstemon albidus**	COLORADO. Baca Co.: 3 mi W of Saunders, KS. *Freeman 475*.	8_{II}	
"	COLORADO. Las Animas Co.: 7 mi N & 3.5 mi W of Andrix. *Freeman 480*.	8_{II}	
"	KANSAS. Grant Co.: NW of Moscow & 1.5 mi S of the Cimarron River along US 270 & 25. *Freeman 140*.	8	
"	KANSAS. Meade Co.: 60 yds W of the Clark Co. Line along US 160. *Freeman 442*.	8	
"	NORTH DAKOTA. Dunn Co.: N of Richardton. *O.A. Stevens s.n.* (NDA)		16
"	TEXAS. Cottle Co.: 10 mi S of Childress along US 62 & 83. *Freeman & Wetter 372*.		16
"	TEXAS. Cottle Co.: 11.7 mi mi NW of jct Farm Rd 1440 & US 62 & 83. *Freeman & Wetter 372*.	8	
"	TEXAS. Motley Co.: ca 2 mi of jct Farm Rds 94 & 1440. *Freeman & Wetter 373*.	8	
Penstemon ambiguus var. *ambiguus*	COLORADO. Yuma Co.: 3.5 mi S of Phillips Co. Line along US 385. *Freeman 507*.		16
"	KANSAS. Kearney Co.: 11.1 mi SW of Lakin along State 25. *Freeman 141*.	8	
"	KANSAS. Morton Co.: Cimarron Nat. Grasslands S of the Cimarron River along State 27. *Freeman 100*.	8	

Table 1 - Continued

Taxon	Locality & Voucher	n	2n
Penstemon ambiguus var. ambiguus (continued)	KANSAS. Morton Co.: Cimarron Nat. Grassland S of Cimarron River along State 27. Freeman 138.	8	
"	NEW MEXICO. Quay Co.: 0.5 mi N of Logan. Stephens 79848. (KANU)		16
Penstemon angustifolius var. angustifolius*	WYOMING. Laramie Co.: 9.7 mi S of Goshen Co. Line along US 85. Freeman 567.		16
"	WYOMING. Laramie Co.: 8.4 mi NE of jct US 85 & I-25. Freeman 569.		16
"	WYOMING. Laramie Co.: 6 mi N of Carpenter. C.L. Porter & M.W. Porter 7677. (RM)		16
Penstemon angustifolius var. caudatus	COLORADO. Huerfano Co.: Lathrop State Park W of Walsenburg. Freeman 433.	8_{II}	
"	COLORADO. Las Animas Co.: 2.5 mi N of Trinidad along I-25. Freeman 434.		16
"	COLORADO. Pueblo Co.: 4.7 mi W of Otero Co. Line along State 10. Freeman 485.		16
"	COLORADO. Yuma Co.: 3.5 mi S of Phillips Co. Line along US 385. Freeman 508.		16
"	NEW MEXICO. Colfax Co.: 1.3 mi E of Springer along US 56. Freeman 432.	8	16
"	NEW MEXICO. Union Co.: 5 mi E of Folsom along State 325. Freeman 437.	8	

Table 1 - Continued

Taxon	Locality & Voucher	n	2n
Penstemon auriberbis*	COLORADO. Las Animas Co. 7 mi N & 2 mi W of Andrix. Freeman 477.	8	16
"	COLORADO. Pueblo Co.: 3.1 mi S of State 165 along I-25. Freeman 487.	8	
Penstemon buckleyi*	KANSAS. Barber Co.: 5.2 mi S of Sayer along US 281. Freeman 381.		16
"	KANSAS. Kiowa Co.: 0.8 mi E of Greensburg along US 54. Freeman 445.		16
"	KANSAS. Meade Co.: 60 yds W of Clark Co. Line along US 160. Freeman 443.	8_{II}	
"	OKLAHOMA. Greer Co.: Quartz Mountain State Park NE of Magnum. Freeman & Wetter 358.	8	
Penstemon cobaea var. cobaea	KANSAS. Ellsworth Co.: 0.9 mi W of CK Ranch & 2 mi S of old US 40. Freeman 327.		16
"	KANSAS. Pottawatomie Co.: E edge Tuttle Creek State Park along State 13. Freeman 897.	8	
"	OKLAHOMA. Jefferson Co.: 15.5 mi E of Waurika along US 70. Freeman & Wetter 342.	8	
"	OKLAHOMA. McClain Co.: Johnson's Pasture. F. Thomas s.n. (KANU)		16
"	OKLAHOMA. Osage Co.: W of Skiatook along State 20. Freeman 417.	8	

Table 1 - Continued

Taxon	Locality & Voucher	n	2n
Penstemon cobaea var. cobaea (continued)	TEXAS. Foard Co.: 26 mi E of Paducah along Farm Rd 654. Freeman 417.		16
Penstemon cobaea var. purpureus*	OKLAHOMA. Bryan Co.: 0.7 mi N of Matoy. Freeman 413.		16
Penstemon digitalis	KANSAS. Neosho Co.: 2 mi E of Erie at the Erie Country Club. Freeman 123.	48	
"	KANSAS. Pottawatomie Co.: E edge of Tuttle Creek State Park along State 13. Freeman 321.		96
"	KANSAS. Pottawatomie Co.: E edge of Tuttle Creek State Park along State 13. Freeman 388.	48	
"	MISSOURI. Johnson Co.: 2 mi W of Warrensburg along US 50. Freeman & Wetter 452.	48	96
Penstemon eriantherus var. eriantherus	SOUTH DAKOTA. Mellette Co.: 10 mi W of Cedar Butte. Stephens 49342. (KANU)		16
"	WYOMING. Platte Co.: Guernsey State Park NW of Guernsey. Freeman 564.		16
Penstemon fendleri*	NEW MEXICO. Quay Co.: 5.2 mi W of Curry Co. Line along State 18 & 88. Freeman 425.	8	
"	NEW MEXICO. Quay Co.: 9.8 mi S of Tucumcari along State 18. Freeman 438.	8	
"	OKLAHOMA. Jackson Co.: N edge of Eldorado along State 44. Freeman & Wetter 355.	8	

Table 1 - Continued

Taxon	Locality & Voucher	n	2n
Penstemon glaber var. glaber	WYOMING. Campbell Co.: 12.9 mi N of Converse Co. Line along State 59. Freeman 555.		16
"	WYOMING. Crook Co.: 1.25 mi E of main entrance to Devil's Tower Nat. Monument. F.S. & C.D. Crosswhite s.n. (RM)		16
Penstemon gracilis var. gracilis	NEBRASKA. Cherry Co.: 1.2 mi E of Nenzel along US 20. Freeman 172.	8	
"	NORTH DAKOTA. Dunn Co.: 10 mi W & 0.5 mi N of Killdeer. Freeman 213.		16
"	NORTH DAKOTA. Emmons Co.: 9.1 mi N of South Dakota State border along US 83. Freeman 226.	8	
"	WYOMING. Crook Co.: 3.7 mi N of Key Hole State Park. Freeman 544.	8_{II}	
Penstemon grandiflorus	IOWA. Bremer Co.: N edge of Waverly along the Cedar River. Freeman 7869. (WET)		16
"	KANSAS. Kiowa Co.: 3.3 mi W of Greensburg along US 54. Freeman 444.	8	
"	KANSAS. Pottawatomie Co.: E side of Tuttle Creek Reservoir 1.5 mi N of Carnahan Cove. Freeman 40.	8_{II}	
"	KANSAS. Pottawatomie Co.: E side of Tuttle Creek Reservoir 1 mi N of Carnahan Cove. Freeman 41.		16
"	NEBRASKA. Buffalo Co.: 4 mi S & 2 mi W of Ravenna. Luce s.n. (*KNSC)		16

Table 1 - Continued

Taxon	Locality & Voucher	n	2n
Penstemon grandiflorus (continued)	NEBRASKA. Sheridan Co.: 0.6 mi E of Clinton along US 20. Freeman 527.		16
"	SOUTH DAKOTA. Gregory Co.: 9 mi N & 9 mi E of Gregory. Smith 40. (SDU)		16
Penstemon haydeni*	NEBRASKA. Hooker Co.: 3.7 mi N of McPherson Co. Line along State 97. Freeman 522.	8	16
Penstemon jamesii	NEW MEXICO. Quay Co.: 9.8 mi S of Tucumcari along State 18. Freeman 427.	8	16
Penstemon laxiflorus	OKLAHOMA. Carter Co.: N edge of Dickson along US 177. Freeman 408.	8	
"	OKLAHOMA. Cleveland Co.: 0.4 mi S of State 9 along 120th Ave in Norman. Freeman 399.		16
"	OKLAHOMA. Marshall Co.: 3 mi N of Woodville. Freeman 410.	8	
Penstemon nitidus var. nitidus	SOUTH DAKOTA. Butte Co.: Shepherd's Monument NE of Belle Fourche along US 85. Freeman 202.		16
Penstemon oklahomensis*	OKLAHOMA. Bryan Co.: 0.25 mi NE & 1 mi E of Caddo. Taylor & Wright 24873. (OKL)		16
Penstemon pallidus	KANSAS. Douglas Co.: 1 mi S of Baldwin City in Baldwin City Cemetary. Freeman 389.		16
"	KANSAS. Wilson Co.: 3.5 mi S of Altoon along US 85. Freeman 390.	8_{II}	

Table 1 - Continued

Taxon	Locality & Voucher	n	2n
Penstemon tubaeflorus var. tubaeflorus	KANSAS. Cloud Co.: 10 mi W & 1 mi N of Miltonvale along US 24. Freeman 605.	16	
"	KANSAS. Coffey Co.: 1.5 mi E of Gridley along State 57. Freeman 118.	16	
"	KANSAS. Harper Co.: 3.5 mi E of Attica along US 160. Freeman 133.	16	
"	KANSAS. Lincoln Co.: 2 mi W of Lincoln along State 18. Freeman 151.	16	
"	KANSAS. Ottawa Co.: 3.5 mi S of Minneapolis along State 106. Freeman 153.	16	
"	KANSAS. Pottawatomie Co.: E edge of Tuttle Creek State Park along State 13. Freeman 155.	16	
"	KANSAS. Wilson Co.: 4.7 mi E of Fall River along State 96. Freeman 96.	16	
"	MISSOURI. Bates Co.: 1 mi N of Butler along US Business 71. Freeman & Wetter 463.	16	
Penstemon virens	COLORADO. Larimer Co.: 5.8 mi W of Poudre Park along State 14 & 0.5 mi S. Freeman 586.	8	
"	WYOMING. Albany Co.: 4.9 mi N of Colorado State border along US 287. Freeman 579.		16

* indicates first reported count for taxon

Table 2

PUBLISHED CHROMOSOME COUNTS FOR GREAT PLAINS SPECIES OF *PENSTEMON**

Taxon	n	2n	Reference
Penstemon ambiguus var. *ambiguus*	8		Nisbet & Jackson, 1960
Penstemon angustifolius var. *caudatus*	8		Nisbet & Jackson, 1960
Penstemon cobaea		64	Piotrowska, 1934
	8		Smith, 1964
Penstemon digitalis	48		Winge, 1925 (*P. laevigatus* var. *digitalis*)
		96	Crosswhite & Kawano, 1965
Penstemon eriantherus		16	La Cour (by Darlington), 1945 (*P. cristatus*)
Penstemon glaber var. *glaber*	8		Winge, 1925, (*P. gordoni*)
Penstemon glaber var. *alpinus*	8		Clausen *et al.*, 1940
Penstemon glaber var. *brandegei*	8		Nisbet & Jackson, 1960 (*P. alpinus* ssp. *brandegei*)
Penstemon gracilis var. *gracilis*		16	Keck, 1945
		16	Crosswhite & Kawano, 1965
Penstemon grandiflorus		16	Crosswhite & Kawano, 1965
Penstemon jamesii	8		Nisbet & Jackson, 1960
Penstemon laxiflorus		16	Crosswhite & Kawano, 1965
Penstemon nitidus	8_{II}		Taylor & Brockman, 1966
Penstemon pallidus		16	Crosswhite & Kawano, 1965
Penstemon procerus var. *procerus*	8	16,32	Clausen *et al.*, 1940
	8	32	Keck, 1945
		16,32	Taylor & Brockman, 1966
	8		Taylor, 1967
Penstemon secundiflorus	8	16	Clausen *et al.*, 1940
	8		Nisbet & Jackson, 1960

Table 2 - Continued

Taxon	n	2n	Reference
Penstemon tubaeflorus		32	Crosswhite & Kawano, 1965
Penstemon virens	8		Clausen et al., 1940
	8_{II}		Keck, 1945
		16	Wiens & Halleck, 1962

* names in parentheses are those used by authors and considered synonyms herein.

Figures 2-9

Camera lucida drawings of meiotic and mitotic chromosomes of Penstemon. All drawings are at a scale of ca 2000x.

2. P. albidus, mitotic metaphase, Stevens s.n., 2n = 16.

3. P. cobaea var. purpureus, mitotic metaphase, Freeman 413, 2n = 16.

4. P. angustifolius var. caudatus, mitotic metaphase, Freeman 485, 2n = 16.

5. P. angustifolius var. angustifolius, mitotic metaphase, Freeman 569, 2n = 16.

6. P. auriberbis, mitotic metaphase, Freeman 477, 2n = 16.

7. P. pallidus, diakinesis, Freeman 390, n = 8_{II}

8. P. cobaea var. cobaea, mitotic metaphase, Freeman 417, 2n = 16.

9. P. ambiguus var. ambiguus, metaphase II, Freeman 138, n = 8.

(2)

(3)

(4)

(5)

(6)

(7)

(8)

(9)

Figures 10-17

Camera lucida drawings of meiotic and mitotic chromosomes of Penstemon. All drawings are at a scale of ca 2000x.

10. P. eriantherus var. eriantherus, mitotic metaphase, Stephens 49342, 2n = 16.

11. P. oklahomensis, mitotic metaphase, Taylor & Wright 24873, 2n = 16.

12. P. gracilis var. gracilis, mitotic metaphase, Freeman 213, 2n = 16.

13. P. glaber var. glaber, mitotic metaphase, Freeman 555, 2n = 16.

14. P. nitidus var. nitidus, mitotic metaphase, Freeman 202, 2n = 16.

15. P. grandiflorus, mitotic metaphase, Luce s.n., 2n = 16.

16. P. jamesii, anaphase I, Freeman 427, n = 8.

17. P. virens, anaphase II, Freeman 586, n = 8.

(10)

(11)

(12)

(13)

(14)

(15)

(16)

(17)

Figures 18-23

Camera lucida drawings of meiotic chromosomes of Penstemon. All drawings are at a scale of ca 2000x.

18. P. tubaeflorus var. tubaeflorus, metaphase II, Freeman 118, n = 16.

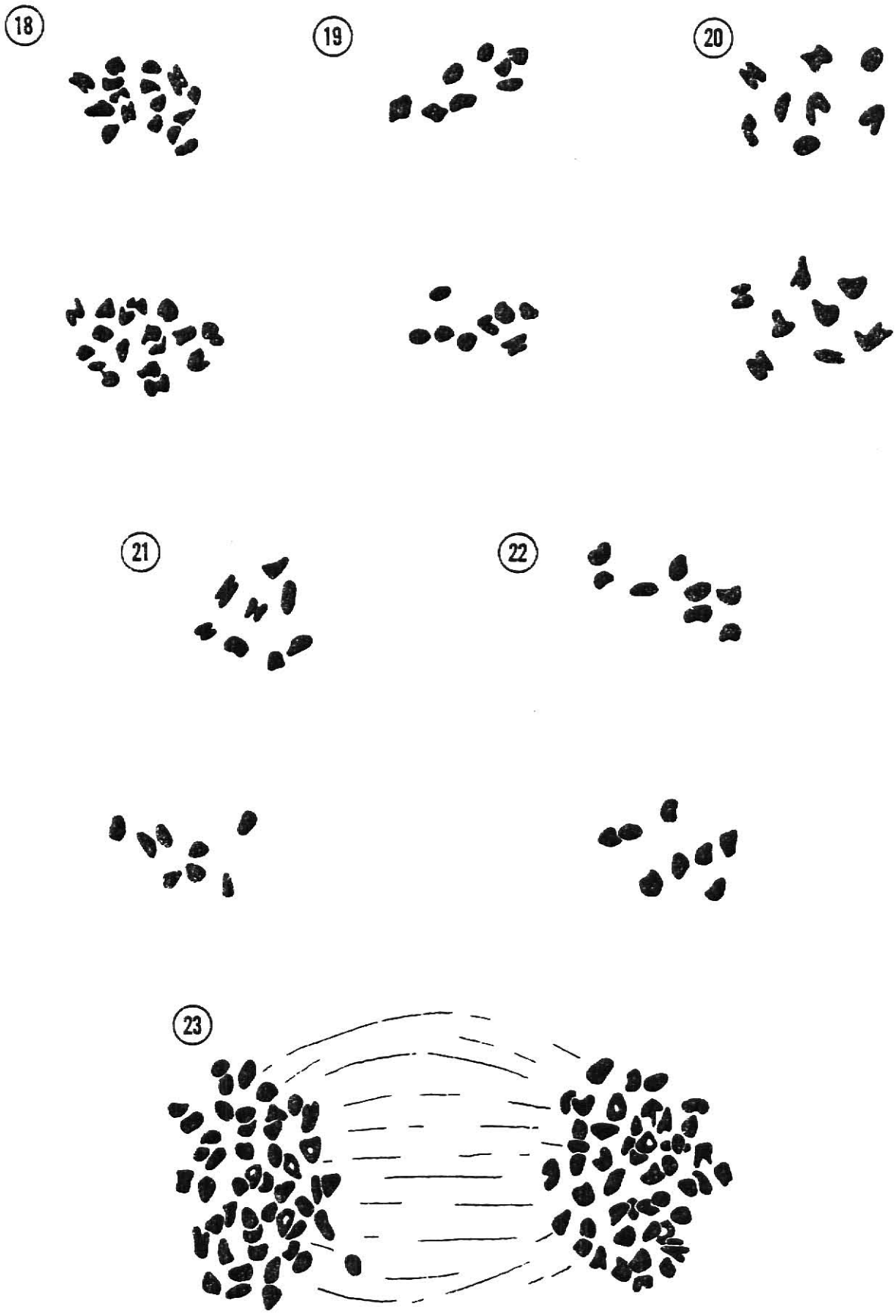
19. P. haydeni, anaphase I, Freeman 522, n = 8.

20. P. fendleri, anaphase I, Freeman 355, n = 8.

21. P. laxiflorus, anaphase I, Freeman 410, n = 8.

22. P. buckleyi, anaphase I, Freeman & Wetter 358, n = 8.

23. P. digitalis, anaphase I, Freeman 388, n = 48.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CHROMATOGRAPHIC STUDIES

Introduction. The use of paper chromatography as an approach to resolve problems in plant systematics has been in vogue since it was dramatically demonstrated by Alston and Turner (1959, 1963a) in their study of interspecific hybridization in the genus Baptisia. Their pioneering study initiated an avalanche of similar investigations in many groups of plants, and the popularity of this approach continues.

The use of chromatographic data as a systematic tool was untested in Penstemon prior to the initiation of this study. For this reason, an investigation of comparative phenolic profiles for Great Plains representatives of the genus was undertaken to ascertain the technique's potential in elucidating sectional affinities and species relationships.

Materials and Methods. Bulk material was collected by the author in the field and allowed to air dry. After drying, ca 3 gm of leaf and stem material was ground to a fine powder in a Waring blender. Phenolic compounds were extracted in 25 ml of absolute methanol for ca 5 hours and the plant material then removed from the extract by filtration. Re-extraction was carried out two additional times whereupon the plant material was discarded and the extracts for the sample combined. The solvent was then removed using a rotary evaporator under air pump vacuum, leaving a viscous green or yellow residue, which was refrigerated overnight. The residue was filtered to remove much of the remaining chlorophyll and used directly or refrigerated at 0° C until used.

Phenolic extracts were spotted on pre-washed 46x57 cm Whatman 3 MM chromatography paper. Pre-washing of the paper involved running excess 15% glacial acetic acid in water through and off of the paper by normal descending chromatography. This process was normally carried out overnight

but could be accomplished in as little as 6 hours. After pre-washing, the paper was allowed to dry thoroughly.

Phenolics were separated by standard procedures for 2-dimensional descending paper chromatography (Mabry et al., 1970). Initial development was in the 57 cm direction and employed 3 parts t-butanol: 1 part glacial acetic acid: 1 part distilled water, v/v/v (TBA), as the solvent system. Development required from 18 to 25 hours. The paper was again allowed to dry thoroughly. Development in the 46 cm direction utilized 15% glacial acetic acid (HOAc) in water for ca 4 hours. The paper was again dried upon completion of development.

Chromatograms were viewed under ultraviolet light (U.V.) and the spots outlined. Under U.V. light, phenolic compounds appeared pale to deep purple, fluorescent blue, fluorescent green, or pink. Chromatograms were also exposed to NH_3 vapors under U.V. and any color changes noted. R_f values (distance between origin and greatest concentraction of spot divided by the distance between the origin and the solvent front) were computed for each spot in each of the two solvents.

Results. Thirty-nine populations distributed among 20 species were examined chromatographically for phenolic compounds (Table 3). Spots recognized in the species examined for phenolic compounds are listed in Table 4, along with each spot's color in U.V. light and U.V. light + NH_3 vapors, as well as R_f values in TBA and HOAc. Spots are numbered for convenience and a total of 46 spots are recognized.

It was found upon examination of the chromatograms that masses of fluorescent blue and green spots frequently appeared near the solvent front and in most cases were not distinct enough to permit analysis. Thus, spots appearing purple in U.V. light received the most scrutiny. However, a

number of spots appearing pink, tan, and blue in U.V. light and positioned well behind the solvent front were included in the analysis.

Table 5 presents the distribution of spots recognized. A composite 2-dimensional paper chromatographic pattern of all spots recognized is given in Figure 24. Patterns for individual species follow in Figures 25-45.

Discussion. It was hoped that an examination of phenolic patterns in Great Plains species of Penstemon might help elucidate sectional and species relationships. While the technique did not result in an overabundance of revelations, it does appear that chromatographic studies of the genus hold potential, particularly if coupled with the identification of compounds.

As a result of this superficial survey, it was found that phenolic profiles substantiate sectional integrity previously inferred from morphological studies and to a lesser extent, cytological studies. Representatives of 5 sections of the genus Penstemon were examined (Section Ambigui - 1 species, Section Cristati - 5 species, Section Coerulei - 7 species, Section Penstemon - 6 species, and Section Glabri - 1 species). Although two of the sections were represented by a single species each, it appears that each of the sections exhibited distinctive phenolic distributions that delimited the sections fairly well.

Phenolic patterns did provide some information concerning species relationships as a number of species could be recognized on patterns alone. Compounds 17, 29, and 46 were found to be present in representatives of all sections examined. Other compounds were found to be section-specific (e.g. compounds 32 and 34 in Section Ambigui) or species-specific (e.g. compound 4 in P. auriberbis).

In P. ambiguus var. ambiguus of Section Ambigui (Figure 25), 11

compounds were recognized. Compounds 32 and 34 were unique to this species, but could be present in other species of the section that were not examined.

Section Cristati, represented by 5 species, showed a greater diversity of compounds than any other section examined (Figures 26-30). Twenty-nine different spots were recognized. In this section, compounds 26 and 35 were unique to the section and found in two or more species. In addition, other species-specific compounds were found only in members of this section. These included compounds 4, 19, and 30 (in P. auriberbis), 14 (in P. jamesii), 27 (in P. cobaea var. cobaea), and 38 (in P. eriantherus var. eriantherus).

Overall, the section showed cohesiveness as a natural unit with compounds 15, 17, and 29 common to all species in the section. The absence of compound 46 from 3 of the 5 members of the Cristati also appeared to be diagnostic.

Section Coerulei showed the least diversity of compounds of the sections examined when one considers the average number of compounds per species (Figures 31-38). In this section, 7 species were examined with a total of 18 compounds recognized for an average number of compounds per species of 9.4.

Gornall and Bohm (1978), in a summary article, emphasized the rather well documented fact that one of the major trends in angiosperm flavonoid evolution is one of reduction both in number of flavonoid classes and structural complexity from primitive to advanced taxa. They indicated this reduction trend has been demonstrated with a wide range of taxa at a multitude of taxonomic levels within the taxonomic hierarchy of the plant kingdom. Whether the reduction in phenolic compound diversity in the Coerulei is significant in terms of phylogenetic advancement remains to be seen.

As stated in the cytological section, the Coerulei are a taxonomically

difficult assemblage. Phenolic compounds bear this out as a close similarity of phenolic patterns in taxa examined was observed. Despite this fact, the examination of phenolic patterns did provide useful information in understanding certain species relationships in the section, particularly concerning P. angustifolius and P. buckleyi. Six populations of P. angustifolius var. angustifolius were examined and found to differ only with respect to the presence or absence of compound 31. A single population of P. angustifolius var. caudatus was examined and found to differ from the nomenclaturally typical variety in the absence of compounds 16 and 31. Penstemon buckleyi was found to exhibit a pattern which was quite distinct from that of either variety of P. angustifolius. Three populations of P. buckleyi were examined and all three lacked compounds 8 and 15, compounds found in all populations of P. angustifolius examined. Additionally, 2 compounds unreported in P. angustifolius were found in P. buckleyi, namely species-specific compounds 40 and 44. Thus, phenolic patterns verify the uniqueness of P. buckleyi.

One other point of interest concerns P. haydeni. A reasonable case for the post-Pleistocene hybrid origin of the species can be generated (see Taxonomic Treatment under P. haydeni). The two suspected parents (P. angustifolius and P. grandiflorus) have nearly identical phenolic patterns, however, P. haydeni displayed a pronounced loss of compounds, including numbers 6, 15, 16, and 20. It also exhibited compounds 37 and 45 which were not found in either of the suspected parents. The lack of an identical or nearly identical pattern in P. haydeni does not preclude consideration of this species as a hybrid between P. angustifolius and P. grandiflorus. Alston and Turner (1963b) indicated that established species of suspected hybrid origin may not necessarily exhibit the additive patterns that are often observed in recent hybrids, due to new genotypes resulting from

natural selection and mutation that may modify or obfuscate the additive hybrid pattern.

In Section Penstemon, represented by 6 species, a total of 25 compounds were recognized (Figures 39-44). The members of the section showed very little variation in phenolic patterns if the polyploid species P. digitalis and P. tubaeflorus are excluded. Patterns exhibited by P. gracilis var. gracilis, P. laxiflorus, P. oklahomensis, and P. pallidus were nearly identical, the species typically showing compounds 1, 9, 12, 15, 17, 28, 31, 37, 45, and 46. Patterns observed in the tetraploid P. tubaeflorus and dodecaploid P. digitalis differed radically from the patterns seen in the other members of the section. Both polyploid species had patterns that were roughly similar although P. digitalis had a number of species-specific compounds not found in any other species surveyed. These species-specific compounds included numbers 11, 13, 18, and 33. Species-specific compounds in P. tubaeflorus included numbers 5 and 7. The relationship of these two polyploid species to the other members of the section remains obscure, however, it is probable that an examination of the remaining species in Section Penstemon might shed some light on this subject.

The final section examined, Section Glabri, was represented by a single species (Figure 45). Eleven compounds were observed in this species, none of which were species-specific. Little can be said about possible phylogenetic ties with the other sections examined as more species need to be surveyed to characterize phenolic diversity in the section.

In summary, it can be said that phenolic studies in Penstemon have potential in elucidating phylogenetic relationships in the genus. Phenolic patterns of Great Plains representative of the genus demonstrate reasonably strong sectional integrity inferred primarily from morphological studies,

and also offer insight into certain species relationships in the genus. It is advisable that future phenolic studies take a populational approach and be tied with the identification of compounds.

Table 3

POPULATIONS OF *PENSTEMON* EXAMINED CHROMATOGRAPHICALLY FOR PHENOLIC COMPOUNDS

Taxon	Locality & Voucher
Penstemon albidus	TEXAS. Cottle Co.: 11.7 mi NW of jct Farm Rd 1440 & US 62 & 83. *Freeman 372*.
Penstemon ambiguus var. *ambiguus*	COLORADO. Yuma Co.: 3.5 mi S of Phillips Co. Line along US 385. *Freeman 507*.
Penstemon angustifolius var. *angustifolius*	COLORADO. El Paso Co.: Jct State 83 & Old Ranch Rd NE of Colorado Springs. *Freeman 494*.
"	NEBRASKA. Arthur Co.: 11.4 mi S of Arthur along State 61 & 92. *Freeman 518*.
"	NEBRASKA. Sheridan Co.: 2.4 mi E of Rushville along US 20. *Freeman 528*.
"	WYOMING. Converse Co.: 10.5 mi S Campbell Co. Line along State 59. *Freeman 558*.
"	WYOMING. Laramie Co.: 8.4 mi SE of jct US 85 and I-25. *Freeman 569*.
"	WYOMING. Weston Co.: 4.3 mi SE of Osage along US 16. *Freeman 537*.
Penstemon angustifolius var. *caudatus*	NEW MEXICO. Colfax Co.: 1.3 mi E of Springer along US 56. *Freeman 432*.
Penstemon auriberbis	COLORADO. Las Animas Co.: 7 mi N & 2 mi W of Andrix. *Freeman 477*.
"	COLORADO. Pueblo Co.: 3.1 mi S of State 165 along I-25. *Freeman 487*.
Penstemon buckleyi	KANSAS. Barber Co.: 5.2 mi S of Sayer along US 281. *Freeman 381*.
"	OKLAHOMA. Greer Co.: Quartz Mountain State Park NE of Magnum. *Freeman 358*.
"	TEXAS. Motley Co.: 5 mi W of Matador along US 62 & 70. *Freeman 421*.

Table 3 - Continued

Taxon	Locality & Voucher
Penstemon cobaea var. cobaea	OKLAHOMA. Jefferson Co.: 0.9 mi E & 3 mi N of Oscar along State 32. Freeman 415.
Penstemon digitalis	KANSAS. Pottawatomie Co.: E edge of Tuttle Creek State Park along State 13. Freeman 606.
"	MISSOURI. Johnson Co.: 2 mi W of Warrensburg along US 50. Freeman 452.
Penstemon eriantherus var. eriantherus	NEBRASKA. Dawes Co.: 5 mi SE of Sioux Co. Line along State 71 & 2. Freeman 530.
"	WYOMING. Converse Co.: 10.5 mi S Campbell Co. Line along State 59. Freeman 557.
Penstemon fendleri	OKLAHOMA. Jackson Co.: N edge of Eldorado along State 44. Freeman 355.
"	TEXAS. Briscoe Co.: 0.3 mi E jct State 86 & Farm Rd 599. Freeman 377.
Penstemon glaber var. glaber	WYOMING. Campbell Co.: 12.9 mi N of Converse Co. Line along State 59. Freeman 555.
Penstemon gracilis var. gracilis	NEBRASKA. Cherry Co.: 1.2 mi E of Nenzel along US 20. Freeman 526.
Penstemon grandiflorus	KANSAS. Riley Co.: 3 mi S & 2.5 mi E of Manhattan along County Rd 911. Freeman 608.
Penstemon haydeni	NEBRASKA. Hooker Co.: 3.7 mi N of McPherson Co. Line along State 96. Freeman 522.
Penstemon jamesii	NEW MEXICO. Quay Co.: 9.8 mi S of Tucumcari along State 18. Freeman 427.
Penstemon laxiflorus	OKLAHOMA. Cleveland Co.: 0.4 mi S of State 9 along 120th Ave in Norman. Freeman 399.

Table 3 - Continued

Taxon	Locality & Voucher
Penstemon laxiflorus (continued)	OKLAHOMA. Johnston Co.: 0.4 mi E of Carter Co. Line along US 70. Freeman 409.
"	OKLAHOMA. Marshall Co.: 3 mi N of Woodville. Freeman 410.
Penstemon nitidus var. *nitidus*	WYOMING. Campbell Co.: 15.8 mi N of Gillette along State 59. Freeman 549.
Penstemon oklahomensis	OKLAHOMA. Marshall Co.: 3 mi E of Kingston along US 70 & 0.25 mi S. Freeman 412.
"	OKLAHOMA. Osage Co.: 4.7 mi E of Hominy along State 20. Freeman 393.
Penstemon pallidus	KANSAS. Douglas Co.: 1 mi S of Baldwin City in Baldwin City Cemetary. Freeman 389.
"	KANSAS. Wilson Co.: 3.5 mi S of Altoon along US 85. Freeman 390.
"	MISSOURI. Johnson Co.: 1 mi NW of Warrensburg along US 50. Freeman 453.
Penstemon secundiflorus	COLORADO. Larimer Co.: 5.8 mi W of Poudre Park along State 14. Freeman 585.
"	COLORADO. Pueblo Co.: 3.1 mi S of State 165 along I-25. Freeman 488.
Penstemon tubaeflorus var. *tubaeflorus*	KANSAS. Pottawatomie Co.: E edge of Tuttle Creek State Park along State 13. Freeman 605.
"	MISSOURI. Bates Co.: 1 mi N of Butler along US Business 71. Freeman 463.

Table 4

SPOTS RECOGNIZED IN GREAT PLAINS SPECIES OF PENSTEMON EXAMINED FOR PHENOLIC COMPOUNDS

Spot	Color		Rf values	
	U.V.	$+NH_3$	TBA	HOAc
1	p	p	.12	.08
2	p	p	.16	.12
3	p	p	.08	.20
4	p	p	.12	.28
5	p	y	.13	.32
6	p	y	.11	.35
7	p	p	.15	.37
8	p	g	.12	.40
9	p	p	.13	.47
10	p	p	.08	.49
11	p	y	.15	.55
12	p	p	.16	.62
13	p	y	.16	.68
14	p	o	.15	.69
15	p	o	.21	.62
16	p	g	.25	.61
17	k	k	.29	.64
18	p	p	.30	.57
19	p	o	.26	.57
20	p	y	.23	.57
21	p	o	.19	.50
22	p	g	.24	.45
23	p	o	.21	.40
24	p	y	.24	.34
25	p	o	.24	.31
26	t	t	.20	.29
27	p	o	.21	.23
28	p	g	.25	.21
29	p	y	.22	.19
30	b	m	.21	.13
31	k	k	.16	.07
32	t	t	.25	.12
33	p	y	.26	.14
34	p	p	.26	.16
35	b	m	.30	.20
36	p	o	.32	.26
37	p	o	.31	.32
38	k	k	.33	.44
39	p	o	.32	.46
40	p	g	.34	.46
41	p	o	.36	.50
42	b	m	.39	.49

Table 4 - continued

Spot	Color		Rf values	
	U.V.	$+NH_3$	TBA	HOAc
43	p	o	.40	.42
44	p	y	.36	.18
45	p	o	.39	.12
46	p	g	.40	.06

Key to color abbreviations:

p = purple
o = purple-olive
y = yellow
g = green
k = pink
t = tan
b = blue
m = mint-green

Table 5

DISTRIBUTIONS OF SPOTS RECOGNIZED IN GREAT PLAINS POPULATIONS OF PENSTEMON

EXAMINED FOR PHENOLIC COMPOUNDS

Spot \ Pop.	amb 507	alb 372	aur 477	" 487	cob 415	eri 530	" 557	jam 427	ana 494	" 518	" 528	" 558	" 569	" 537	anc 432	buc 381	" 358	" 421	fen 355	" 377	grn 608	hay 522	nit 549	sec 585	" 488	dig 606	" 452	grc 526	lax 399	" 409	" 410	okl 412	" 393	pal 389	" 390	" 453	tub 605	" 463	gla 555
1	X					X	X																			X	X		X	X	X	X	X	X	X	X			
2	X		X	X	X	X	X																																
3																										X											X	
4			X	X																																		
5																																					X	
6	X	X				X	X		X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X													X
7																																				X	X	
8		X				X	X		X	X	X	X	X	X	X									X														X
9																												X	X	X	X	X	X	X	X	X		X
10		X			X																				X													
11																										X	X											
12					X																			X				X	X	X	X	X	X	X	X	X		
13																										X	X											
14								X																														
15		X	X	X	X	X	X	X	X	X	X	X	X	X	X						X		X	X	X	X	X		X	X	X	X	X	X	X	X	X	X
16	X								X	X	X	X	X	X		X		X			X																
17	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X	X	X	X	X		X	X		X
18																										X	X											
19			X	X																																		
20	X								X	X	X	X	X	X	X	X	X	X	X	X	X		X															
21																										X	X									X	X	
22																				X	X			X	X													
23			X	X																						X	X									X	X	
24	X								X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X													
25			X	X				X																		X	X											

Table 5 - Continued

Spot \ Pop.	amb 507	alb 372	aur 477	" 487	cob 415	eri 530	" 557	jam 427	ana 494	" 518	" 528	" 558	" 569	" 537	anc 432	buc 381	" 358	" 421	fen 355	" 377	grn 608	hay 522	nit 549	sec 585	" 488	dig 606	" 452	grc 526	lax 399	" 409	" 410	okl 412	" 393	pal 389	" 390	" 453	tub 605	" 463	gla 555
26						X		X																														
27					X																																	
28		X				X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X	X	X	X	X	X	X	X			X
29	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X											X
30				X																																		
31		X	X	X		X	X				X	X		X		X	X		X	X			X	X	X			X	X	X	X	X	X	X	X	X			X
32	X																																						
33																										X	X												
34	X																																						
35			X	X	X	X	X																																
36			X	X	X																					X	X										X	X	
37			X	X	X		X	X														X		X		X	X	X	X	X	X	X	X	X	X	X	X	X	X
38						X																																	
39			X	X	X			X																		X	X												
40																		X																					
41								X																		X	X										X	X	
42						X	X																																X
43			X	X				X																		X	X												
44																	X	X																					
45								X															X					X	X	X	X	X	X	X	X	X			
46		X				X	X	X		X	X	X	X	X	X	X	X	X	X			X	X	X	X	X			X	X	X	X	X	X	X	X	X			X

amb = P. ambiguus var. ambiguus
alb = P. albidus
aur = P. auriberbis
cob = P. cobaea var. cobaea
eri = P. eriantherus var. eriantherus
jam = P. jamesii
ana = P. angustifolius var. angustifolius
anc = P. angustifolius var. caudatus
buc = P. buckleyi
fen = P. fendleri
grn = P. grandiflorus
hay = P. haydeni
nit = P. nitidus var. nitidus
sec = P. secundiflorus
dig = P. digitalis
grc = P. gracilis var. gracilis
lax = P. laxiflorus
okl = P. oklahomensis
pal = P. pallidus
tub = P. tubaeflorus var. tubaeflorus
gla = P. glaber var. glaber

Figures 24-27

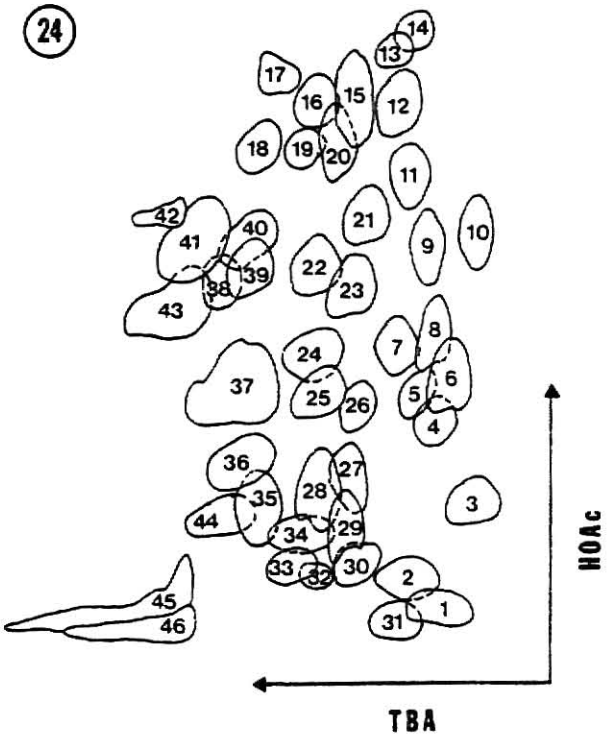
Phenolic compound patterns recognized in Great Plains species of *Penstemon*.

24. Composite chromatogram of all phenolic compounds recognized in study.

25. *P. ambiguus* var. *ambiguus*

26. *P. albidus*

27. *P. auriberbis*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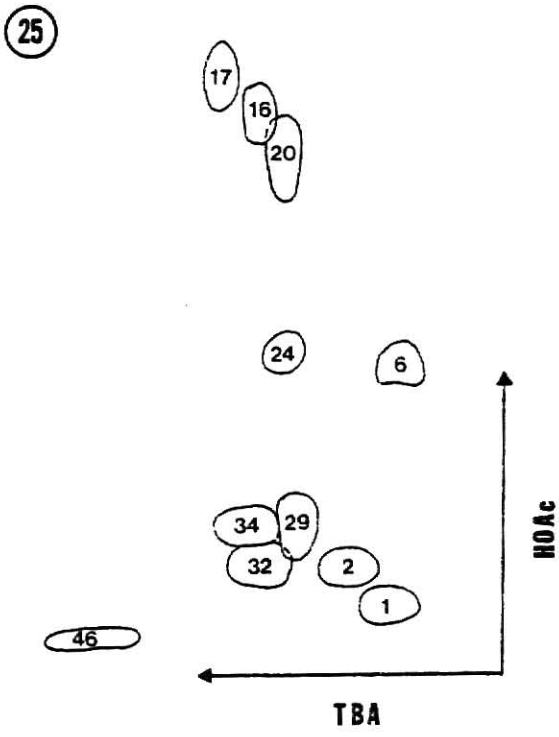
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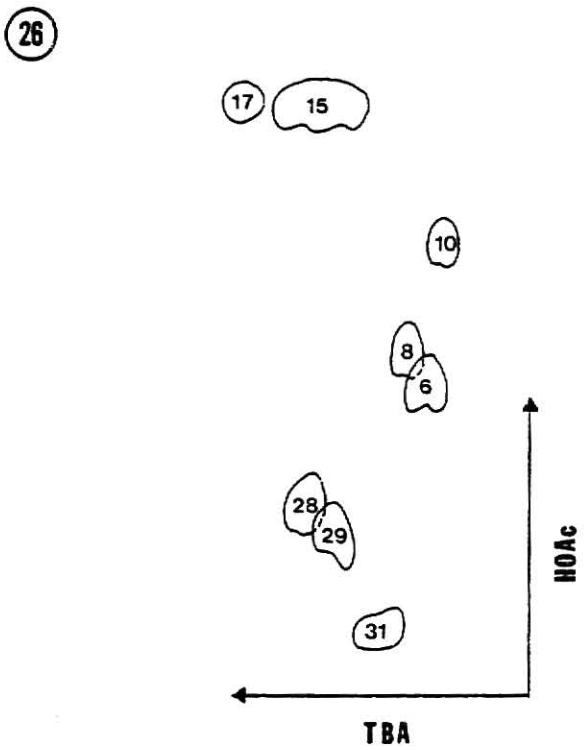
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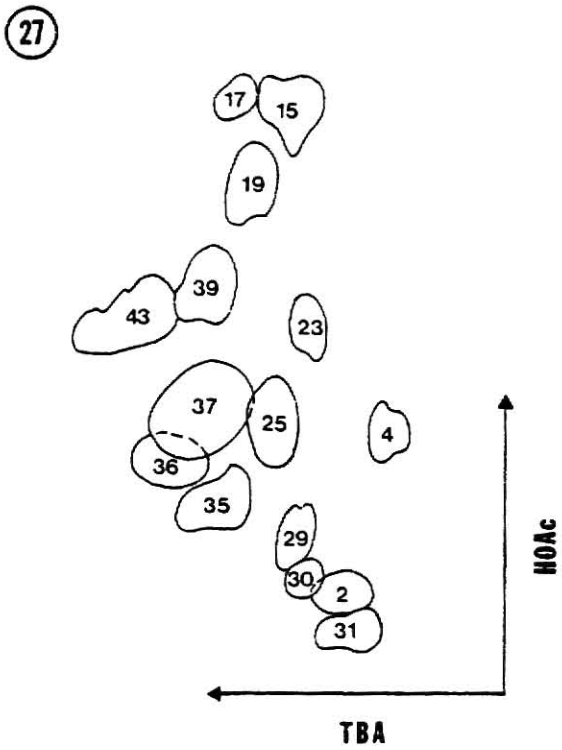
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Figures 28-31

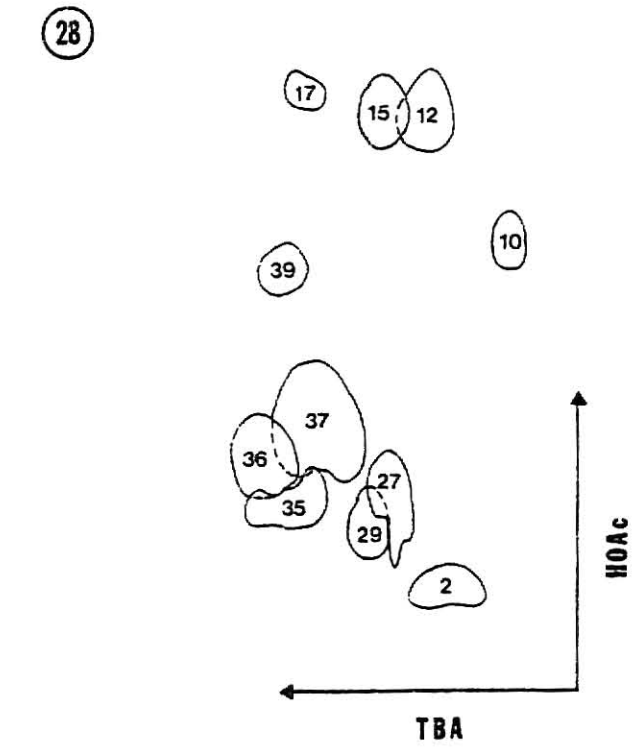
Phenolic compound patterns recognized in Great Plains species of *Penstemon*.

28. *P. cobaea* var. *cobaea*

29. *P. eriantherus* var. *eriantherus*

30. *P. jamesii*

31. *P. angustifolius* var. *angustifolius*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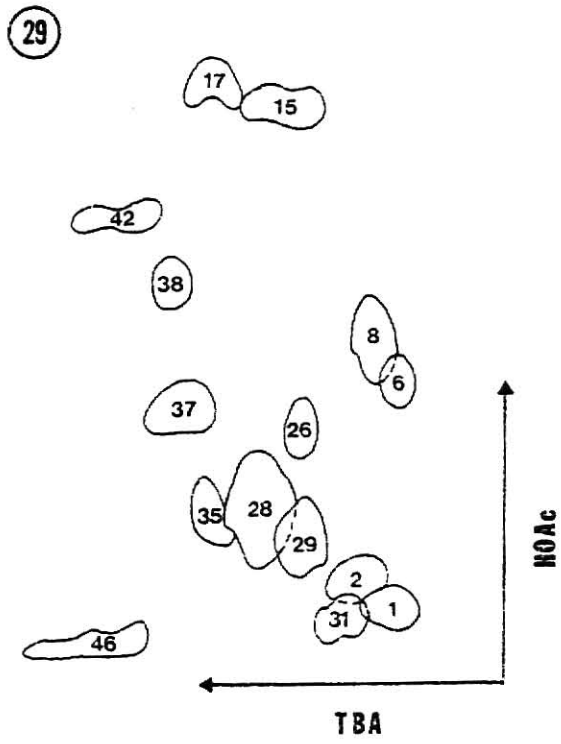
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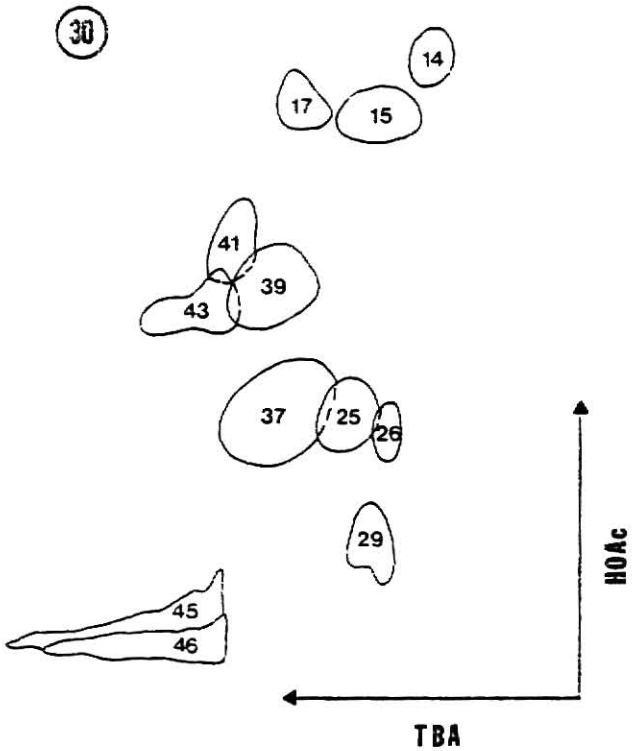
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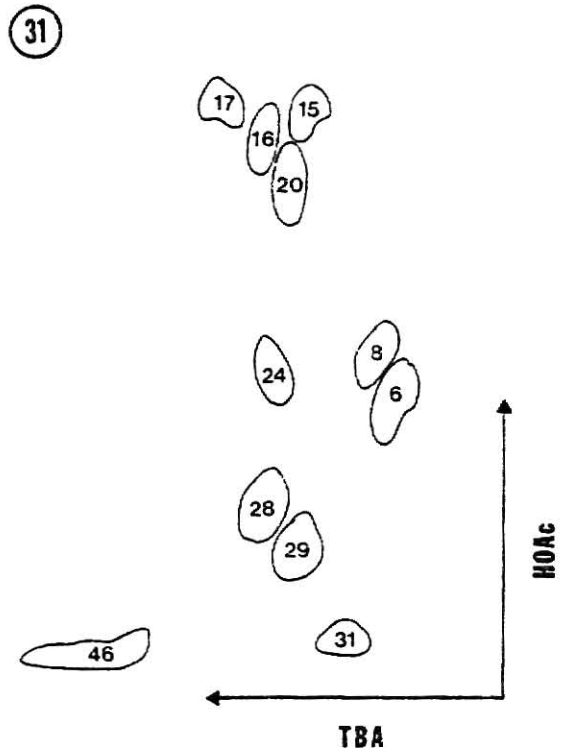
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Figures 32-35

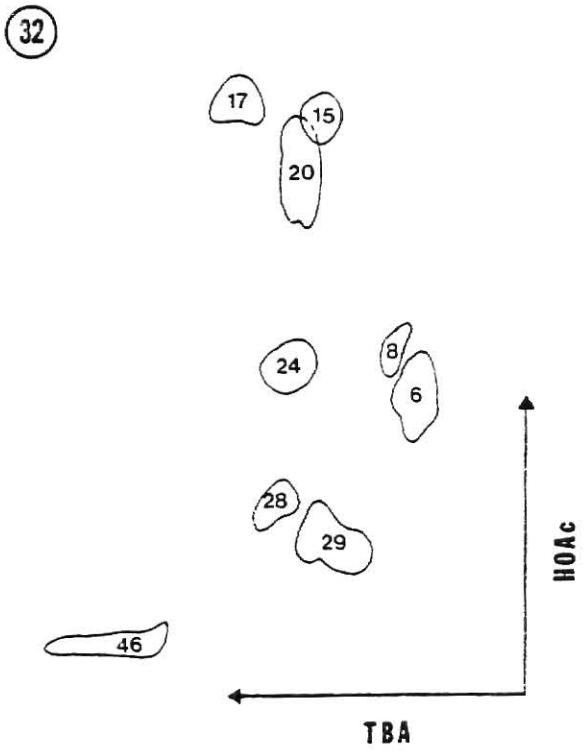
Phenolic compound patterns recognized in Great Plains species of *Penstemon*.

32. *P. angustifolius* var. *caudatus*

33. *P. buckleyi*

34. *P. fendleri*

35. *P. grandiflorus*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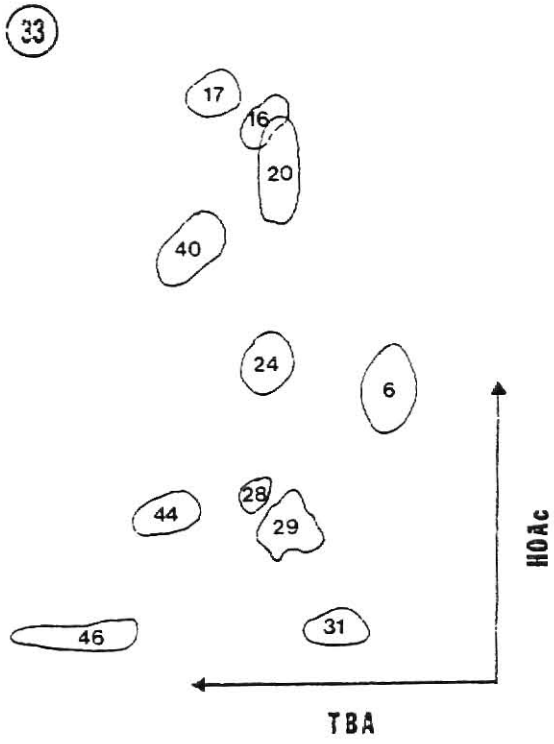
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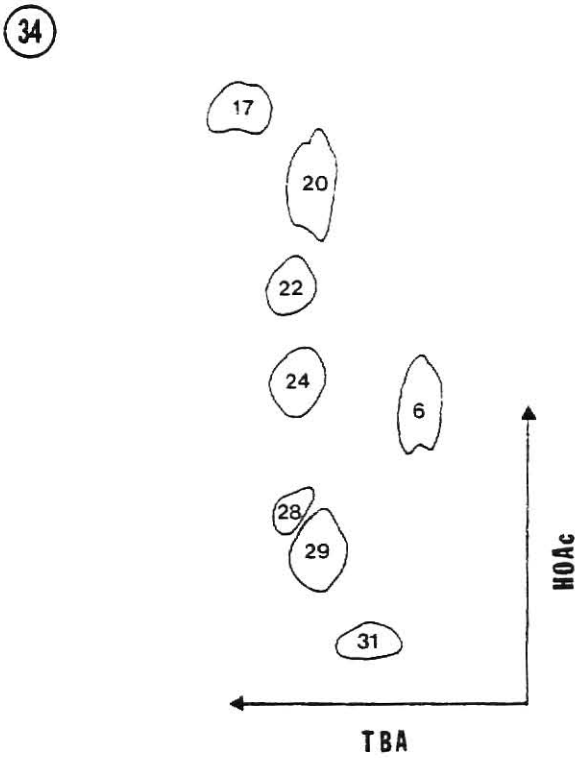
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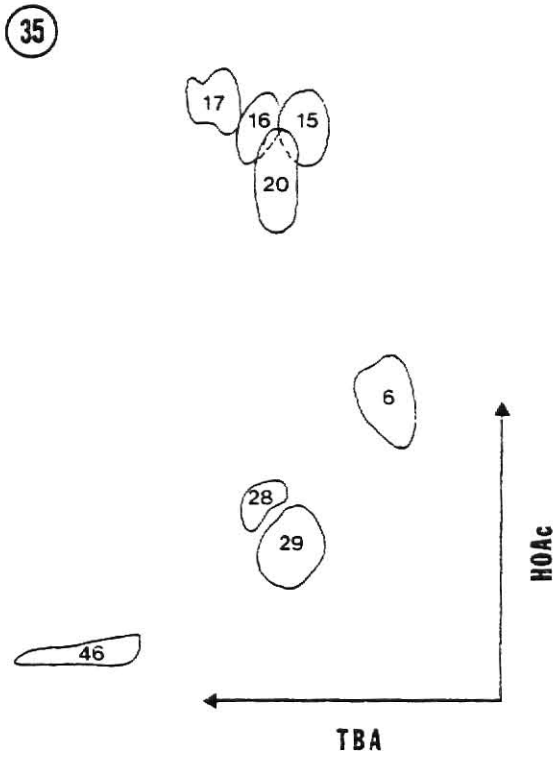
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HOAc
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Figures 36-39

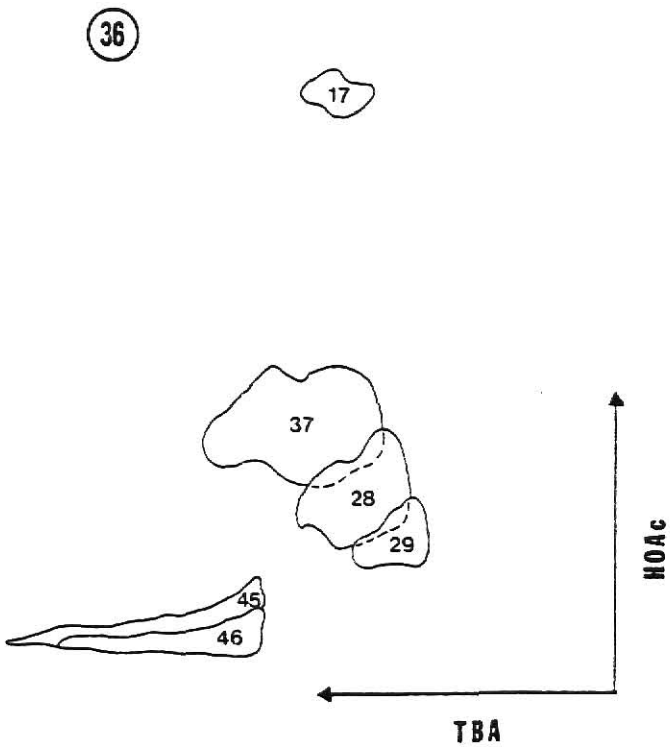
Phenolic compound patterns recognized in Great Plains species of *Penstemon*.

36. *P. haydeni*

37. *P. nitidus* var. *nitidus*

38. *P. secundiflorus*

39. *P. digitalis*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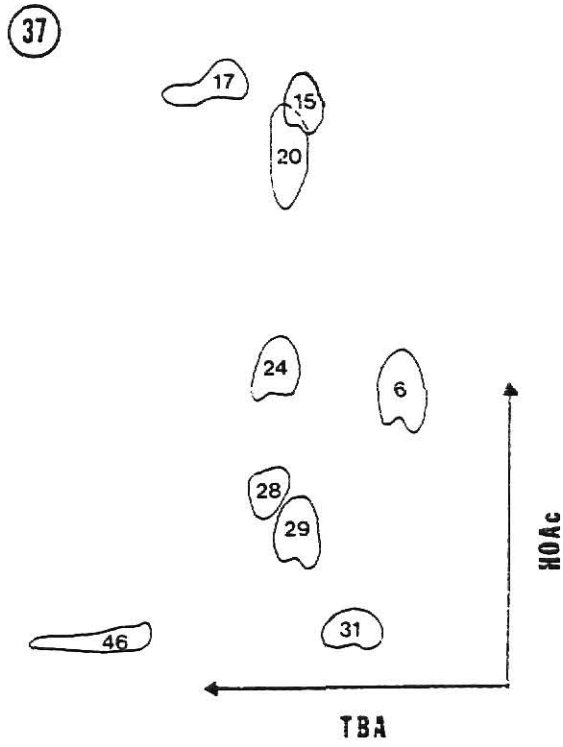
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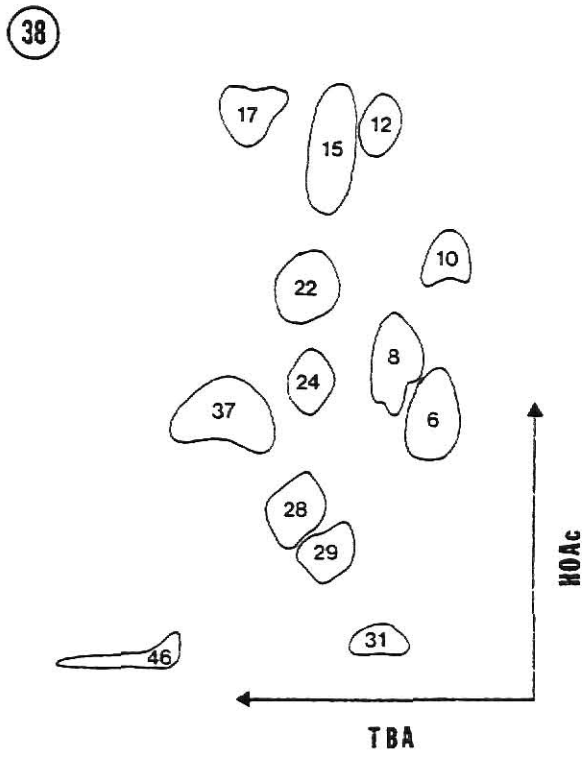
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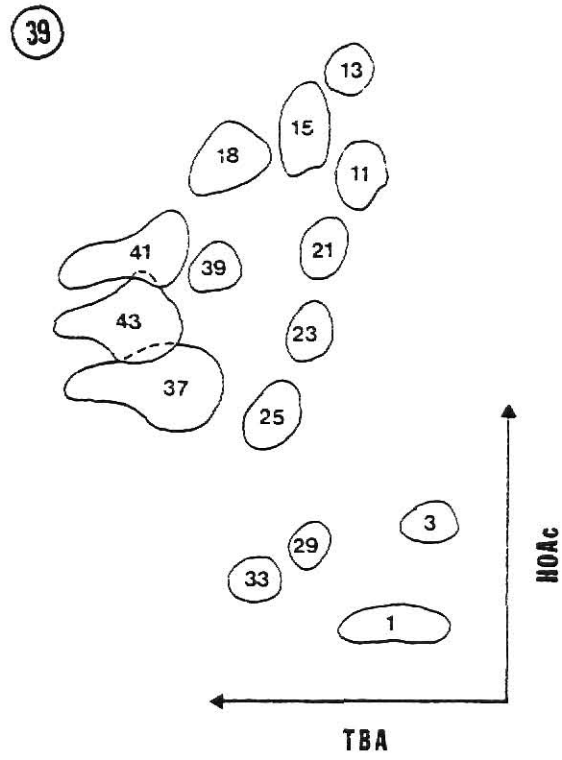
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Figures 40-43

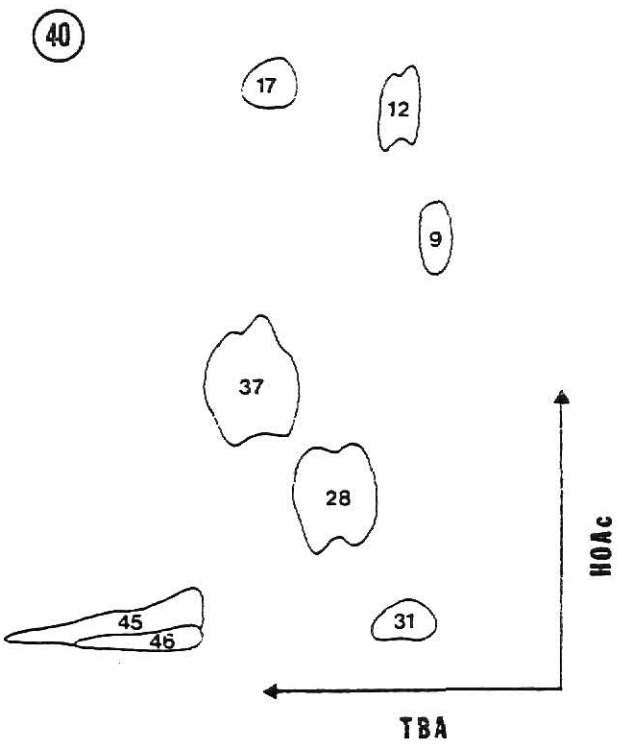
Phenolic compound patterns recognized in Great Plains species of Penstemon.

40. P. gracilis var. gracilis

41. P. laxiflorus

42. P. oklahomensis

43. P. pallidus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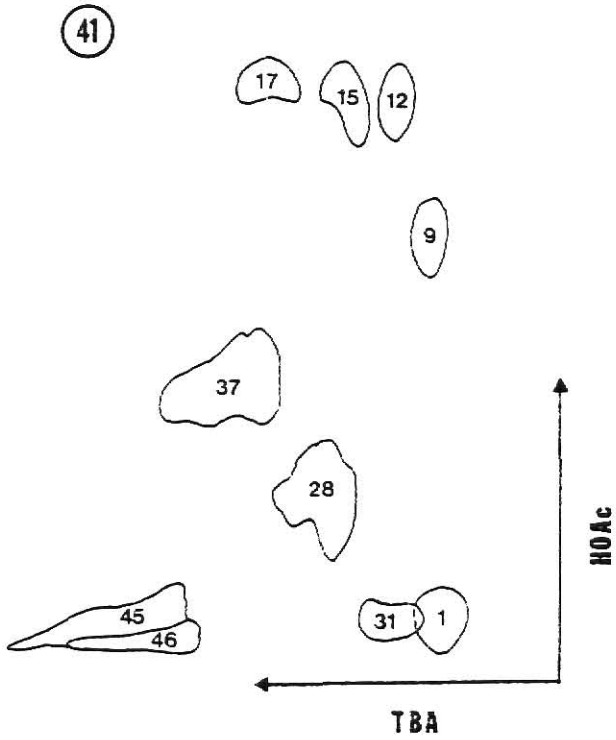
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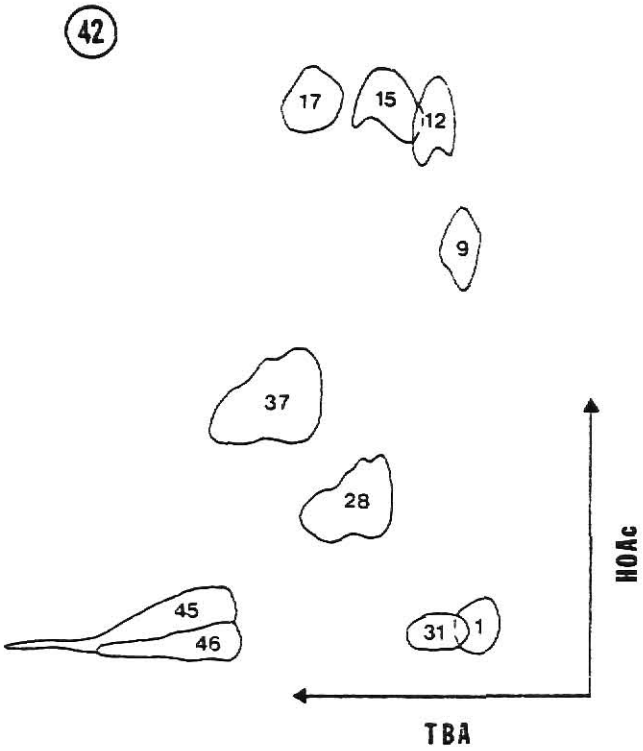
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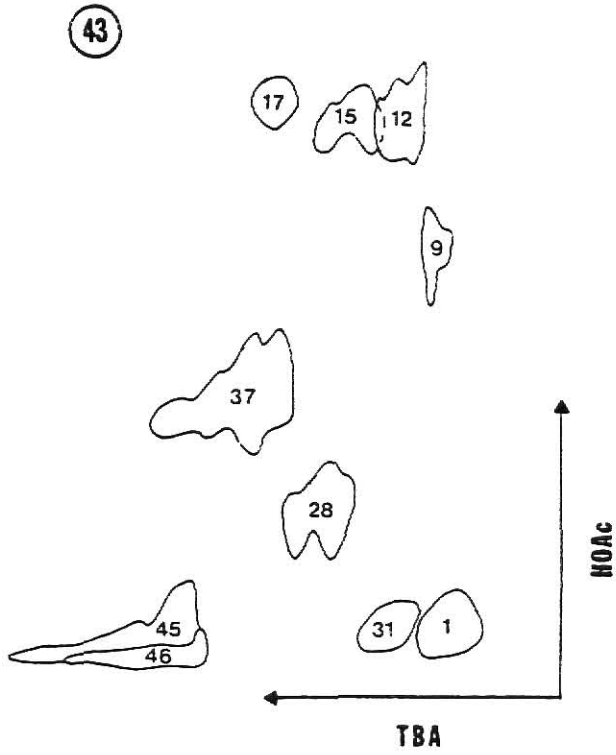
43
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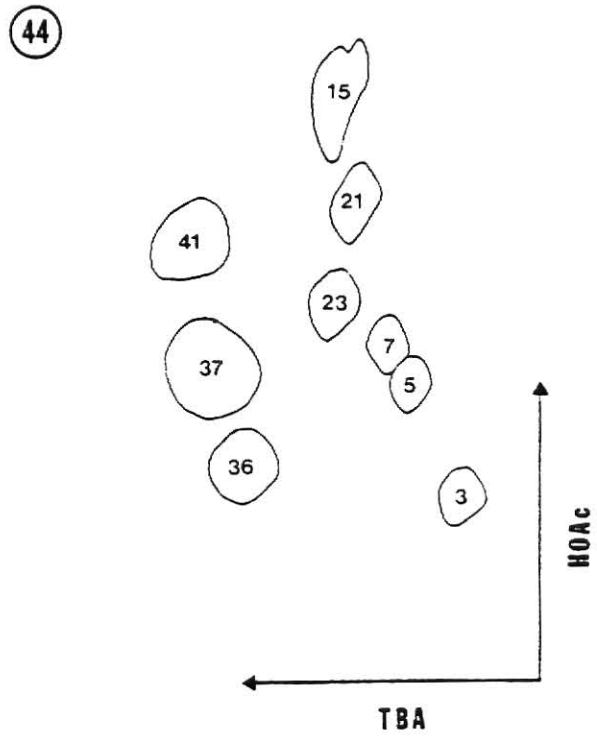
Figures 44-45

Phenolic compound patterns recognized in Great Plains species of *Penstemon*.

44. *P. tubaeflorus* var. *tubaeflorus*

45. *P. glaber* var. *glaber*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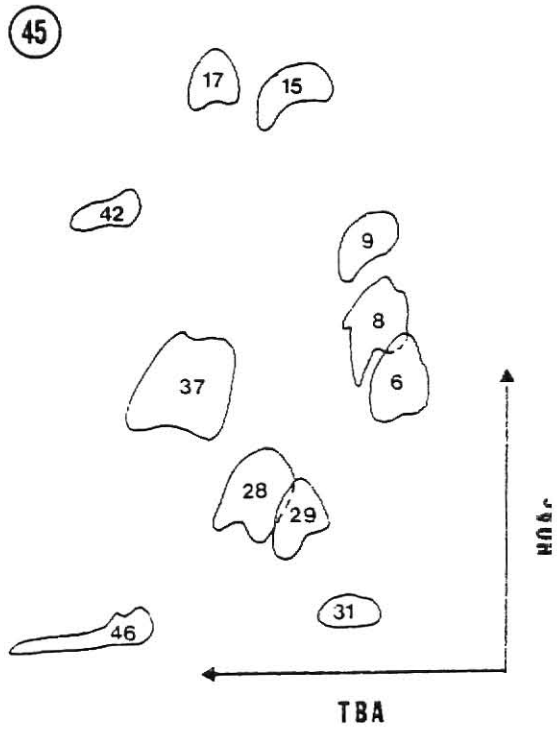
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PALYNOLOGY

Introduction. The use of pollen as a potentially significant taxonomic character is well ingrained in plant systematics. The utility of palynology as a systematic tool goes back to the early 1900's, but its widespread adoption began only some 25 years ago.

Palynological studies in the Scrophulariaceae are limited. Erdtman (1966) described the pollen of a number of scrophulariaceous taxa in his survey of plant pollen. Varghese (1968) examined the pollen of 32 species distributed among 21 genera in 10 tribes in the Scrophulariaceae. While his paper was primarily descriptive, it did point to the potential of palynological studies in resolving systematic problems in the family. Niezgoda & Tomb (1975) explored the use of pollen morphology in understanding taxonomic relationships in the Tribe Leucophylleae. More recently, Argue (1980) demonstrated the taxonomic utility of pollen morphology in the genus Mimulus.

Prior to the present study, no examination of the taxonomic potential of pollen in the genus Penstemon had been undertaken. Niezgoda (1974) included a description of pollen of an unnamed species of Penstemon, along with several scanning electron micrographs, and Argue (1980) mentioned the endoapertures in several species of Penstemon. However, these reports are typical of the palynological information available for the genus. Thus, a survey of the pollen of Great Plains Penstemons of the genus was carried out.

Materials and Methods. Unopened flower buds were removed from herbarium specimens and from the author's dried field collections. Prior to pollen processing, anthers were dissected from each bud so as to reduce the possibility of introducing contaminating pollen, especially in those species with

externally viscid corollas. Extracted anthers were softened a minimum of 18 hours in 10% KOH and then processed through the Erdtman method of acetolysis (1960) as modified by Faegri and Iverson (1964). Following acetolysis, pollen samples were stored in 70% ethanol.

Samples were examined using light microscopy (LM) and scanning electron microscopy (SEM). For LM analysis, acetolyzed aqueous pollen was mounted in warm glycerin jelly on a slide and cover-slipped. Permanent slides were made by ringing the coverslip with clear fingernail polish. Four slides were made for each population studied. Thirty measurements of polar and equatorial diameters were taken from each population. Measurements were made within 4 weeks after slide preparation using a Zeiss Universal microscope at a magnification of 800x.

For SEM examination, acetolyzed aqueous pollen was placed on circular cover slips cemented to aluminum SEM stubs with silver paste. Initially, samples were air-dried and then vapor coated with gold-paladium alloy while rotating the stub from +90° to -90° with respect to the vapor source. However, this usually resulted in collapsed grains. This problem was corrected by freeze-drying the aqueous sample immediately after placing it on the cover slip. Pollen micrographs were made using an ETEC Autoscan scanning electron microscope.

Results. Sixty-nine populations of Great Plains Penstemon were examined in LM and/or SEM (Table 6). These populations were distributed among 21 species. Polar and equatorial measurements obtained from LM are provided in Table 7 for those populations examined. Pollen samples preceded by an asterisk in Table 6 were examined by SEM. Scanning electron micrographs of selected taxa are shown in Figures 46-54.

The pollen of those Penstemon species examined was generally found to

vary from oblate spheroidal to prolate spheroidal in equatorial view with P:E ratios from 0.97-1.15. The only exception to this was the population of P. glaber var. alpinus examined (Ownbey 782) with a P:E ratio of 0.81. Pollen varied from spherical to angular in polar view. Grains were tricolpate with variable endoapertures, some species normally with a simple regular to irregular endoaperture per colpus while others exhibited a tendancy towards multiple endoapertures. In all cases, the aperture(s) was(were) located equatorially and an exinous bridge was often observed over the aperture. Sculpturing of the exine varied from microperforate to perforate or occasionally approached foveolate.

Discussion. An examination of the pollen of Great Plains representatives of Penstemon suggests the genus to be stenopalynous, as only minor variations in grain size and exine sculpturing were noted among the species.

Perhaps the only character of taxonomic significance was stumbled upon quite by accident during preparation of pollen for SEM examination. Initially, pollen samples were air-dried on aluminum stubs prior to examination in the scanning electron microscope. It was noted that most grains collapsed using such a procedure, however, representatives of Sections Penstemon and Cristati tended to be less susceptible to collapse than representatives of Sections Ambigui and Coerulei. This phenomenon may reflect fundamental differences in the exines among these sections and certainly warrants investigation using transmission electron microscopy. Aside from this observation, little else of significance can be said concerning palynological differences among sections. As a point in passing, the smallest grains were observed in Section Ambigui. Average grain size gradually increased in Sections Penstemon, Coerulei, Cristati, and Glaber (in that order), however, the difference between equatorial or polar diameters from smallest to largest grain was only about 15 microns.

In summary, the pollen of Penstemon appears to be quite uniform in exomorphology with grains varying only with respect to size and minor sculpturing details among species. No trends congruent with recognized sectional boundaries were noted other than the tendency of the pollen walls of Sections Penstemon and Cristati to resist collapse when air-dried. Future work should include transmission electron microscopy of sectional exines of selected species.

Table 6

POLLEN STUDY SPECIMENS

Taxon	Voucher
Penstemon albidus	Freeman 85, Rooks Co., Kansas (KSC) *Freeman 207, Slope Co., North Dakota (KSC) *McDougal 35, Lubbock Co., Texas (KSC) Slagg 10, Arapaho Co., Colorado (KSC)
Penstemon ambiguus var. ambiguus	*Weber 6455, Logan Co., Colorado (RM) *Stephens 75861, Curry Co., New Mexico (KANU)
Penstemon angustifolius var. angustifolius	*Stephens 77791, Fallon Co., Montana (KANU) Williams 1546, Kidder Co., North Dakota *Stephens 22596 & Brooks, Elbert Co., Colorado (KANU) Stephens 38241, Sioux Co., Nebraska (KANU)
Penstemon angustifolius var. caudatus	*Stephens 75516, Union Co., New Mexico, (KANU) Stephens 21908 & Brooks, Las Animas Co., Colorado (KANU) Stephens 64697, Cheyenne Co., Colorado (KANU) *Kiener 26967, Scotts Bluff Co., Nebraska (NEB)
Penstemon auriberbis	*Stephens 22163, Huerfano Co., Colorado (KANU) *Stephens 22066 & Brooks, Las Animas Co., Colorado (KANU) Weber 4683, Fremont Co., Colorado (KANU)
Penstemon buckleyi	Goodman 2092, Caddo Co., Oklahoma (OKL) *McGregor 28916, Russell Co., Kansas (NY)
Penstemon cobaea var. cobaea	*Stephens 20443, Wichita Co., Texas (KANU) *Barber 805, Greer Co., Oklahoma (OKL)
Penstemon digitalis	*Freeman 124, Neosho Co., Kansas (KSC) *Goodman 7447, Sequoyah Co., Oklahoma (KANU) Einemann s.n., Cuming Co., Nebraska (NEB)

Table 6 - Continued

Taxon	Voucher
Penstemon eriantherus var. eriantherus	*Freeman 182, Sioux Co., Nebraska (KSC) *Stephens 40241 & Brooks, McKenzie Co., North Dakota (KANU) Stephens 23786 & Brooks, Powder River Co., Montana (KANU)
Penstemon fendleri	*Waterfall 16933, Briscoe Co., Texas (KSC) *Hopkins, Nelson & Nelson 232, Caddo Co., Oklahoma (RM) Correll 24090, Hartley Co., Texas (NY)
Penstemon glaber var. glaber	*Freeman 197, Lawrence Co., South Dakota (KSC) *Porter & Porter 8294, Big Horn Co., Wyoming (RM) Stephens 12273, Dewey Co., South Dakota (KANU)
Penstemon glaber var. alpinus	*Stephens 22933 & Brooks, Goshen Co., Wyoming (KANU) Ownbey 782, Platte Co., Wyoming (RM)
Penstemon gracilis var. gracilis	*Freeman 164, Thomas Co., Nebraska (KSC) Freeman 205, Harding Co., South Dakota (KSC) *Freeman 219, McLean Co., North Dakota (KSC) Moore & Thatcher 14340, Norman Co., Minnesota (KSC)
Penstemon grandiflorus	*Freeman 220, McLean Co., North Dakota (KSC) *Freeman 39, Riley Co., Kansas (KSC) Harms 2492, Charles Mix Co., South Dakota (KANU)
Penstemon haydeni	*Barnes & Heinisch s.n., Hooker Co., Nebraska (NEB) *Tolstead 45, Cherry Co., Nebraska (NEB)
Penstemon jamesii	*Nelson & Nelson 4701, Colfax Co., New Mexico (RM) *Bare 2276, Morton Co., Kansas (KANU) Barrington s.n., Las Animas Co., Colorado (OKLA)

Table 6 - Continued

Taxon	Voucher
Penstemon laxiflorus	Massey & Perino 2675, Johnston Co., Oklahoma (OKL) *Stephens 20217, Canadian Co., Oklahoma (KANU) *Thomas P6809, McCurtain Co., Oklahoma (OKL)
Penstemon nitidus var. nitidus	*Harner 61, Campbell Co., Wyoming (RM) *Hegstad 7640, Mountrail Co., North Dakota (NDA)
Penstemon oklahomensis	*Shaddy 94, Payne Co., Oklahoma (KSC) *Stephens 20343, Comanche Co., Oklahoma (KANU) Waterfall 2642, Oklahoma Co., Oklahoma (OKL)
Penstemon pallidus	Palmer 49035, Dade Co., Missouri (KSC) *Bare 766, Douglas Co., Kansas (KANU) Stephens 52640, Wilson Co., Kansas (KANU) *Henderson 66-346, Johnson Co., Missouri (KANU)
Penstemon procerus var. procerus	*Stephens 78254, Daniels Co., Montana (KANU) Stephens 78276, Valley Co., Montana (KANU) Zaczkowski 948, Carbon Co., Montana (NDA)
Penstemon secundiflorus	*Stephens 22826 & Brooks, Laramie Co., Wyoming (KANU) *Nisbet 27, Harding Co., New Mexico (NY) Ripley & Barneby 8394, Pueblo Co., Colorado (NY)
Penstemon tubaeflorus var. tubaeflorus	*Freeman 151, Lincoln Co., Kansas (KSC) Hawk 10, Tulsa Co., Oklahoma (KSC) *Freeman 133, Harper Co., Kansas (KSC) Freeman 119, Anderson Co., Kansas (KSC)

Table 7

POLLEN GRAIN MEASUREMENTS

Taxon & Population	Equatorial		Polar		Grand Eq. Mean	Grand Polar Mean	Polar to Eq. Ratio (P:E)
	Mean Dia.	Stand. Dev.	Mean Dia.	Stand. Dev.			
P. albidus							
Freeman 85 (KSC)	21.1	0.90	22.6	1.05			
Freeman 207 (KSC)	20.5	1.17	22.5	1.04			
McDougal 35 (KSC)	20.9	0.94	23.4	0.82			
Slagg 10 (KSC)	21.5	1.09	23.5	0.94	21.0	23.0	1.10
P. ambiguus var. *ambiguus*							
Weber 6455 (RM)	14.4	1.01	15.0	0.94			
Stephens 75861 (KANU)	15.9	0.68	17.1	0.72	15.2	16.1	1.06
P. angustifolius var. *angustifolius*							
Stephens 77791 (KANU)	19.4	0.69	21.6	1.47			
Williams 1546 (KANU)	19.9	1.13	21.1	0.65			
Stephens 22596 & Brooks (KANU)	18.8	0.73	20.8	0.78			
Stephens 38241 (KANU)	19.4	1.08	21.5	1.22	19.4	21.3	1.10
P. angustifolius var. *caudatus*							
Stephens 75516 (KANU)	19.9	0.79	19.5	1.08			
Stephens 21908 & Brooks (KANU)	19.3	1.10	21.4	1.24			
Stephens 64697 (KANU)	18.3	0.96	21.8	1.19			
Kiener 26967 (NEB)	18.0	0.88	20.1	1.19	18.9	20.9	1.10
P. auriberbis							
Stephens 22163 (KANU)	21.2	1.39	21.6	1.35			
Stephens 22066 & Brooks (KANU)	20.8	0.99	25.0	2.11			
Weber 4683 (KANU)	21.7	1.22	24.2	1.25	21.2	23.6	1.11

Table 7 - Continued

Taxon & Population	Equatorial		Polar		Grand Eq. Mean	Grand Polar Mean	Polar to Eq. Ratio (P:E)
	Mean Dia.	Stand. Dev.	Mean Dia.	Stand. Dev.			
P. buckleyi							
Goodman 2092 OKL)	20.3	0.97	20.4	0.72			
McGregor 28916 (NY)	20.8	1.30	21.9	1.43	20.6	21.2	1.03
P. cobaea var. *cobaea*							
Barber 805 (OKL)	27.3	1.58	28.0	1.91			
Stephens 20443 (KANU)	26.0	2.10	28.8	1.94	26.7	28.4	1.06
P. digitalis							
Freeman 124 (KSC)	28.6	1.21	29.3	1.35			
Goodman 7447 (KANU)	28.7	1.52	30.9	1.13			
Einemann s.n. (NEB)	26.1	1.14	30.6	0.96	27.8	30.3	1.09
P. eriantherus var. *eriantherus*							
Freeman 182 (KSC)	22.8	0.98	24.1	1.02			
Stephens 23786 & Brooks (KANU)	22.6	1.39	23.6	1.30			
Stephens 40241 & Brooks (KANU)	23.4	1.45	26.3	1.39	22.9	24.7	1.08
P. fendleri							
Waterfall 16933 (KSC)	22.7	1.29	27.3	1.17			
Hopkins, Nelson, & Nelson 232 (RM)	21.6	1.50	23.1	0.94			
Correll 24090 (NY)	21.4	1.05	22.6	1.11	21.9	24.3	1.11
P. glaber var. *glaber*							
Freeman 197 (KSC)	25.1	1.75	28.0	1.77			
Porter & Porter 8294 (RM)	26.5	1.41	26.1	1.28			
Stephens 12273 (KANU)	28.0	1.50	26.6	1.67	26.5	26.9	1.02
P. glaber var. *alpinus*							
Ownbey 782 (RM)	30.1	1.40	24.5	1.32	30.1	24.5	0.81

Table 7 - Continued

Taxon & Population	Equatorial		Polar		Grand Eq. Mean	Grand Polar Mean	Polar to Eq. Ratio (P:E)
	Mean Dia.	Stand. Dev.	Mean Dia.	Stand. Dev.			
P. gracilis var. *gracilis*							
Freeman 164 (KSC)	18.3	1.00	19.6	0.87			
Freeman 205 (KSC)	18.7	0.69	19.5	0.58			
Freeman 219 (KSC)	19.6	1.23	22.0	0.66			
Moore & Thatcher 14340 (KSC)	20.8	0.99	21.9	1.04	19.4	20.8	1.07
P. grandiflorus							
Freeman 39 (KSC)	28.4	1.81	29.8	1.70			
Freeman 220 (KSC)	30.5	1.46	30.3	0.95			
Harms 2492 (KSC)	29.1	2.07	30.0	2.14	29.3	30.0	1.02
P. haydeni							
Barnes & Heinish s.n. (NEB)	26.4	1.35	25.0	1.27			
Tolstead 45 (NEB)	25.9	0.71	28.6	1.29	26.2	26.8	1.02
P. jamesii							
Nelson & Nelson 4701 (RM)	27.6	1.49	27.1	2.04			
Bare 2276 (KANU)	23.2	2.21	23.8	1.40			
Barrington s.n. (OKLA)	22.2	1.17	24.1	1.23	24.3	25.0	1.03
P. laxiflorus							
Massey & Perino 2675 (OKL)	19.5	1.06	21.4	1.22			
Stephens 20217 (KANU)	22.0	0.75	21.2	0.91			
Thomas P6809 (OKL)	21.8	1.03	21.3	1.12	21.1	21.3	0.99
P. nitidus var. *nitidus*							
Hegstad 7640 (NDA)	20.9	1.12	23.7	1.30			
Harner 61 (RM)	20.3	1.14	23.7	0.93	20.6	23.7	1.15

Table 7 - Continued

Taxon & Population	Equatorial		Polar		Grand Eq. Mean	Grand Polar Mean	Polar to Eq. Ratio (P:E)
	Mean Dia.	Stand. Dev.	Mean Dia.	Stand. Dev.			
P. oklahomensis							
Stephens 20343 (KANU)	19.9	0.90	21.1	1.27			
Shaddy 94 (KSC)	22.3	1.25	22.2	1.03			
Waterfall 2642 (OKL)	20.9	1.03	20.8	1.27	21.0	21.4	1.02
P. pallidus							
Palmer 49035 (KSC)	19.8	0.61	21.4	1.19			
Stephens 52640 (KANU)	18.8	1.06	20.1	1.42			
Bare 766 (KANU)	20.2	0.70	20.4	1.18	19.6	20.6	1.05
P. procerus var. *procerus*							
Stephens 78254 (KANU)	18.5	1.36	18.9	0.84			
Stephens 78276 (KANU)	17.6	1.03	18.5	1.09			
Zaczkowski 948 (NDA)	19.7	1.33	21.5	1.09	18.6	19.6	1.05
P. secundiflorus							
Ripley & Barneby 8394	23.0	1.33	21.3	1.20			
Stephens 22826 & Brooks (KANU)	23.5	1.27	23.1	1.37			
Nisbet 27 (NY)	22.6	1.24	22.2	0.85	23.0	22.2	0.97
P. tubaeflorus var. *tubaeflorus*							
Freeman 151 (KSC)	21.6	1.18	25.0	0.49			
Hawk 10 (KSC)	22.7	0.99	23.1	1.33			
Freeman 133 (KSC)	21.6	0.93	23.7	1.14			
Freeman 119 (KSC)	21.4	1.45	24.0	1.67	21.8	24.0	1.10

Figure 46. SEM micrograph of pollen of P. pallidus, equatorial view, Henderson 66-346 (KANU)

Figure 47. SEM micrograph of pollen of P. digitalis, equatorial view, Freeman 124 (KSC)

Figure 48. SEM micrograph of pollen of P. auriberbis, equatorial view, Stephens 22066 & Brooks (KANU)

Figure 49. SEM micrograph of pollen of P. glaber var. glaber, equatorial view, Freeman 197 (KSC)

Figure 50. SEM micrograph of pollen of P. ambiguus var. ambiguus, equatorial view, Stephens 75861 (KANU)

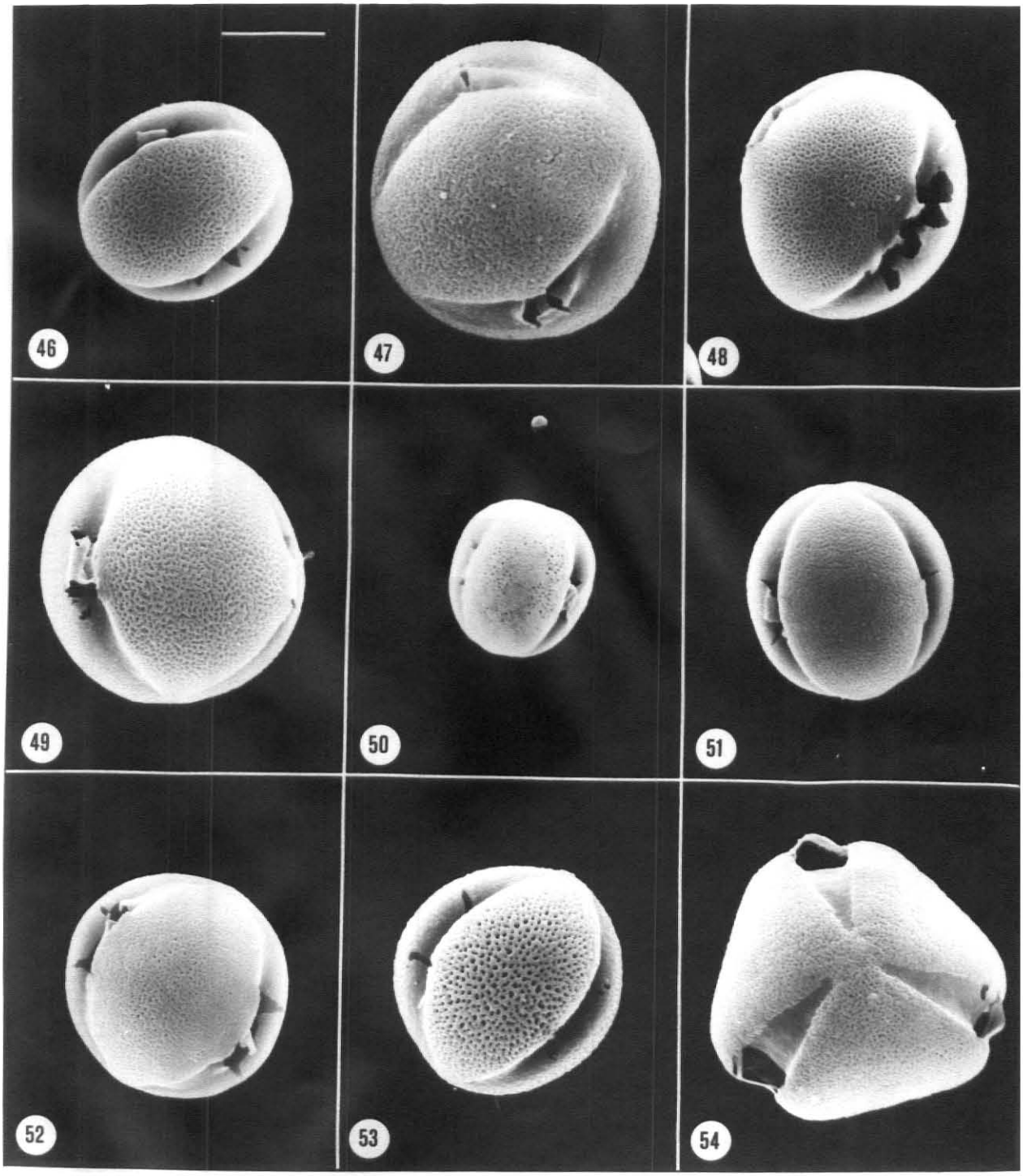
Figure 51. SEM micrograph of pollen of P. eriantherus var. eriantherus, equatorial view, Stephens 40241 & Brooks (KANU)

Figure 52. SEM micrograph of pollen of P. haydeni, equatorial view, Barnes & Heinish s.n. (NEB)

Figure 53. SEM micrograph of pollen of P. fendleri, equatorial view, Waterfall 16933 (KSC)

Figure 54. SEM micrograph of pollen of P. grandiflorus, polar view, Freeman 39 (KSC)

line equals 10 microns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INTRODUCTION TO TAXONOMIC TREATMENT

Some 7500 herbarium specimens were examined in the course of this study. In light of this number, the citation of all specimens examined would be a cumbersome list indeed. Therefore, only a limited number of representative specimens are cited although a complete list of specimens examined is available at the Kansas State University Herbarium.

In citing specimens, priority was given to the author's collections and voucher specimens used in cytological, palynological, and chromatographic studies. The author's collections are deposited at the Kansas State University Herbarium (KSC) with duplicates yet to be distributed. Citation priority was next given to widely distributed collections followed by collections not widely distributed but needed to document the range of each species. In the case of Penstemon haydeni S. Wats., all specimens examined are cited due to the rarity of the species and the limited number of specimens representing the taxon.

Species descriptions are written based on examination of extensive herbarium materials from the Great Plains and field observations in the region. Descriptions for taxa not restricted to the Great Plains incorporate data from limited herbarium specimens collected outside the study area and written descriptions. Thus, species descriptions in this study circumscribe the entire range of morphological variation exhibited by a species both within and outside the Great Plains. Morphological features that distinguish Great Plains taxa from related peripheral taxa are provided in the discussions that follow the species descriptions. All measurements given in the species descriptions and keys are taken from herbarium specimens.

Complete synonomies are provided for all taxa known to occur in the

Great Plains. Additionally, synonomies for each taxon reflect the original orthography as used by each author. No generic synonomy was compiled, but works including such information or discussions pertinent to a generic synonomy of Penstemon may be found in the works of Krautter (1908), Pennell (1935), Straw (1966), and Crosswhite (1967d).

Species distributions that immediately follow habitat information for each species are written to include the total range of the species, including all of its subspecific taxa, if any. Where species have subspecies or varieties occurring outside and within the Great Plains, distributions for those taxa occurring wholly or partially in the Great Plains are given in detail. Additional distribution information for subspecific taxa outside the study area is occasionally supplied.

Table 8 is a synopsis of the genus Penstemon in the Great Plains.

Table 8

SYNOPSIS OF THE GENUS *PENSTEMON* IN THE GREAT PLAINS

Genus *Penstemon* Mitchell

Subgenus *Penstemon*

Section *Penstemon*

Species

7. *digitalis* Nuttall ex Sims
11. *gracilis* Nuttall var. *gracilis*
15. *laxiflorus* Pennell
17. *oklahomensis* Pennell
18. *pallidus* Small
19. *procerus* Douglas ex Graham var. *procerus*
21. *tubaeflorus* Nuttall var. *tubaeflorus*
22. *virens* Pennell

Section *Ambigui* (Rydberg) Pennell

2. *ambiguus* Torrey var. *ambiguus*

Section *Cristati* (Rydberg) Pennell

1. *albidus* Nuttall
4. *auriberbis* Pennell
6. *cobaea* Nuttall var. *cobaea*
8. *eriantherus* Pursh var. *eriantherus*
14. *jamesii* Bentham in DC.

Section *Coerulei* Pennell

3a. *angustifolius* Nuttall ex Pursh var. *angustifolius*
3b. *angustifolius* var. *caudatus* (Heller) Rydberg
5. *buckleyi* Pennell
9. *fendleri* Torrey & Gray
12. *grandiflorus* Nuttall
13. *haydeni* S. Watson
16. *nitidus* Douglas ex Bentham in DC. var. *nitidus*
20. *secundiflorus* Bentham in DC.

Subgenus *Habroanthus* Crosswhite

Section *Glabri* (Rydberg) Pennell

10a. *glaber* Pursh var. *glaber*
10b. *glaber* var. *alpinus* (Torrey) Gray
10c. *glaber* var. *brandegei* (Porter ex Rydberg) Freeman

TAXONOMIC TREATMENT OF *PENSTEMON* IN THE GREAT PLAINS

Penstemon Mitchell, Acta Phys.-Med. Acad. Leopold. Nat. Cur. 8, Append. 214. 1748.

Ours herbaceous or suffrutescent perennials. Stems decumbent or erect, solitary to many from an herbaceous or woody caudex surmounting a taproot. Leaves opposite, exstipulate, entire to toothed; basal leaves absent to well developed or tufted, subpetiolate or more frequently petiolate; cauline leaves filiform to broadly ovate, sessile and frequently clasping. Inflorescence a compact to open thyrse with few to many flowers, with indistinct to distinct verticillasters (false whorls composed of a pair of opposed cymes), rarely secund; bracts much-reduced to prominent. Flowers perfect, zygomorphic; calyx equally to subequally 5-lobed, sepals entire to erose; corolla sympetalous and salverform, funnelform, or tubular-funnelform, slightly to prominently ampliate, occasionally ventricose, nearly regular to strongly bilabiate, the upper lip 2-lobed, the lower lip 3-lobed, unlined or more frequently lined internally with nectar guides, palate (the lower prominent lip) rounded to plicate and glabrous to villose; staminode (sterile stamen) attached to the posterior (upper) inner surface of the corolla and reduced or frequently flattened and bearded distally, included to prominently exserted; fertile stamens 4, didynamous, inserted on or at the base of the corolla, alternate with the lobes, anthers with 2 locules (anther-sacs), the sacs becoming divaricate and dehiscing longitudinally either incompletely or completely, occasionally becoming explanate (spread out flat), filaments arching. Pistil with 2 fused carpels, stigma capitate, style slender and elongate, ovary hypogynous, 2-loculed, placentation axiallary. Fruit a 2-valved septicidal capsule. Seeds numerous ($\pm$100), slightly rounded to angular. Pollen tricolpate. Base chromosome number, $\underline{x} = 8$.

Key to the Great Plains Species of Penstemon

1. Anthers glabrous or if anthers pubescent then the corolla also glandular-pubescent externally.
    2. Corolla salverform; the staminode glabrous and well-included; leaves filiform; the stems much-branched from a distinctly woody base . . . . . I. Section Ambigui
    2. Corolla funnelform, tubular-funnelform, tubular-salverform, ampliate or otherwise, but never merely salverform; the staminode sparsely to densely bearded and included or exserted; leaves linear or wider; stems neither much-branched nor arising from a distinctly woody base.
        3. Corolla glandular-pubescent externally or if glabrous then the inflorescence capitate or elongate-cylindrical with dense verticillasters; leaves glabrous to canescent but never obviously glaucous and firm.
            4. Seeds 0.5-1.3 mm long, tan to dark brown; the throat of the corolla slightly to distinctly flattened and scarcely to prominently plicate anteriorly within, or if the throat not flattened and plicate then the stems glabrous below . . . . . II. Section Penstemon
            4. Seeds 2-3.5 mm long, dark brown to black; the throat of the corolla rounded and not plicate anteriorly within; stems glabrate to villose-canescent . . . III. Section Cristati
        3. Corolla glabrous externally; the inflorescence thyrsoid; leaves glaucous and firm . . . . . IV. Section Coerulei
1. Anthers hirsute; corolla glabrous externally . . . . V. Section Glabri

I. Section Ambigui (Rydberg) Pennell

A single species . . . . . 2. P. ambiguus

II. Section Penstemon

1. Corolla glabrous externally, 6-11 mm long, deep blue to violet-blue . . . . . 19. P. procerus

1. Corolla glandular-pubescent externally, usually exceeding 10 mm in length, white to anthocyanic.

    2. Stems glabrous toward the base.

        3. Corolla glandular-pubescent internally, the throat barely inflated, unlined and unridged anteriorly within; anther-sacs becoming explanate . . . . . 21. P. tubaeflorus

        3. Corolla sparsely to moderately pubescent internally but the hairs eglandular, the throat abruptly inflated, lined with reddish-purple guidelines and barely 2-ridged anteriorly within; anther-sacs not becoming explanate . . . . . 7. P. digitalis

    2. Stems puberulent to villose toward the base.

        4. Corolla white or yellowish-white and unlined internally, 24-32 mm long . . . . . 17. P. oklahomensis

        4. Corolla white to anthocyanic and lined internally, 10-30 mm long.

            5. Stems glandular-villose toward the base, the stems and leaves often appearing velvety . . . . . 18. P. pallidus

            5. Stems merely puberulent toward the base, the stems and leaves glabrous to puberulent and not appearing velvety.

                6. Staminode 15-20 mm long and prominently exserted; corolla 20-30 mm long, peduncles ascending or spreading . . . . . 15. P. laxiflorus

                6. Staminode 8-12 mm long and included or barely exserted; corolla 10-22 mm long, peduncles appressed or erect.

7. Corolla pale to dark blue or violet, the throat weakly 2-ridged anteriorly within, stems arising from a much-branched, well-developed suffrutescent caudex . . . . . 22. P. virens

7. Corolla pale lavender to mauve, the throat prominently 2-ridged anteriorly within, stems arising from a usually slender herbaceous caudex . . . . . 11. P. gracilis

III. Section Cristati (Rydberg) Pennell

1. Throat of the corolla glandular internally but not pilose; staminode sparingly bearded and included or slightly exserted.
   2. Corolla over 35 mm long, white to pink, lilac, or dark violet-purple; the throat abruptly much-inflated; cauline leaves 3.5-15 cm long, 1-5.4 cm wide . . . . . 6. P. cobaea
   2. Corolla 12-20 mm long, white or occasionally faint pink or violet; the throat funnelform and moderately ampliate; cauline leaves 2.5-6.5 cm long, 0.3-2 cm wide . . . . . 1. P. albidus
1. Throat of the corolla pilose internally or at the orifice; staminode densely bearded and slightly to prominently exserted.
   3. Ovary and style glabrous; stems glabrate to pubescent.
      4. Corolla 24-35 mm long, the throat ventricose-ampliate; anther-sacs dehiscing throughout and across the connective, becoming explanate . . . . . 14. P. jamesii
      4. Corolla 16-24 mm long, the throat moderately ampliate; anther-sacs not becoming explanate . . . . . 4. P. auriberbis
   3. Ovary and occasionally the proximal 1/4 to 1/2 of the style glandular-puberulent; stems canescent to villose-canescent.8. P. eriantherus

IV. Section Coerulei Pennell

1. Sepals 7-13 mm long at anthesis; throat of the corolla distinctly inflated and ventricose posteriorly.
   2. Corolla 35-48 mm long; sepals lanceolate to lance-ovate; capsule 16-20(25) mm long . . . . . 12. P. grandiflorus
   2. Corolla 23-25 mm long; sepals linear to linear-lanceolate; capsule 13-16 mm long . . . . . 13. P. haydeni
1. Sepals 3.5-7(8) mm long at anthesis; throat of the corolla scarcely to moderately ampliate and neither distinctly inflated nor ventricose posteriorly.
   3. Throat of the corolla barely ampliate and slightly decurved, distinctly decurved in mature unopened corollas just prior to anthesis; thyrse elongate and distinctly interrupted; upper cauline leaves trullate, widely spaced, and normally much shorter than the internodes . . . . . 9. P. fendleri
   3. Throat of the corolla slightly to moderately ampliate, not distinctly decurved in open or unopened corollas; thyrse compact to elongate; upper cauline leaves lanceolate to ovate but seldom ever trullate, compact to moderately spaced and normally longer than the internodes.
      4. Inflorescence secund, loose to moderately compact . . . . . 20. P. secundiflorus
      4. Inflorescence cylindrical and not secund, distinctly interrupted and moderately compact.
         5. Bracts lance-ovate to orbiculate; corolla usually lavender but occasionally pale pink to very pale blue, never deep blue; thyrse elongate and frequently distinctly interrupted . . . . . 5. P. buckleyi

5. Bracts lanceolate to lance-ovate; corolla deep blue to blue or less commonly lavender to pink; thyrse elongate to moderately compact and seldom distinctly interrupted.

6. Cauline leaves linear to lanceolate or lance-ovate, short to long acuminate or acute; anther-sacs (0.9)1.1-1.5 mm long . . . . . 3. P. angustifolius

6. Cauline leaves lanceolate to ovate, acuminate or more frequently mucronate; anther-sacs 0.7-1.2 mm long . . . . . 16. P. nitidus

V. Section Glabri (Rydberg) Pennell

A single species . . . . . 10. P. glaber

1. Penstemon albidus Nuttall

Pentstemon albidum Nutt., Gen. N. Amer. Pl. 2: 53. 1818. Chelone albida (Nutt.) Spreng., Syst. Veg. 2: 813. 1825. Type: "On the plains of the Missouri, common, from the confluence of the river Platte to the Mountains." (Holotype: not located by Pennell).

Penstemon teretiflorum Nutt., in Fras. Catal. 2. 1813. nomen nudum.

Penstemon viscidulus Nees in Neuweid, Reise Nord-Amer. 2: 444. 1841. Type: "Auf dem Missouri mit zuruckgebrachte." (Type: not seen).

Perennial herb. Stems erect or ascending, (1)1.5-5(5.5) dm tall, retrorsely puberulent below and glandular-pubescent near the inflorescence, 1-5 stems arising from a short-branched caudex surmounting a taproot. Leaves entire to obscurely or obviously serrate, nearly glabrous to puberulent or scabrous; basal leaves (ob)lanceolate to obovate, 2-8.5(11) cm long overall, (0.4)0.7-1.8(2) cm wide, acute to obtuse, tapering to a petiolate base; cauline leaves lanceolate to lance-ovate, 2.5-6.5 cm long, (0.3)0.7-1.9(2.1) cm wide, acute, sessile and clasping. Thyrse 4-24(30) cm long, with (2)3-9(10)

verticillasters, narrow, elongate, scarcely to distinctly interrupted, individual cymes 2-7 flowered, peduncles and pedicels glandular-pubescent, peduncles appressed or erect, to 1.2 cm long, pedicels 0.2-0.8(1) cm long; bracts lanceolate, the lower ones to 3.5 cm long and 1.5 cm wide, acute. Calyx glandular-pubescent, sepals lanceolate to lance-ovate, 4-7 mm long, 1.5-3 mm wide, acute, entire, herbaceous throughout, tinged red along the midvein and toward the base; corolla (12)16-20 mm long, funnelform, weakly bilabiate, white to faintly pink or violet, glandular-pubescent externally and glandular internally, throat (4)6-8 mm broad, moderately ampliate, lined internally on the anterior surface with red or reddish-purple nectar guides, palate densely glandular-pubescent and rounded, lobes of the upper lip spreading, lobes of the lower lip spreading or slightly projecting, the limb often appearing flat; staminode 8-9 mm long from its point of attachment, included, flattened only slightly at the tip, the distal 2-6 mm sparsely to moderately bearded with tortuous sordid-yellow to yellow hairs to 1 mm long; fertile stamens included or the longer pair reaching the orifice, anther-sacs 0.7-0.9 mm long, black, smooth, dehiscing the entire length and across the connective, becoming explanate; style 9-11(13) mm long, glabrous. Capsule 8-12 mm long. Seeds 2-3 mm long, angular, finely reticulate, dark brown to black. $n = 8$.

Sandy-loam to sand or gravel in open prairies and hills. Southern Manitoba, Saskatchewan, and Alberta south to western Oklahoma, Texas (Howard County), and northeastern New Mexico. Flowering from late April in Texas and Oklahoma to early July in North Dakota and Canada.

Penstemon albidus is the most widespread of the Great Plains Penstemons and is a quite common constituent of prairie plant communities throughout its range. The species exhibits relatively little phenotypic variation considering its range, although, specimens may vary noticeably as to flower

color, serration of the leaves, and degree of puberulence of leaves and stems.

REPRESENTATIVE SPECIMENS:

UNITED STATES:

COLORADO: Adams Co.: 2 mi S & 2 mi W Leader, 13 June 1968, Stephens 22563 & Brooks (KANU). Arapahoe Co.: 12 mi S Bennett, 12 June 1968, Stephens 22518 & Brooks (KANU). Baca Co.: 3 mi W Saunders, 3 June 1980, Freeman 475 (KSC). Bent Co.: Rule Creek, 21 May 1913, Osterhout 4871 (RM). Boulder Co.: Eldorado Springs, 24 June 1917, Clokey 2795 (NY, MO, RM). Cheyenne Co.: 2 mi W Cheyenne Wells, 25 May 1973, Stephens 64679 (KANU). Denver Co.: Denver, 17 June 1917, Clokey 2791 (MO-3, NY, RM-2). Douglas Co.: 2 mi N Franktown, 21 June 1937, Beetle & Snyder 37 (RM, MO). Elbert Co.: 26.3 mi W Limon, 4 June 1980, Freeman 501 (KSC); 3 mi NW Fondis, 17 June, 1935, Ownbey 1278 (NY, MO, RM). El Paso Co.: 30 mi SE Colorado Springs, 14 July, 1930, Keck 873 (MO, NY). Kiowa Co.: Eads, 19 June 1898, Baker, Earle & Tracy 813 (MO, NY). Kit Carson Co.: 3.4 mi N Siebert, 4 June 1980, Freeman 504 (KSC). Las Animas Co.: 7 mi N & 3.5 mi W Andrix, 3 June 1980, Freeman 479 (KSC); 7 mi N & 3.5 mi W Andrix, 3 June 1980, Freeman 480 (KSC). Lincoln Co.: 10 mi NW Limon, 16 June 1937, Ramaley & Gambill 16082 (MO). Logan Co.: Sterling, 11 June 1896, Osterhout 988 (NY, CS, RM). Morgan Co.: 2 mi S Brush, 15 June 1967, Stephens 11515 & Brooks (KANU). Otero Co.: 7.5 mi S Higbee, 7 June 1968, Stephens 22047 & Brooks (KANU). Phillips Co.: 0.5 mi E Holyoke, 6 June 1954, Harrington 7457 (CS). Prowers Co.: 25 mi S Lamar, 21 May 1914, Osterhout 5060 (RM). Sedgwick Co.: 2.5 mi S Julesburg, 5 June 1980, Freeman 511 (KSC). Washington Co.: 4 mi W Cope, 14 June 1953, Keck 6501 (NY). Weld Co.: Pawnee Buttes, 1 July 1906, Dodds 2081 (NY, RM). Yuma Co.: Bonny State Recreation Area 20 mi N Burlington, 5 June 1980, Freeman 505 (KSC).

IOWA: Plymouth Co.: S of Westfield, 29 May 1938, Goodman 3038 (NY, MO). Sioux Co.: N of Oak Grove State Park along Little Sioux River, 23 July 1937, Hayden 9033 (NY, MO).

KANSAS: Barber Co.: 41 mi W Medicine Lodge, 28 May 1957, McGregor 12876 (NY). Barton Co.: 1 mi N Olmitz, 2 June 1973, Stephens 65183 (KANU). Cheyenne Co.: 2 mi W & 1.4 mi N St. Francis, 5 June 1980, Freeman 506 (KSC). Clark Co.: 20 mi NW Ashland, 8 June 1979, Freeman 134 (KSC); 5 mi N Ashland, 29 May 1967, Stephens 11190 (NY, OKLA). Comanche Co.: 17 August 1896, Hitchcock s.n. (KSC). Decatur Co.: Sappa State Park, 28 June 1954, McGregor 9489 (KANU). Ellis Co.: Near Hays, 14 June 1935, Shepherd 88 (IND, OKL, MO, RM, OKLA). Ellsworth Co.: Near Wilson, 1927, Weber 27 (KSC-2). Finney Co.: 4 mi W Kalvesta, 2 June 1967, Stephens 11293 (NY, OKLA). Ford Co.: Dodge City, May 1891, Ellis s.n. (KSC-2, NY). Gove Co.: 22 July 1895, Hitchcock 377a (KSC-2, NY, MO, RM). Graham Co.: 20 June 1897, Hitchcock s.n. (KSC). Grant Co.: 1.5 mi S Cimarron River along Hwy 270 & 25, 9 June 1979, Freeman 140 (KSC). Gray Co.: 2.5 mi W Cimarron, 19 May 1972, Stephens 53068 (KANU). Greeley Co.: 3.5 mi E Tribune, 5 June 1971, Stephens 47970 (KANU). Haskell Co.: 6 mi SW Satanta, 6 June 1961, McGregor 16944 (NY, KANU). Hamilton Co.: Hamilton Co. State Fishing Lake 3 mi W & 2 mi N Syracuse, 3 June 1980, Freeman 474 (KSC). Hodgeman Co.: 2 mi S & 3 mi E Jetmore, 15 May 1975,

Stephens 84059 (KANU). Kearney Co.: 2.1 mi N Lakin, 2 June 1980, Freeman 473 (KSC). Kiowa Co.: 5 mi SW Belvidere, 19 May 1972, McGregor 24256 (KANU). Lane Co.: Dighton Cemetary 1.6 mi E Dighton, 2 June 1980, Freeman 469 (KSC). Lincoln Co.: 100 yds E Lincoln Co. Line, 23 May 1980, Freeman 449 (KSC). Logan Co.: 16.9 mi S Oakley, 10 June 1979, Freeman 146 (KSC); 11 May 1895, Hitchcock 377 (KSC, NY, MO, RM). Meade Co.: Sec. 1, T32S, R26W, 2 June 1979, Freeman & Freeman 97 (KSC); 3 mi E Meade State Park, 8 June 1979, Freeman 136 (KSC); 11 mi E Meade, 6 May 1942, Horr E444 (OKL, NY, RM, SDC, KSP, OKLA, KANU-2, IND). Morton Co.: 1 mi N Cimarron River along Hwy 27, 3 June 1979, Freeman 101 (KSC); Cimarron River N of Elkhart on Point Rock, 12 July 1929, Rydberg & Imler 969 (NY, KANU). Ness Co.: 2 mi W Beeler, 1 June 1973, Stephens 65087 (KANU). Norton Co.: 3 mi W Dellvale along Prairie Dog Creek, 23 May 1935, Gates 18059 (KSC). Osborne Co.: 1.5 mi W Alton, 1 June 1979, Freeman 80 (KSC). Pawnee Co.: 1 mi E & 0.5 mi S Ash Valley, 4 June 1974, Brooks 5944 (KANU). Phillips Co.: 4 mi E Logan, 28 June 1954, McGregor 9551 (KANU). Pratt Co.: 3 mi SW Preston, 14 May 1954, Atkins 1 (KSC). Rawlins Co.: 7 mi N Atwood, 7 June 1971, Stephens 48029 (KANU). Rooks Co.: 0.5 mi SW Stockton, 1 June 1979, Freeman 81 (KSC); Rooks State Fishing Lake, 1 June 1979, Freeman 85 (KSC). Rush Co.: 1.5 mi NW Bison, 2 June 1980, Freeman 468 (KSC). Russell Co.: 100 yds W Lincoln Co. Line, 23 May 1980, Freeman 448 (KSC). Scott Co.: Lake Scott State Park, 9 June 1979, Freeman 143 (KSC). Seward Co.: 3 mi E Hayne, 8 May 1942, Horr s.n. (KANU). Sheridan Co.: Sheridan State Fishing Lake 3.9 mi W Studley, 10 June 1979, Freeman 148 (KSC). Sherman Co.: 7 mi S, 2 mi W, & 3 mi S Goodland, 25 May 1971, McGregor 23727 (OKL, KANU). Smith Co.: 5.9 mi S Nebraska State Line on Hwy 8, 21 June 1979, Freeman 157 (KSC). Stafford Co.: 6 mi N St. John, 26 May 1974, McGregor 26005 (KANU). Stanton Co.: 1 mi N Saunders, 9 July 1975, Brooks 10726 & Hauser (KANU). Stevens Co.: NE of Richfield along Cimarron River, 9 June 1979, Freeman 139 (KSC). Thomas Co.: Prairie Dog Creek 3 mi NW Rexford, 21 May 1935, Gates 18000 (KSC). Trego Co.: 3 mi S Wakeeney, 4 June 1967, Stephens 11344 (NY). Wallace Co.: 4 mi S Wallace, 4 June, 1969, Stephens 31317 & Brooks (KANU). Wichita Co.: 11 mi S Leoti, 31 May 1973, Stephens 65007 (KANU).

MINNESOTA: Big Stone Co.: Ortonsville, 14 July 1940, Gleason 9488 (NY). Chippewa Co.: Montevideo, June 1894, Moyer s.n. (RM, NY, MO-2). Clay Co.: 6 mi E & 1 mi S Glyndon, 16 June 1969, Barker 5341 (NDA).

MONTANA: Carter Co.: 8 mi S Ekalaka, 14 June 1974, Stephens 77715 (KANU). Cascade Co.: Great Falls, 18 July 1887, Anderson 6113 (NY). Chouteau Co.: 6 mi N Loma, 23 July 1973, Stephens 68577 (KANU). Custer Co.: 8 mi NE Miles City, 29 June 1968, Stephens 23715 & Brooks (KANU). Daniels Co.: 4.5 mi E Flaxville, 18 June 1974, Stephens 78221 (KANU). Dawson Co.: 18 mi E Glendive, 15 June 1974, Stephens 77880 (KANU). Fallon Co.: 28 mi S Baker, 25 June 1968, Stephens 23266 & Brooks (KANU). Garfield Co.: 32 mi E Jordan, 21 June 1974, Stephens 78491 (KANU). McCone Co.: 5 mi SE Ft. Peck Dam, 20 June 1974, Stephens 78374 (KANU). Meagher Co.: Between White Sulphur Springs & Harlowton, 2 July 1945, Hitchcock & Muhlick 11887 (RM, NY, MO). Musselshell Co.: 25 mi S Roundup, 25 June 1955, Booth 55141 (RM). Park Co.: 2 mi E Livingston, 5 June 1959, Booth s.n. (RM). Powder River Co.: 24.8 mi W Broadus, 10 June 1980, Freeman 547 (KSC). Prairie Co.: Between Terry & mouth of Powder River, 14 June 1937, Pennell 20459 (NY). Richland Co.: 14 mi W Lambert, 16 June 1974, Stephens 77984 (KANU). Roosevelt Co.:

Culbertson, 19 June 1927, Larsen 125 (MO). Sheridan Co.: Westby, 16 June 1927, Larsen 15 (RM, MO). Stillwater Co.: 2 mi E Columbus, 18 June 1946, Ripley & Barneby 8053 (NY). Valley Co.: 21 mi S Opheim, 19 June 1974, Stephens 78311 (KANU). Wheatland Co.: 10 mi S Harlowton, 2 July 1947, Hitchcock 16008 (RM, NY, MO). Wibaux Co.: 21 mi S Wibaux, 26 June 1968, Stephens 23368 & Brooks (NDS, KANU). Yellowstone Co.: Custer, 30 May 1890, Blankinship 47 (MO).

NEBRASKA: Adams Co.: 1 mi N Ayr, 28 May 1975, Churchill 5460 (NEB, NY). Antelope Co.: Royal, 31 May 1924, Wernecke s.n. (KSC, FHKSC); Grove Lake N of Royal, 1 June 1974, Churchill 3261 (NEB, NDA, NY). Arthur Co.: 11.4 mi S Arthur, 5 June 1980, Freeman 517 (KSC). Banner Co.: 1 mi S & 8 mi E Harrisburg, 29 June 1970, Stephens 40873 & Brooks (KANU). Blaine Co.: 7 mi E Dunning along Middle Loup River, 3 June 1975, Kolstad 3777 (*KNSC). Boone Co.: 1 mi S St. Edward, 31 May 1974, Churchill 3230 (NEB). Box Butte Co.: N of Hemingford, 18 June 1953, Kiener 29386a (NEB). Boyd Co.: 3 mi S & 1 mi E Monowi, 3 June 1970, Stephens 38708 & Brooks (KANU). Brown Co.: 9.4 mi NW Long Pine, 26 June 1979, Freeman 233 (KSC). Buffalo Co.: 2 mi S & 3 mi W Ravenna, 12 July 1975, Luce s.n. (*KNSC). Butler Co.: 3 mi W & 5 mi N Rising City, 31 May 1968, Stephens 21543 (KANU). Cedar Co.: 1 mi NW & 1 mi N Obert, 7 June 1974, Sutherland 3751 & Churchill (NEB). Chase Co.: 2 mi S Enders, 24 May 1966, McGregor 19859 (KANU). Cherry Co.: Merritt Reservoir 30 mi SW Valentine, 22 June 1979, Freeman 171 (KSC); 1.2 mi E Nenzel, 22 June 1979, Freeman 173 (KSC). Cheyenne Co.: Sidney, 23 May 1922, Nelson s.n. (RM). Cumings Co.: 0.5 mi S & 4 mi W Wisner, 28 May 1974, Churchill 3099 (NDA, NEB, NY). Custer Co.: 2 mi SE Merna, 9 June 1931, Pennell 15052 (RM). Dawes Co.: N of Crawford along Hwy 71 & 2 & 5 mi SE Sioux Co. Line, 7 June 1980, Freeman 531 (KSC); 0.25 mi SW Chadron State College campus, 28 May 1973, Mason 102 (SDU, NDA). Dawson Co.: 1 mi NW Gothenburg, 1 June 1934, Morrison 1061 (NEB). Devel Co.: 27 June 1891, Rydberg s.n. (NY). Douglas Co.: Omaha, 23 May 1875, Cleburne s.n. (NEB). Dundy Co.: 8 mi E & 1 mi S Haigler, 10 June 1973, Stephens 65504 (KANU). Franklin Co.: 7 mi S & 1 mi E Hildreth, 23 May 1971, Stephens 47429 (KANU). Frontier Co.: 2 mi S Stockville, 9 June 1973, Stephens 65413 (KANU). Garden Co.: 5 mi SW Lewellen, 25 May 1966, McGregor 19894 (KANU). Gosper Co.: 20 June 1891, Rydberg s.n. (NY). Harlan Co.: 5 mi N Harlan Co. Dam, 20 May 1977, Kolstad 4675 (*KNSC). Hitchcock Co.: 14 mi NW Culbertson, 12 July 1968, Bare & McGregor 1389 (KANU). Holt Co.: 3 mi E & 22 mi N Atkinson, 3 June 1970, Stephens 38781 & Brooks (KANU). Hooker Co.: 3 mi W Thomas Co. Line along Hwy 2, 5 June 1980, Freeman 523 (KSC). Howard Co.: 2.5 mi S St. Paul, 14 May 1970, Stephens 37941 (KANU). Kearney Co.: Minden, 28 May 1937, Hapeman 835 (OKLA). Keith Co.: 17.1 mi S Arthur, 5 June 1980, Freeman 515 (KSC). Keya Paha Co.: 7.5 mi E & 7 mi S Springview, 4 June 1970, Stephens 38916 & Brooks (KANU). Kimball Co.: 2.5 mi W Kimball interchange on I-80, 15 June 1972, Pierce 1949 (RM). Knox Co.: 0.5 mi E & 7 mi N Crofton, 3 June 1970, Stephens 38658 & Brooks (KANU). Lincoln Co.: 5.7 mi N North Platte, 18 August 1915, Pennell 6408 (NY). McPherson Co.: 2 mi N Tryon, 5 June 1980, Freeman 521 (KSC). Merrick Co.: 5 June 1936, Mueller s.n. (NEB). Morrill Co.: 0.5 mi S Angora, 1 June 1973, Churchill 861 (NEB). Nuckolls Co.: 3 mi W & 2 mi N Superior, 24 May 1971, Stephens 47497 (KANU). Perkins Co.: 0.25 mi E Grainton, 6 June 1976, Forney 320 (*KNSC). Phelps Co.: 5 mi S Holdrege, 22 May 1940, Brown 1229 (NEB-2). Pierce Co.: 1 mi E & 1.5 mi N Hadar,

2 June 1970, Stephens 38635 & Brooks (KANU, NDA). Platte Co.: S of Monroe, 23 May 1971, Sutherland 2912 & Parker (NY). Rock Co.: 6 mi E Bassett, 4 June 1970, Stephens 38879 & Brooks (KANU). Scotts Bluff Co.: 3 mi W Gering, 27 May 1951, Kiener 26966 (NEB). Sheridan Co.: 0.2 mi E of Dawes Co. Line along Hwy 74, 6 June 1980, Freeman 529 (KSC). Sherman Co.: 2 mi E & 1.5 mi N Litchfield, 26 June 1967, Beck 87 (*KNSC). Sioux Co.: Smiley Canyon in Ft. Robinson State Park, 23 June 1979, Freeman 178 (KSC); 2 mi N Harrison, 23 June 1979, Freeman 181 (KSC). Thomas Co.: Along Loup River at Halsey, 9-10 June 1931, Pennell 15058 (NY). Webster Co.: 4 mi S Red Cloud, 13 May 1976, Kolstad s.n. (*KNSC). Wheeler Co.: 7 mi N & 6 mi E Bartlett, 11 July 1968, Stephens 24241 & Brooks (KANU). York Co.: 1 mi W & 1 mi N Lushton, 22 May 1971, Stephens 47365 (KANU).

NEW MEXICO: Quay Co.: 8 mi N Nara Visa, 28 May 1973, Higgins 6920 (NY). Union Co.: 2 mi W Clayton, 11 June 1941, Mankin 856 (NY).

NORTH DAKOTA: Adams Co.: 2 mi W Reeder, 21 June 1970, Stephens 40390 & Brooks (KANU). Barnes Co.: 15.5 mi N Valley City at Ashtabula Lake, 18 June 1971, Godfread 831 (NDA). Benson Co.: Leeds, 15 June 1909, Lunell s.n. (NY, MO). Billings Co.: Near Medora & Theodore Roosevelt National Memorial Park, 7-10 June 1967, Porter & Porter 10350 (RM, NY). Bottineau Co.: Turtle Mts., 16 June 1960, Stevens s.n. (NDA). Bowman Co.: 6 mi S Scranton, 28 July 1969, Zaczkowski 1268 (NDA). Burke Co.: 0.5 mi S Canadian Border in Des Lacs National Wildlife Refuge, 20 June 1969, Hegstad 1436 (NDA). Burleigh Co.: 3.5 mi SE Baldwin, 25 July 1970, Morrison 24 (NDA). Cavalier Co.: 2 mi S & 1 mi W Olga, 18 June 1970, Stephens 40028 & Brooks (KANU). Cass Co.: 6 mi S & 2 mi W Alice, 17 June 1970, Seiler 1585 (NDA, KANU). Divide Co.: 3 mi W Ambrose, 23 June 1970, Hegstad 5053 (NDA). Dunn Co.: 7 mi W & 1.5 mi N Killdeer, 25 June 1979, Freeman 216 (KSC). Eddy Co.: Hamar, 13 June 1960, Stevens s.n. (NDA). Emmons Co.: Lake Oahe Beaver Creek Public Use Area, 25 June 1979, Freeman 224 (KSC); 3 mi S Glencoe Church in NW Emmons Co., 7 June 1971, Williams 125 (KANU, NDA). Golden Valley Co.: 5 mi W Sentinel Butte, 10 June 1970, Zaczkowski 2530 (NDA). Grand Forks Co.: Turtle River State Park, 16 June 1953, Stevens 1423 (NDA). Grant Co.: 4 mi NW Raleigh, 20 June 1970, Morrison 91 (NDA). Griggs Co.: Cooperstown, 29 July 1965, Stevens s.n. (NDA). Kidder Co.: 5 mi E & 6 mi N Tappen, 5 June 1972, Williams 968 (KANU, MO, NDA). LaMoure Co.: Adrian, 27 June 1912, Bergman 1794 (RM, MO, NDA). Logan Co.: 5 mi W & 0.5 mi S Burnstad, 13 June 1975, Williams 2605 (NDA). McHenry Co.: 1 mi N Towner, 21 July 1951, Boivin & Dore 8154 (NDA). McIntosh Co.: 14 mi W & 0.5 mi S Wishek, 8 June 1972, Williams 1016 (MO, NDA). McKenzie Co.: Elbowoods, 17 June 1935, Heidenreich s.n. (NDA). McLean Co.: 2 mi N & 6 mi W Wilton, 14 June 1974, Larson 4449 (NDA). Mercer Co.: 15 mi N Hazen, 17 June 1974, Larson 4487 (NDA). Morton Co.: Mandan, 12 June 1937, Pennell 20442 (NY). Mountrail Co.: 3 mi S & 2 mi E Powers Lake, 9 June 1969, Hegstad 3042 (NDA). Nelson Co.: Stump Lake, 25 July 1911, Haigh 298 (RM). Oliver Co.: 2 mi S & 5 mi E Center near Nelson Lake, 13 June 1974, Larson 4395 (NDA). Pembia Co.: 5 mi W Cavalier, 17 June 1969, Barker 5374 (NDA, KANU). Pierce Co.: Lake Girard, 17 June 1960, Stevens s.n. (NDA). Ransom Co.: Lisbon, 7 July 1891, Lee 532 (NDA). Renville Co.: 12 mi W Mohall, 10 June 1976, Larson 5585 & Lind (NDA). Richland Co.: 5 mi W & 3 mi S Kindred, 10 June 1970, Seiler 1578 (NDA, KANU). Rollette Co.: 1.5 mi W Belcourt, 18 June 1970, Stephens 40046 & Brooks (KANU). Sargent Co.: Rutland, 11 June 1891,

Waldron s.n. (RM). Sheridan Co.: Central Sheridan Co., 9 June 1958, Stevens & Moir 1899 (NDA). Slope Co.: 3 mi W Amidon, 24 June 1979, Freeman 207 (KSC); 4 mi W & 12 mi N Amidon, 24 June 1979, Freeman 211 (KSC). Stark Co.: 0.5 mi S Dickinson, 14 June 1969, Seiler 72 (NDA). Steele Co.: Luverne, 9 June 1966, Stevens s.n. (NDA). Stutsman Co.: Kensal, 11 June 1972, Bergman 1731 (MO, NDA). Towner Co.: Rock Lake, 12 June 1958, Stevens & Moir 1920 (NDA). Walsh Co.: Homme Reservoir near Park River, 21 June 1974, Godfread 5666 (NDA-2). Ward Co.: Minot, 17 August 1891, Bolley s.n. (RM). Wells Co.: Hurdsfield, 9 June 1958, Stevens & Moir 1820 (NDA). Williams Co.: 1 mi S & 2 mi E McGregor, 18 June 1970, Hegstad 4782 (NDA).

OKLAHOMA: Beaver Co.: 15 mi SW Beaver, 8 May 1913, Stevens 353 (OKLA, MO, OKL). Beckham Co.: 8 mi N Sayre, 18 May 1959, Wiedeman 147 (OKLA, OKL). Cimarron Co.: 2 mi W Kenton, 22 May 1980, Freeman 438 (KSC); 12 mi N & 3 mi W Boise City along Cimarron River, 29 May 1967, Taylor & Taylor 3775 (OKLA, OKL). Comanche Co.: Wichita National Forest, 9 May 1937, Eskew 1711 (OKL, OKLA, IND). Custer Co.: 1.5 mi N Clinton, 13 May 1939, Hopkins & Van Valkenburgh 4069 (OKL). Dewey Co.: 2 mi N Leedey, 28 April 1974, Stephens 74725 (KANU, OKL). Ellis Co.: Canadian River Valley at Pack Saddle Bridge, 26 May 1935, Goodman 2590 (MG, OKL). Greer Co.: 2 mi S Magnum, 29 May 1957, Waterfall 13128 (OKLA-3, OKL-2). Harmon Co.: 13.2 mi W Magnum, 19 June 1947, Waterfall 7178 (OKLA, OKL). Harper Co.: Near Buffalo, 4 May 1913, Stevens 304 (OKLA, MO, OKL). Jackson Co.: 1.2 mi S jct Hwy 44 & 34, 3 May 1975, Barber 752 (OKLA, OKL). Roger Mills Co.: Antelope Hills, 26 May 1935, Goodman 2604 (NY, OKL, MO). Texas Co.: 10 mi W Guymon, 18 May 1941, Hopkins & Van Valkenburgh 5832 (RM). Woods Co.: Waynoka, 1 May 1936, Demaree 12383 (MO, FHKSC, NY, OKL). Woodward Co.: 3 mi SE Woodward, 29 April 1974, Stephens 74756 (KANU, OKL).

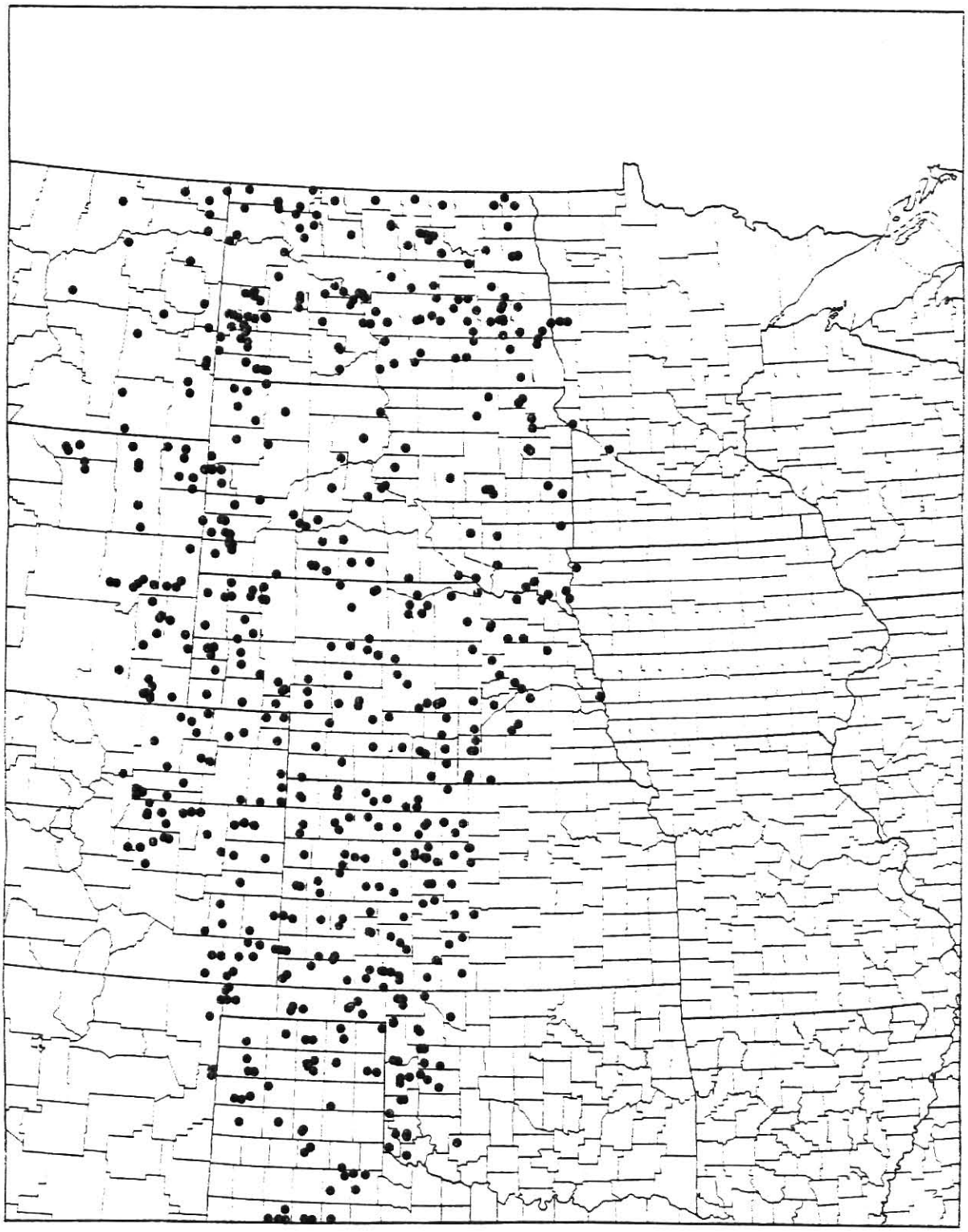
SOUTH DAKOTA: Aurora Co.: 1891, Wilcox 3191 (SDU). Beadle Co.: 11 mi SE Huron, 12 July 1959, Van Bruggen 4720 (SDU). Bennett Co.: LaCreek National Wildlife Refuge, 28 July 1976, Leach s.n. (SDU). Brookings Co.: Brookings, 16 June 1893, Williams s.n. (RM). Brown Co.: Aberdeen, June 1896, Griffiths s.n. (RM). Butte Co.: Shepherds' Monument NE of Belle Fourche along Hwy 85, 24 June 1979, Freeman 203 (KSC). Charles Mix Co.: 1 mi E Pickstown, 5 July 1967, Van Bruggen 5078 (SDU). Clay Co.: Vermillion, 22 May 1911, Visher 4045 (MO). Codington Co.: Horseshoe Lake, 30 May 1958, Dugle 540 (SDU). Corson Co.: Missouri River near Mobridge, 7 June 1960, Van Bruggen 4824 (SDU). Custer Co.: 2.5 mi N Pringle, 23 June 1979, Freeman 187 (KSC). Davidson Co.: Near Mitchell, 6 June 1929, Palmer 36077 (NY, MO). Day Co.: Near Owens Creek 1 mi E Blue Dog Lake, 12 June 1973, Roberts 4 (SDC). Dewey Co.: Sec. 20, T16N, R25E, 4 June 1971, Taylor 10865 (SDC). Fall River Co.: Along Hwy 71 7.6 mi SW jct with Hwy 18, 23 June 1979, Freeman 184 (KSC); Hot Springs, 16 June 1892, Rydberg 918 (NY, SDC, NEB). Gregory Co.: 3 mi N Bonesteel, 21 June 1967, Stephens 11976 & Brooks (KANU). Haakon Co.: 10 mi E Billsburg, 24 June 1967, Stephens 12152 & Brooks (KANU). Hand Co.: Near Miller, June 1907, Case 34 (RM). Harding Co.: 4.1 mi S Ludlow, 24 June 1979, Freeman 206 (KSC). Hutchinson Co.: 1 mi N Tripp, 30 May 1968, Stephens 21506 (KANU). Hughes Co.: Pierre, 1892, Adams 19 (SDC). Jackson Co.: Cedar Pass, 2 June 1914, Over 6294 (SDU). Lawrence Co.: 10 mi W Spearfish, 7 September 1937, Pennell 21377 (NY). Marshall Co.: 7 mi SE Lake City, 15 June 1969, Stephens 31871 & Brooks (NY, NDA). Meade Co.: 1 mi E Mud Butte, 15 June 1970, Stephens 39836 & Brooks (KANU). Mellette Co.:

6 mi N Norris, 7 June 1970, Stephens 39172 & Brooks (KANU). Minnehaha Co.: Dell Rapids, August 1892, Thorber s.n. (SDC). Pennington Co.: NE entrance to Badlands National Monument, 10 June 1957, Lindstrom 84 (SDU). Perkins Co.: 1 June 1912, Visher 555 (RM). Potter Co.: Gettysburg, 1 September 1892, Griffiths & Schlosser 215 (SDC). Shannon Co.: 25 mi NW Sharps Corner, 8 June 1970, Stephens 39342 & Brooks (NY, KANU). Stanley Co.: 25 mi SE Ft. Pierre, 23 June 1967, Stephens 12089 & Brooks (KANU). Sully Co.: Sutton Ranch, 21 May 1938, Snyder 33 (SDC). Todd Co.: 1 mi S By The Way, 28 May 1966, Stanley 146 (KSP). Tripp Co.: 4 mi E & 2 mi N Wewelan, 6 June 1970, Stephens 39048 & Brooks (NY, KANU). Union Co.: Sec. 16, T92N, R49W along Big Sioux River, 27 May 1970, Van Bruggen 5631 (SDU). Washabaugh Co.: Eagle Nest Butte, 30 May 1914, Over 2084 (SDU). Yankton Co.: 5 mi W Yankton, 23 June 1965, McGregor 19457 (KANU). Ziebach Co.: 7.5 mi S Eagle Butte, 25 June 1967, Stephens 12220 & Brooks (KANU).

TEXAS: Armstrong Co.: Palo Duro Canyon 17 mi SSW Claude, 21 May 1966, Rowell 11009 (TTC-2, OKLA). Briscoe Co.: 10 mi NE Silverton, 10 June 1954, Holland 726 (KSP). Comanche Co.: 1 mi S Comanche, 28 April 1934, Tharp s.n. (MO, NY). Cottle Co.: 10 mi S Childress, 26 April 1980, Freeman & Wetter 365 (KSC); 11.7 mi NW jct Farm Rd 1440 & Hwy 83 & 62, 26 April 1980, Freeman & Wetter 372 (KSC). Crosby Co.: 5 mi W Crosbyton, 4 May 1963, Pilcher 29 (OKLA). Dallam Co.: 10 mi NW Dalhart, 12 May 1974, Stephens 75452 (KANU). Deaf Smith Co.: S Bridwell Ranch, 30 July 1967, Waller 1480 (TTC). Dickens Co.: 6 mi W Dickens, ——— , Brown 24 (TTC). Garza Co.: 3 mi NW Post, 29 April 1965, Hutchins 392 (TTC, OKLA). Gray Co.: 24 mi S Pampa, 24 May 1965, Rowell 10815 (TTC-2, OKLA). Hall Co.: 14.1 mi SE Turkey, 26 April 1980, Freeman & Wetter 376 (KSC). Hansford Co.: 6 mi S & 4 mi W Gruver, 14 May 1955, Cutter 29 (OKL). Hartley Co.: 4 mi E Channing, 25 May 1961, Correll 24074 (NY). Hemphill Co.: 1.5 mi S Gem, 24 May 1961, Correll 24030 (NY). Howard Co.: Near Big Spring, 11 June 1900, Eggert s.n. (MO). Hutchinson Co.: Near Stinnett, 21 April 1946, McFarland 41 (OKL, RM). Kent Co.: 11 mi SW Clairemont, 4 May 1963, Pritchard s.n. (OKLA). Lipscomb Co.: 16 mi SE Darrouzett, 6 May 1960, Wallis 8453 (TTC). Lubbock Co.: Buffalo Spring canyon 16 mi NE Lubbock, 23 April 1963, Rowell 8528 (OKLA, OKL). Lynn Co.: Between Tahoka & Lubbock, 29 April 1925, Small & Wherry 12157 (NY). Motley Co.: Along Farm Rd 94 2 mi W jct with Farm Rd 1440, 26 April 1980, Freeman & Wetter 373 (KSC); 5 mi W Matador, 20 May 1980, Freeman 421 (KSC). Ochiltree Co.: Near Perryton, 17 May 1941, Hopkins & Van Valkenburgh 5772 (OKL, NY, RM). Oldham Co.: 7.4 mi W Adrian, 28 May 1964, Rowell 10068 (OKLA). Potter Co.: Ady, 23 May 1920, Pennell 10549 (NY). Randall Co.: Head of Palo Duro Canyon near Canyon, 22 May 1920, Pennell 10545 (NY, MO). Roberts Co.: 27 mi S Perryton, 15 July 1957, Wallis 4954 (TTC). Sherman Co.: Along Farm Rd 2232 2 mi S Hwy 15, 21 May 1970, Flyr 1455 (MO).

WYOMING: Albany Co.: Laramie Hills, 17 June 1891, Buffum s.n. (RM). Campbell Co.: 15.8 mi N Gillette, 10 June 1980, Freeman 548 (KSC); S of Gillette on Hwy 59 along Belle Fourche River, 10 June 1980, Freeman 554 (KSC). Converse Co.: 13.2 mi NE Douglas, 10 June 1980, Freeman 559 (KSC). Crook Co.: Keyhole State Park, 7 June 1980, Freeman 542 (KSC); Near Hulett, 14 June 1935, Ownbey 676 (RM, NY, MO). Goshen Co.: 4.8 mi W Ft. Laramie, 11 June 1980, Freeman 566 (KSC). Johnson Co.: N end Lake DeSmet, 1 July 1953, Porter 6283 (RM, MO). Laramie Co.: 9.6 mi NE jct Hwy 85 & I-25,

Figure 55. Great Plains Distribution of Penstemon albidus



11 June 1980, Freeman 568 (KSC); 5 mi S Cheyenne, 21 June 1935, Ownbey 677 (RM, MO). Niobrara Co.: 40 mi N Lusk, 8 June 1956, Porter 6943 (RM). Platte Co.: Glendo State Park SE Glendo, 10 June 1980, Freeman 561 (KSC); Guernsey State Park NW Guernsey, 11 June 1980, Freeman 565 (KSC); 20 mi SW Wheatland, 19 June 1945, Porter 3542 (NY, OKLA, MO, RM). Sheridan Co.: Mouth Big Goose Canyon, 21 May 1934, Rollins 446 (RM). Weston Co.: 1 mi W South Dakota State Line along Hwy 16, 7 June 1980, Freeman 535 (KSC).

CANADA:

MANITOBA: N of Carberry, 14 June 1906, Macoun & Herriot 78449 (NY).

SASKATCHEWAN: Tribune Dam near Goodwater, 18 June 1959, Bird 455 (OKL).

2. Penstemon ambiguus Torrey

Pentstemon ambiguum Torr., Ann. Lyceum Nat. Hist. New York 2: 228. 1828. Leiostemon purpureus Raf., Atlantic J. 1: 145. 1832. Leiostemon ambiguus Greene, Leafl. Bot. Observ. Crit. 1: 223. 1906. Type: "Hab. Near the Rocky Mountains (E.P. James in 1820).", in eastern Colorado. (Holotype: NY!).

Pentstemon ambiguus β foliosus Benth. in DC., Prod. Syst. Nat. Regn. Veg. 10: 321. 1846. Type: "On high level prairie, July 7 1844", collected by Fremont, no. 623, in Cheyenne County, Colorado, fide Pennell (1935). (Holotype: NY!).

Long-lived suffrutescent perennial. Stems erect or ascending, (2)3-4 (6) dm tall, slender, glabrous to retrorsely scabrous below and glabrous to puberulent near the inflorescence, much-branched from a woody base surmounting a thick, woody creeping rootstock. Leaves filiform, (3)5-30(40) mm long, 0.5-1(2.5) mm wide, entire, acuminate to mucronate, glabrous to scabrid-puberulent, margins glabrous to scaberulent and involute with a very fine scarious edge. Thyrse 6-15 cm long, with 6-10 verticillasters, interrupted, loose, narrow, individual cymes reduced to 2-3 flowers, peduncles glabrous to scaberulent, ascending, to 1.8 cm long, pedicels glabrous to scaberulent, to 0.8 cm long; bracts filiform, resembling the cauline leaves, the lower ones to 2.5 cm long. Calyx glabrous, sepals ovate, 1.5-3.5 mm long, 1-1.5 mm wide, acuminate to mucronate, green with broad white edges, margins

broadly scarious and occasionally erose; corolla (14)16-22(28) mm long, salverform, scarcely bilabiate, glabrous externally, the tube exceptionally slender, throat (3)4-5 mm broad, barely ampliate, pale to deep pink, lined internally with reddish-purple nectar guides and two pubescent reddish or magenta guides on the anterior surface extending back to the tube, pubescent laterally at the orifice, the face of the limb very pale milky pink to milky white, lustrous, oblique to the throat and appearing flat, palate rounded and pubescent, lobes of the upper lip rounded and reflexed, lobes of the lower lip rounded and projecting-spreading; staminode 7-9 mm long from its point of attachment, well included, glabrous; fertile stamens included, anther-sacs 0.5-0.6 mm long, glabrous, deep purple, appearing black, dehiscing the entire length and across the connective, becoming explanate; style 8-10 mm long, glabrous and very slender. Capsule 7-9 mm long. Seeds 1.2-2 mm long, angular, finely reticulate, very dark brown. n = 8.

Sandy plains and hills. Eastern Colorado from the South Platte River southeast to southwestern Kansas in the Arkansas and Cimarron River valleys and east to Ellis, Roger Mills, and Comanche (?) Counties, Oklahoma; western Texas (south to Presidio County) and west to Arizona and Nevada. Two specimens labeled "Wichita Mts., June 1853" and collected by Marcy s.n. (NY) are purportedly from Comanche County, Oklahoma (Pennell, 1935). This is over 100 miles southeast of the next eastern locality (Roger Mills County, Oklahoma) and it should be re-investigated. Flowering from early May to August.

Our plants in the Great Plains are referable to var. ambiguus. In southcentral and western New Mexico, the northern Rio Grande and Pecos River valleys of west Texas, and west to Arizona and Nevada, var. ambiguus is replaced by var. laevissimus (Keck) Holmgren. The latter variety differs

from the nomenclaturally typical variety by having glabrous stems, and with the leaf margins tending to be smooth or only minutely scabrous.

REPRESENTATIVE SPECIMENS:

UNITED STATES:

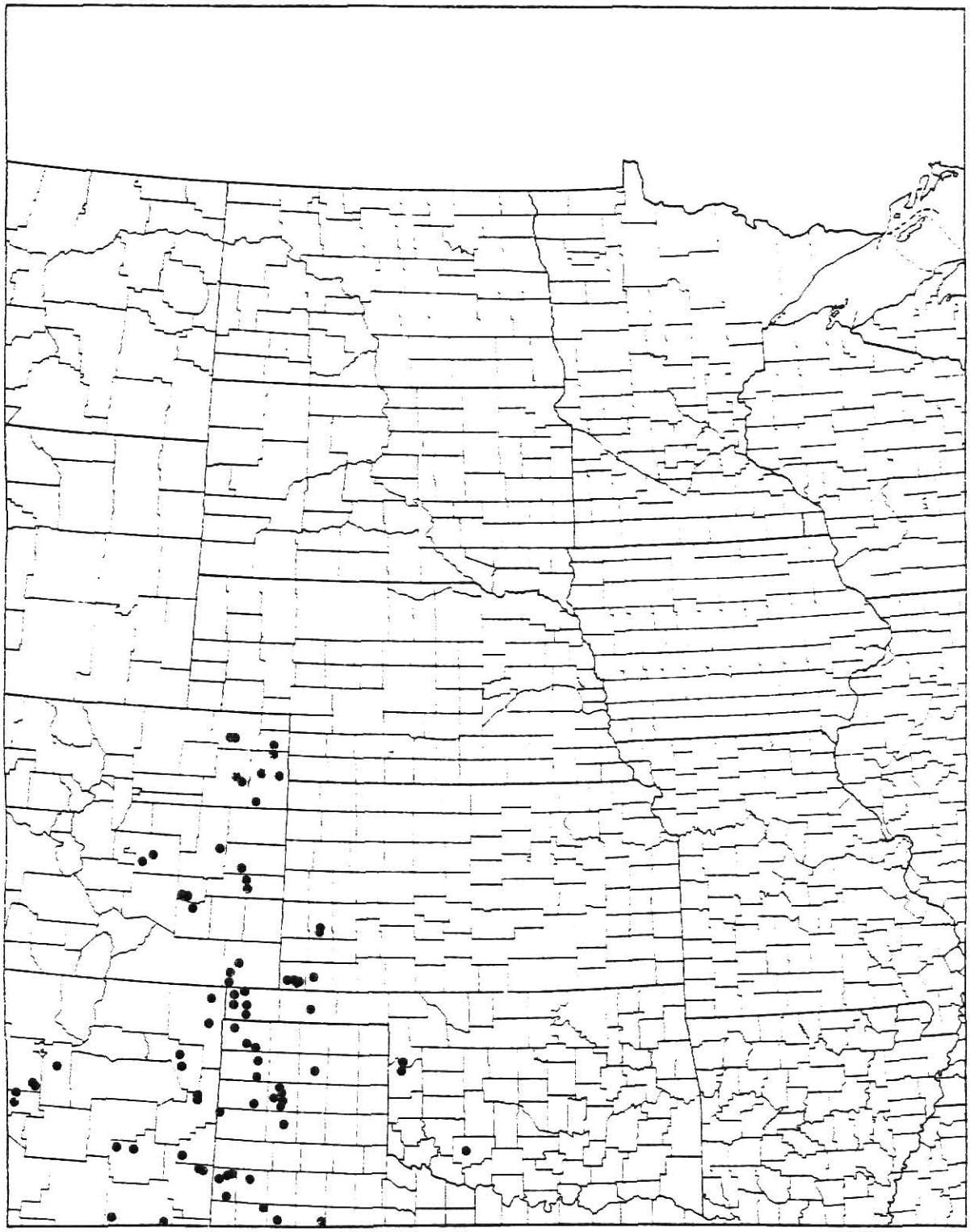
COLORADO: Baca Co.: 6 mi W and 23 mi S of Pritchett, 5 June 1972, Stephens 54266 (KANU, NDA, NY). Cheyenne Co.: 10 mi S of Kit Carson, 10 July 1947, Porter 4268 (RM). Crowley Co.: 5 mi N and 1 mi E of Fowler, 23 June 1961, Lane G1-61 (CS). El Paso Co.: 15 mi E of Fountain, 14 July 1930, Keck 872 (MO). Kiowa Co.: 2 mi E, 3 mi S, and 3 mi E of Eads, 10 June 1972, Stephens 54512 (KANU, NDA). Lincoln Co.: S of Boyero, 1 August 1935, Ward 1835 (CS). Logan Co.: Sterling, 10 June 1896, Osterhout 990 (RM-2, NDA, CS). Otero Co.: Rocky Ford, 18 June 1900, Osterhout 2088 (RM-2, NY). Phillips Co.: 8.5 mi S of Holyoke, 24 June 1972, Stephens 55651 (KANU). Washington Co.: 3 mi S of Otis, 26 September 1972, Stephens 62548 (KANU). Yuma Co.: 3.5 mi S of Yuma-Phillips Co. Line, 5 June 1980, Freeman 507 (KSC); Wray, 21 June 1910, Osterhout 4332 (RM, NY).

KANSAS: Kearney Co.: 11.1 mi SW of Lakin, 9 June 1979, Freeman 141 (KSC); Near Lakin, 12 June 1928, Howe s.n. (NEB, NY). Morton Co.: Cimarron River N of Elkhart, 12 July 1929, Rydberg & Imler 901 (KSC, KANU, NEB, NY, MO); Cimarron River N of Elkhart, 3 June 1979, Freeman 100 (KSC); Cimarron River N of Elkhart, 9 June 1979, Freeman 138 (KSC); 5 mi WNW of Rolla, 18 June 1957, Hulbert 2845 (KSC, KANU, OKLA).; 3 mi N of Elkhart, 1 June 1967, Stephens 11267 (KANU, NY, NDA, OKLA). Stevens Co.: 5 mi NW of Hugoton, 26 August 1951, McGregor 5093 (KANU).

NEW MEXICO: Bernalillo Co.: Albuquerque, 6 September 1909, Rusby s.n. (NY). Chaves Co.: 40 mi E of Roswell, 27 May 1938, Palmer 55 (MO). Curry Co.: 2.5 mi S of Melrose, 18 May 1974, Stephens 75861 (NY, KANU). DeBaca Co.: 15 mi W of Fort Sumner, 6 June 1974, Higgins 8634 (NY). Harding Co.: Mosquero to Bueyeros, 23 June 1924, Eggleston 20192 (NY). Lea Co.: Tatum, 27 May 1934, Reed 3692 (TTC-2). Quay Co.: 0.5 mi N Logan, 14 July 1974, Stephens 79848 (KANU). Roosevelt Co.: 5 mi NE of Portales, 14 June 1930, Goodman & Hitchcock 1122 (NY, MO, RM). Sandoval Co.: E of Bernalillo, 31 August 1956, Barneby 12834 (NY). Santa Fe Co.: 2 mi S of Santa Fe, Summer 1939, Morgan s.n. (OKL). Union Co.: 3 mi SW of Clayton, 12 July 1974, Stephens 79655 (KANU). Valencia Co.: 40 mi E of Grants, 23 June 1940, Hitchcock & Stanford 6766 (NY).

OKLAHOMA: Cimarron Co.: 7 mi E of Kenton, 9 July 1975, Brooks 10728 & Hauser (KANU, NY); 14 mi N and 2 mi W of Boise City, 21 June 1955, Schemnitz s.n. (OKL, OKLA). Comanche Co.: Witchita Mts, June 1853, Marcy s.n. (NY-2). Ellis Co.: 0.5 mi N of Packsaddle Bridge along US 283, 18 June 1973, Goodman & Lawson 8420 (KANU, OKL). Roger Mills Co.: 23 May 1939, Engelman 2001 (OKL). Texas Co.: 3 mi N of Guymon, 14 June 1973, Sanders 20 (OKL).

Figure 56. Great Plains Distribution of *Penstemon ambiguus* var. *ambiguus*



TEXAS: Andrews Co.: 15 mi SW of Andrews, 11 June 1965, Canales 14 (KSC, OKL). Bailey Co.: 8.1 mi E of Muleshoe, 30 May 1964, Rowell 10003 (TTC, OKLA, OKL). Crosby Co.: 7 mi E of Crosbyton, 11 May 1963, Rowell 8593 (OKLA). Culberson Co.: 21.25 mi W of Kent, 9 May 1946, Cory 52273 (NY). Deaf Smith Co.: 1.5 mi SSE of Glenrio, 25 June 1967, Waller 1410 (TTC). Dallam Co.: 4.5 mi NW of Dalhart, 5 August 1974, Stephens 82212 (KANU). Garza Co.: 12 mi N of Post, 6 May 1963, McNabb 148 (OKLA, OKL). Hartley Co.: 2.3 mi W of Channing, 13 June 1964, Roberts 57 (OKLA, OKL). Hockley Co.: Anton, 18 June 1931, Reed 3472 (TTC). Howard Co.: Big Springs, 12 May 1902, Tracy 7995 (NY, NEB, MO-2). Hutchinson Co.: 2.4 mi SE of Sinnett, 31 May 1966, Wiles 434 (TTC). Lamb Co.: 2 mi S of Earth, 14 May 1967, Paetzold 105 (TTC). Lubbock Co.: Vicinity of Lubbock, 4 June 1930, Demaree (OKL, TTC-2). Martin Co.: Stanton, 13 June 1900, Eggert s.n. (MO). Midland Co.: 4 mi E of Midland, 4 June 1943, Cory 42038 (RM, NY). Oldham Co.: 28 mi S of Channing, 28 June 1962, Turner & Melchert 4793 (TTC). Potter Co.: 15 mi N of Amarillo, 30 July 1934, Goodman 2223 (NY, OKL, RM, MO); 2 mi N of Canadian River Bridge on Hwy 287, 3 June 1945, Jepersen & Jepersen 2691 (RM, MO, NY). Presidio Co.: 2 mi W of Marfa, 1 June 1938, Cutler 1953 (NY, MO). Randall Co.: 12 mi NE of Canyon, 30 June 1972, Higgins 5676 (NY). Terry Co.: Meadow, 4 July 1935, Reed 4197 (RM, TTC-2).

3. Penstemon angustifolius Nuttall ex Pursh

Slender to stout herbaceous perennial. Stems erect to assurgent, (1)1.5-4.5(6.5) dm tall, glabrous or scabrid-puberulent and usually distinctly glaucous, 1-5(10) stems arising from a woody crown or short-branched woody caudex surmounting a taproot. Leaves entire, glabrous to sparingly scabrid-puberulent and usually glaucous, thick; basal leaves linear to spatulate or oblanceolate, (2.5)4-9 cm long, 0.2-1.8 cm wide, acute to obtuse, subsessile to petiolate, the petioles usually winged; cauline leaves linear to lanceolate or lance-ovate, 3-11 cm long, 0.2-2.4(4) cm wide, acuminate to acute or caudate, sessile to cordate-clasping, upper cauline leaves equaling or commonly much longer than the internodes. Thyrse 4-30(37) cm long, with (3)5-15(26) verticillasters, distinctly interrupted to compact, cylindrical and not secund, individual cymes (2)4-8(10) flowered, peduncles and pedicels glabrous or scabrid-puberulent, peduncles absent or if present then less than 1 cm long, pedicels 1-10 mm long; bracts lanceolate to lance-ovate or seldom ovate, gradually reduced upward, the lower ones to 9.8 cm

long and 3 cm wide, acute to long-acuminate, bases scarcely clasping to cordate-clasping and overlapping, lower bracts occasionally concealing the pedicels in wide-bracted plants. Calyx glabrous and glaucous to scarcely scabrid-puberulent, sepals lanceolate to lance-ovate, 4-8 mm long, 1-2.5 mm wide, acute or more frequently acuminate, margins narrowly to moderately scarious particularly near the base, entire to suberose, green or tinged lavender; corolla 14-20(23) mm long, tubular-salverform, bilabiate, pink to lavender or blue to deep blue, glabrous externally, throat 4-6 mm broad, moderately ampliate and scarcely ventricose anteriorly, pale internally and lined on the anterior and posterior surfaces with violet or reddish-purple guidelines, the guidelines passing barely onto the lobes of limb, lobes of the upper and lower lips projecting to spreading, palate glabrous or sparingly pubescent with whitish eglandular hairs; staminode 8-10 mm long from its point of attachment, reaching the orifice, broadly flattened and recurved distally, densely bearded at the tip with golden-yellow hairs to 1 mm long and more sparingly bearded for slightly more than 1/2 its length; fertile stamens included or the longer pair reaching the orifice, anther-sacs (0.9) 1.1-1.5 mm long, purple, lined with white or tan along the sutures, papillose along the sutures, divergent, dehiscing nearly to the apices and across the connective, not becoming explanate; style 10-12 mm long, glabrous. Capsule 9-14(15) mm long. Seeds 2.5-3.5 mm long, angular, finely reticulate, brown to dark brown. $\underline{n} = 8$.

As pointed out by Holmgren (1979b), Penstemon angustifolius has a rich nomenclatural history, a fact attributable to the wide range of phenotypic variability exhibited by the species. In the Great Plains, two varieties are recognized and may be separated as indicated.

1. Cauline leaves linear to linear-lanceolate; stem and leaves occasionally

scabrid-puberulent; corolla 14-18 mm long; bracts mostly gradually tapering from the base to an acuminate or acute tip . 3a. var. angustifolius

1. Cauline leaves lanceolate to lance-ovate; stem and leaves glabrous or very rarely scabrid-puberulent; corolla 16-20(23) mm long; bracts usually broadened above the base and tapering to a short or long-acuminate tip . . . . . 3b. var. caudatus

3a. Penstemon angustifolius Nutt. ex Pursh var. angustifolius

Penstemon angustifolium Nutt., in Fras. Catal. 2. 1813. nomen nudum. Pentstemon angustifolia Nutt. ex Pursh, Fl. Amer. Sept. 738. 1814. Chelone angustifolia (Nutt. ex Pursh) Steudel, Nom. Bot. ed. 1. 186. 1821. Type: Collected by Bradbury on his trip up the Missouri in 1811, "near the Minataree village", possibly in Mercer County, North Dakota, fide Pennell (1935). (Holotype: PH, not seen).

Pentstemon caeruleum Nutt., Gen. N. Amer. Pl. 2: 52. 1818. Chelone coerulea (Nutt.) Sprengel, Syst. Veg. 2: 813. 1825. Type: "On the plains of the Missouri, near Fort Mandan and the Indian towns." (Type: not seen).

Sandy to gravelly soil in open prairies and sandhills. Southeastern North Dakota in Barnes County, west to eastern Montana and central Wyoming; south to southern Colorado on the east slope of the Rocky Mountains. Flowering from mid-May to late June.

Penstemon angustifolius var. angustifolius is commonly encountered in the western half of the northern Great Plains, having an eastern limit in North Dakota and South Dakota roughly bounded by the maximum southern limit of the Wisconsin glacier. Throughout most of its range, the variety is consistently narrow-leaved and populations typically exhibit little variation in flower color, most plants possessing flowers that are blue to deep blue, although plants with pink flowers can be found in limited numbers among blue flowered plants in populations. Additionally, plants of var. angustifolius commonly possess scabrid-puberulence on the stem, leaves, bracts, and

sepals, and tend to be shorter in stature than their southern relatives, although occasionally robust specimens may be encountered.

REPRESENTATIVE SPECIMENS:

UNITED STATES:

COLORADO: Adams Co.: Barr, 5 June 1909, Clemens s.n. (RM). Boulder Co.: White Rocks, 21 May 1933, James s.n. (CS). Denver Co.: Denver, 17 June 1917, Clokey 2796 (NY, RM). Douglas Co.: 3.5 mi S Parker, 2 June 1961, Brunquist B-128 (CS). Elbert Co.: 26.3 mi W Limon, 4 June 1980, Freeman 502 (KSC); 31.8 mi W Limon, 4 June 1980, Freeman 500 (KSC). El Paso Co.: Calahan, June 1893, Saunders s.n. (NEB-3, SDC); Along Hwy 83 NE Colorado Springs, 4 June 1980, Freeman 494 (KSC); Along Hwy 115, 0.1 mi NE of El Paso Co. Line, 4 June 1980, Freeman 491 (KSC). Kit Carson Co.: 13.5 mi S & 4 mi E Siebert, 11 June 1972, Stephens 54744 & Brooks (KANU-2). Larimer Co.: 4.3 mi S Wyoming State Line along Hwy 287, 11 June 1980, Freeman 584 (KSC); N of LaPorte, 30 May 1926, Nelson 10764 (MO, RM). Las Animas Co.: Stonewall, July 1912, Beckwith 165 (NY). Morgan Co.: 2 mi S Brush, 15 June 1967, Stephens 11730 (NY, OKLA, KANU). Phillips Co.: 7.5 mi S Holyoke, 7 June 1974, Stephens 77247 (KANU). Sedgwick Co.: Julesburg, 17 August 1915, Pennell 6399 (NY, RM). Washington Co.: 1 mi W Otis, 11 June 1973, Stephens 65549 (NY, KANU). Weld Co.: Evans, 14 June 1909, Johnson 556 (MO-2, NY, RM). Yuma Co.: Along Hwy 51 1 mi S Phillips Co. Line, 10 June 1978, Wilken 13343 (CS).

MONTANA: Carter Co.: 7 mi S Ekalaka, 14 June 1974, Stephens 77742 (KANU). Dawson Co.: 1 mi NE Dawson, 27 May 1965, McMullin 315 (OKL, OKLA). Fallon Co.: 28 mi S Baker, 25 June 1968, Stephens 23245 & Brooks (KANU, NY).

NEBRASKA: Antelope Co.: August 1887, Webber 5564 (NEB). Arthur Co.: 11.4 mi S Arthur, 5 June 1980, Freeman 518 (KSC). Box Butte Co.: N of Hemingford, 1 June 1950, Kiener 25627 (NEB). Brown Co.: 2 mi W & 8.5 mi N Long Pine, 5 June 1970, Stephens 38967 & Brooks (KANU). Buffalo Co.: South Loup River on US 183, 15 July 1966, Levin 70 (FHKSC). Chase Co.: 2 mi S Enders, 24 May 1966, McGregor 19860 (KANU). Cherry Co.: Along Hwy S-16B between Kennedy & Brownlee, 22 June 1979, Freeman 168 (KSC); Merritt Reservoir ca 30 mi SW Valentine, 22 June 1979, Freeman 170 (KSC); 1.2 mi E Nenzel, 22 June 1979, Freeman 174 (KSC); 1.2 mi E Nenzel, 22 June 1979, Freeman 175 (KSC). Custer Co.: Gavin, 9 June 1931, Pennell 15054 (RM). Dawes Co.: 4.5 mi S & 2 mi E Chadron, 5 June 1973, Spires 341 (NDA). Deuel Co.: 20 June 1889, Bodin s.n. (KSC). Garden Co.: 2 mi S Lewellen, 10 June 1967, Stephens 11499 (OKLA, NY, KANU). Grant Co.: 10 mi S Hyannis, 19 June 1961, Lemaire 1909 (NEB). Greeley Co.: 9 mi N Greeley, 21 June 1965, McGregor 19346 (KANU). Holt Co.: Swan Lake, 16 June 1968, Koch 4799 (NEB, OKLA, OKL, KANU). Hooker Co.: 3 mi W Thomas Co. Line along Hwy 2, 5 June 1980, Freeman 524 (KSC); 16.5 mi W Mullen, 20 June 1975, Churchill 6016 (NEB, KANU). Keith Co.: 17.6 mi S Arthur, 5 June 1980, Freeman 516 (KSC); NE of Ogallala, 17 August 1915, Pennell 6402 (NY, RM). Kimball Co.: 8 mi SW & 1.5 mi S Bushnell, 5 June 1969, Stephens 31482 & Brooks (NDA, KANU).

Lincoln Co.: 12 mi NE North Platte, 16 May 1970, Stephens 38015 (KANU, NY). Logan Co.: Along US 83 at Stapleton, 28 May 1972, Churchill 98 (NEB, MO). McPherson Co.: 9.7 mi W Tryon, 5 June 1980, Freeman 519 (KSC). Morrill Co.: 18 mi S & 3 mi E Alliance, 14 July 1972, Larson 483 (*KNSC). Perkins Co.: 0.75 mi E Grainton, 17 May 1970, Stephens 38042 (KANU, NY). Platte Co.: S of Monroe, 23 May 1971, Sutherland & Parker 2902 (NY). Rock Co.: 10.8 mi S Bassett, 31 May 1973, Churchill 805B (NEB). Scotts Bluff Co.: 40.2 mi S jct Hwy 2 & 71 along Hwy 71, 27 May 1972, Churchill 75 (NEB). Sheridan Co.: 2.4 mi E Rushville, 6 June 1980, Freeman 528 (KSC). Sioux Co.: Smiley Canyon in Ft. Robinson State Park, 23 June 1979, Freeman 177 (KSC). Thomas Co.: 13.6 mi SW Thedford, 22 June 1979, Freeman 165 (KSC); 9.7 mi SW Thedford, 22 June 1979, Freeman 166 (KSC); 16.7 mi SW Thedford, 22 June 1979, Freeman 162 (KSC).

NORTH DAKOTA: Barnes Co.: Valley City, 3 July 1891, Lee 530 (NDA). Billings Co.: Along Little Missouri River near Medora, 7-10 June 1967, Porter & Porter 10362 (NY, RM). Bowman Co.: 2.5 mi S & 2 mi W Griffin, 9 June 1969, Zaczkowski 354 (NDA). Burke Co.: Lostwood Game Reserve, 17 June 1971, Hegstad 8004 (NDA). Burleigh Co.: Menoken, 8 May 1966, Graves s.n. (NDA). Dunn Co.: 8 mi S & 4 mi Halliday, 12 June 1975, Larson 5131 (KANU, NDA). Emmons Co.: 18 mi W & 5.5 mi S Strasburg, 27 May 1972, Williams 901 (MO, KANU, NDA); N of Linton Cemetary 1 mi W of Linton, 31 May 1971, Williams 93 (KANU, NDA). Golden Valley Co.: Sentinel Butte, 22 May 1936, Hanson s.n. (RM). Grant Co.: NW of Lark, 18 June 1968, Stevens s.n. (NDA-2). Hettinger Co.: New England, 24 June 1897, Siger 1072 (NDA). Kidder Co.: Dawson Refuge 8 mi S Dawson, 2 June 1973, Williams 1546 (NDA-2, KANU). Logan Co.: Shell Butte 13.5 mi S & 3 mi W Napoleon, 7 June 1972, Williams 978 (NDA, KANU). McKenzie Co.: Gorham, 2 June 1938, Moran 417 (OKL, RM, NDA). Mercer Co.: 0.5 mi S Stanton, 7 June 1974, Larson 4223 (*KNSC, NDA). Morton Co.: 2 mi E New Salem, 12 June 1937, Pennell 20446 (NY). Sioux Co.: Cannon Ball, 30 May 1912, Bergman 1562 (MO, NDA). Slope Co.: 4 mi W & 12 mi N Amidon, 24 June 1979, Freeman 210 (KSC). Stark Co.: 0.5 mi S Dickinson, 16 June 1969, Seiler 107 (NDA).

SOUTH DAKOTA: Bennett Co.: 8 mi W Martin, 7 June 1970, Stephens 39218 & Brooks (KANU). Butte Co.: Sec. 4, T14N, R3E, 17 June 1975, Sisk s.n. (SDU). Corson Co.: 1 mi N & 4 mi E McLaughlin, 26 June 1967, Stephens 12352 & Brooks (KANU). Fall River Co.: Cheyenne River valley 12 mi SW Hot Springs, 23 May 1930, McIntosh 1375 (SDU, NY). Harding Co.: Cave Hills, 17 July 1920, Over & Solem 12668 (SDU). Meade Co.: Confluence Belle Fourche & Cheyenne Rivers, 5 May 1930, McIntosh s.n. (SDU). Pennington Co.: Sheep Mt. Table in Badlands Nat. Monument, 5 June 1957, Lindstrom 52 (SDU). Perkins Co.: 1 June 1912, Visher 579 (RM). Shannon Co.: 10 mi SE Manderson, 8 June 1970, Stephens 39373 & Brooks (KANU). Stanley Co.: Ft. Pierre, 22 June 1853, Hayden s.n. (MO). Todd Co.: 1 mi S By-The-Way, 23 May 1966, Stanley 109 (KSP, SDU). Tripp Co.: 2.5 mi W Rahn Lake, 26 June 1979, Freeman 230 (KSC). Washabaugh Co.: Eagle Nest Butte, 14 May 1853-4, Hayden s.n. (MO, NY).

WYOMING: Albany Co.: 14 mi N Colorado State Line along Hwy 287, 11 June 1980, Freeman 577 (KSC); Sand Creek, 31 May 1900, Nelson 6973 (NEB, NY, MO, RM); E of Laramie, 14 June 1943, Porter 3195 (NY, OKLA, MO); Red Buttes, June 1903, Nelson 8938 (NY, NDA, MO, RM-3); Laramie Plains, 7 June 1894,

Nelson 179 (NY, RM, MO). Campbell Co.: 12 mi N Converse Co. Line along Hwy 59, 6 June 1963, Porter & Porter 9271 (RM). Carbon Co.: 6.7 mi N Medicine Bow, 13 June 1971, Reveal 2331 (NY). Converse Co.: 10.5 mi S Campbell Co. Line along Hwy 59, 10 June 1980, Freeman 558 (KSC). Crook Co.: 10 mi E & 0.2 mi N Moorcroft, 7 June 1980, Freeman 540 (KSC). Fremont Co.: 22 mi NW Lander, 8 June 1959, Wetherell 29 (RM). Goshen Co.: 8 mi N Jay Em, 10 June 1974, Stephens 77456 (KANU). Laramie Co.: 9.7 mi S Goshen Co. Line along Hwy 85, 11 June 1980, Freeman 567 (KSC); 8.4 mi NE jct Hwy 85 & I-25, 11 June 1980, Freeman 569 (KSC); Ft. Laramie, 28 June 1901, Nelson 8304 (NEB, NY, MO); 6 mi N Carpenter, 19 August 1958, Porter & Porter 7677 (RM). Natrona Co.: 1 mi W Powder River, 5 June 1967, Tresler 367 (RM). Niobrara Co.: Near Van Tassel, 11 June 1957, Porter 7265 (NY, RM). Platte Co.: Glendo State Park, 10 June 1980, Freeman 563 (KSC). Weston Co.: 4.3 mi SE Osage, 7 June 1980, Freeman 537 (KSC).

3b. Penstemon angustifolius var. caudatus (Heller) Rydberg

Pentstemon caudatus Heller, Minnesota Bot. Stud. 2: 34. 1898. Pentstemon angustifolius (f.) caudatus (Heller) Rydb., Bull. Torrey Bot. Club 33: 151. 1906. Pentstemon angustifolius (var.) caudatus (Heller) Rydb., Flora of Colorado. (Agric. Exp. Stat. Colorado Agric. College 100:) 309. 1906. Pentstemon secundiflorus (var.) caudatus (Heller) A. Nels., Coult. & Nels. New Manual Bot. Centr. Rocky Mts. 444. 1909. Penstemon angustifolius subsp. caudatus (Heller) Keck in Kearney & Peebles, J. Wash. Acad. Sci. 29: 490. 1939. Type: "The type is our no. 3580, collected May 26, 1897, at Barrance, Taos county, (New Mexico) altitude 6900 feet." Type specimen is actually A.&E. Heller 3581. (Holotype: MIN; Isotypes: KANU!, KSC!, MO!, NY-2!).

Sandy to gravelly soil in open prairies and in the foothills on the east slope of the Rocky Mountains. Northwestern Nebraska, southwest to the foothills of the Rocky Mountains; south through extreme western Kansas and Oklahoma to northern New Mexico. Flowering from early May to mid-June.

Morphologically, this variety of Penstemon angustifolius is a slightly more robust southern relative of the nomenclaturally typical plants of the northwestern Great Plains. In Holmgren's (1979b) succinct recapitulation of the nomenclatural history of this variety, the troublesome nature of this taxon is immediately apparent.

In northeastern New Mexico, Oklahoma (Cimarron County), and the southeastern quarter of Colorado, P. angustifolius var. caudatus is ordinarily

quite distinct from var. angustifolius. In this region, var. caudatus tends to be taller and more robust, have wider leaves, broader bracts that are widened above the base and tapering to a short or long-acuminate tip, and slightly larger flowers than var. angustifolius. In addition, these southern plants typically exhibit more flower color variability than is usually seen in var. angustifolius; var. caudatus having flowers commonly ranging in color from pink to deep blue. Penstemon angustifolius var. caudatus also normally lacks the scabrid-puberulence commonly observed in var. angustifolius.

From eastcentral Colorado north to the panhandle of Nebraska, the distinction between the two varieties is often quite obscure as the two taxa meet and intergrade. Penland, writing in Harrington (1954), summarized well the situation as it exists in this area of sympatry, stating, "The broader, and often caudate, bracts upon which P. caudatus was based, show such complete intergradation with the narrower ones of the species that the assignment of many specimens in the overlapping ranges is wholly arbitrary." Indeed, the assignment of varietal epithets to specimens from this area can be quite difficult.

My own collections from northeastern Colorado and the southern panhandle of Nebraska indicate that specimens easily referable to one or the other variety can be collected in the same population along with specimens intermediate between the two extremes. Other populations may consist of a preponderance of one variety with a few individuals approaching the other variety while still other populations consist entirely of morphologically intermediate individuals.

Flower color in the area of sympatry ranges from pink to deep blue and puberulence is occasionally associated with wide leaved and bracted plants

although this character seems to show less intergradation between varieties than most other characters. For the most part, plants bearing the scabrid-puberulence normally associated with var. angustifolius can be referred to that variety reasonably well.

In light of the above information, the best one can do with many specimens from this area is be content with an understanding of the cause for the long-standing confusion associated with the taxonomy of Penstemon angustifolius in the area of varietal sympatry and assign specimens the varietal epithet that seems most appropriate. If the taxa were allopatric, they would undoubtedly represent distinct species, however, the situation as it exists represents one in which the entities concerned are clearly best considered varieties.

REPRESENTATIVE SPECIMENS:

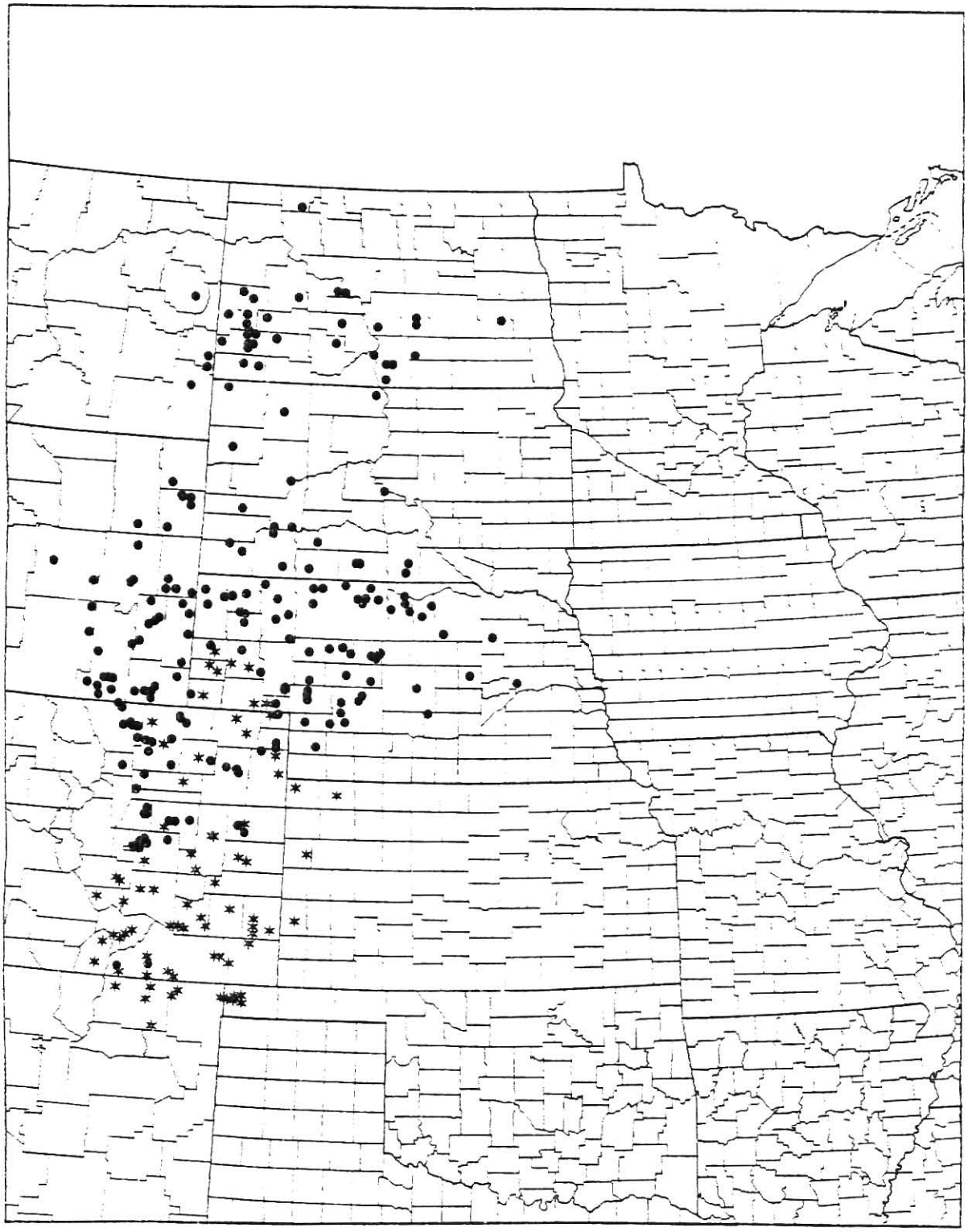
UNITED STATES:

COLORADO: Adams Co.: 2 mi S & 2 mi W Leader, 13 June 1968, Stephens 22562 & Brooks (KANU). Baca Co.: Two Buttes Reservoir, 17 June 1955, Harrington 8002 (CS). Bent Co.: 3 mi S Hasty, 3 May 1947, Harrington 2488 (CS). Cheyenne Co.: 6 mi E Kit Carson along Eureka Creek, 25 May 1973, Stephens 64697 (NY, KANU). Costilla Co.: San Luis Valley, 19 June 1935, Ramaley & Johnson 14649 (NY). Custer Co.: Wet Mt. Valley near Westcliffe, 11 June 1926, Erlanson 1786 (NY). Elbert Co.: 3 mi W Fondis, 17 June 1937, Ownbey 1280 (MO, NY, RM). El Paso Co.: 30 mi SE Colorado Springs, 14 July 1930, Keck 874 (MO, NY). Fremont Co.: 1-2 mi NW Canyon City, 3 August 1915, Pennell 6311 (NY, RM). Huerfano Co.: Lathrop State Park W of Walsenburg, 22 May 1980, Freeman 433 (KSC); Cuchara River above LaVeta, 31 May 1900, Rydberg & Vreeland 5643 (NY, NEB). Kiowa Co.: 10 mi W Haswell, 26 June 1935, Williams 2289 (MO, RM). Kit Carson Co.: 3.4 mi N Siebert, 4 June 1980, Freeman 503 (KSC). Las Animas Co.: Along I-25 2.5 mi N Trinidad, 22 May 1980, Freeman 434 (KSC); 7 mi N & 3 mi E Andrix, 3 June 1980, Freeman 476 (KSC); 7 mi N & 3 mi W Andrix, 3 June 1980, Freeman 478 (KSC). Lincoln Co.: 4 mi N Punkin Center, 11 June 1972, Stephens 54657 (KANU). Logan Co.: 8 mi W Fleming, 1 June 1975, Semple & Semple 1287 (MO). Morgan Co.: Ft. Morgan, 9 May 1910, Johnson s.n. (NY). Otero Co.: 4.4 mi E Pueblo Co. Line along Hwy 10, 3 June 1980, Freeman 482 (KSC). Prowers Co.: 25 mi S Lamar, 21 May 1914, Osterhout 5071 (RM). Pueblo Co.: 4.7 mi W Otero Co. Line, 3 June 1980, Freeman 485 (KSC); Near Pueblo, 12 May 1900, Rydberg & Vreeland 5646 (NY, RM). Sedgwick Co.: 3 mi W Julesburg, 6 June 1954, Harrington

Figure 57. Great Plains Distribution of Penstemon angustifolius

• = var. angustifolius

* = var. caudatus



7469 (CS). Weld Co.: South Platte River valley 18 mi E Greeley, 11 May 1881, Cleburne s.n. (NEB). Yuma Co.: 3.5 mi S Phillips Co. Line, 5 June 1980, Freeman 508 (KSC).

KANSAS: Cheyenne Co.: 12 mi W & 12 mi N St. Francis, 23 June 1971, McGregor 23902 (KANU). Hamilton Co.: 1.5 mi S Syracuse, 8 June 1961, Richards 2594 (KANU). Rawlins Co.: Atwood, Fry s.n. (MO). Wallace Co.: Wallace, 5 July 1885, Kellerman s.n. (NY, KSC).

NEBRASKA: 3 mi E & 9.5 mi N Harrisburg, 5 June 1969, Stephens 31491 & Brooks (KANU). Cheyenne Co.: 2 mi W & 0.75 mi N Sunol, 18 May 1970, Stephens 38103 (KANU). Deuel Co.: 27 June 1891, Rydberg 275 (NEB). Garden Co.: Oshkosh, 8 June 1915, Bates s.n. (NEB). Kimball Co.: 2 mi W Kimball, 14 June 1967, Stephens 11666 & Brooks (KANU). Morrill Co.: Courthouse Rock, 1 June 1973, Churchill 869B (NEB). Scotts Bluff Co.: 3 mi W Gering, 27 May 1951, Kiener 26967 (NEB).

NEW MEXICO: Colfax Co.: 1.3 mi E Springer, 21 May 1980, Freeman 432 (KSC); Raton Pass N of Raton, 4 September 1940, Pennell 26530 (RM, NY). San Juan Co.: Aztec, 6 May 1899, Baker 603 (RM, MO). Union Co.: 5 mi E Folsom, 22 May 1980, Freeman 437 (KSC).

OKLAHOMA: Cimarron Co.: Black Mesa State Park, 22 May 1980, Freeman 439 (KSC); 10.3 mi W Boise City, 22 May 1980, Freeman 440 (KSC); Tesequite Canyon, 15 May 1948, Goodman & Waterfall 4851 (OKL, OKLA).

4. Penstemon auriberbis Pennell

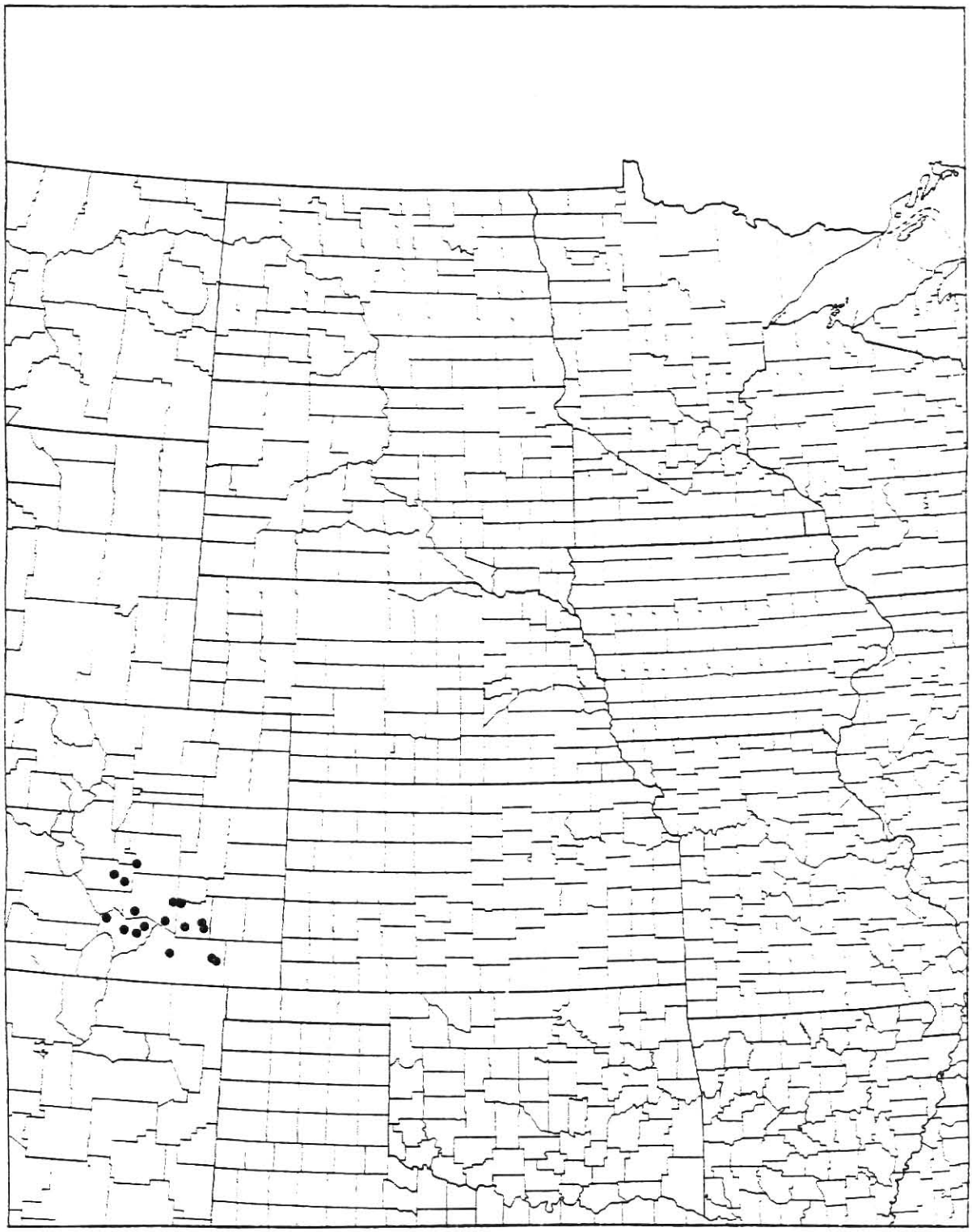
Penstemon auriberbis Penn., Contr. U.S. Natl. Herb. 20: 399. 1920. Type: "collected on a dry sandy sagebrush slope, east of Fountain Creek, northeast of Pueblo, Pueblo County, Colorado, altitude about 1,400 meters, in flower, June 5, 1915, by F.W. Pennell (no. 5731)." (Holotype: NY; Isotypes: GH, RM, US, not seen).

Compact herbaceous perennial. Stems erect to assurgent, 1-3(3.5) dm tall, retrorsely puberulent below and glandular-pubescent near the inflorescence, 1-6(15) stems arising from a simple or branched woody caudex surmounting a taproot. Leaves entire or the upper cauline leaves occasionally denticulate, glabrous to puberulent; basal leaves linear to lanceolate and usually noticeably narrower than the cauline leaves, (1.5)3-6(10) cm long overall, (1)2-5(7) mm wide, acute to obtuse, subpetiolate to petiolate, tufted; cauline leaves linear to linear-lanceolate, (2.5)4-8 cm long, 2-7 mm

wide, attenuate to acute, sessile to slightly clasping. Thyrse (5)7-23 cm long, with 3-8 verticillasters, compact to interrupted, somewhat secund, leafy-bracted, individual cymes 2-4 flowered, peduncles and pedicels glandular-pubescent, peduncles appressed or erect, to 1.5 cm long, pedicels 1-4 mm long; bracts linear to linear-lanceolate, the lower ones to 10 cm long and 1.2 cm wide, acuminate to acute. Calyx densely glandular-pubescent, sepals linear-lanceolate to ovate, (6)7-9 mm long, 1-2 mm wide, long-acuminate, entire, margins narrowly scarious towards the base, midveins frequently reddish-purple at anthesis; corolla (16)18-22(24) mm long, tubular-funnelform, scarcely bilabiate, pale lilac to purplish-blue, the tube and inside paler, glandular-pubescent externally, throat 7-9 mm broad, scarcely inflated and moderately ampliate, lined internally with magenta or bluish-purple guidelines on the anterior and posterior surfaces, the guidelines passing barely onto the lobes of both lips, palate white or pale lavender and pilose near the base of the lobes of the lower lip with eglandular straw-yellow hairs, lobes of the upper and lower lip spreading, the limb appearing rather flat; staminode 13-16 mm long from its point of attachment, barely to conspicuously exserted, distally flattened and recurved, bearded most of its length with stiff or twisted yellow-orange hairs to 2.5 mm long; fertile stamens included or the longer pair reaching the orifice, anther-sacs 1.2-1.5 mm long, tan tinged with purple, papillose along the sutures, widely divaricate, dehiscent nearly the entire length and across the connective, not becoming explanate; style 11-14 mm long, glabrous. Capsule (6)8-10 mm long. Seeds 2-3 mm long, angular, finely reticulate, black. $\underline{n} = 8$.

Sandy-loam to sand in high plains, foothills, and on sagebrush slopes. Southeastern Colorado in the Arkansas and Rio Grande River Valleys south to Union County, New Mexico. Flowering from mid-May to early August.

Figure 58. Great Plains Distribution of Penstemon auriberbis



Common to locally abundant throughout its range, this species frequently forms a striking lilac or bluish carpet, visible from a mile or more away, in the foothills of the Rocky Mountains.

Penstemon auriberbis can be distinguished from all other members of Section Cristati in the Great Plains by having anther-sacs which become widely divaricate but not explanate at maturity. The other members possess anther-sacs which become explanate.

REPRESENTATIVE SPECIMENS:

UNITED STATES:

COLORADO: El Paso Co.: 0.1 mi NE of El Paso Co. Line, 4 June 1980, Freeman 491 (KSC). Fremont Co.: 1.4 mi W of intersection Hwy 120 & 50, 4 June 1980, Freeman 489 (KSC); 29 mi SW of Colorado Springs, 21 May 1949, Weber 4683 (KANU, IND). Huerfano Co.: 1.6 mi E of Cuchara River along Hwy 10, 3 June 1980, Freeman 486 (KSC). Las Animas Co.: 7 mi N & 2 mi W Andrix, 3 June 1980, Freeman 477 (KSC); Sec. 6, T33S, R55W, 7 June 1977, Barrington s.n. (OKLA). Otero Co.: 11.2 mi S of LaJunta, 3 June 1980, Freeman 481 (KSC); 4.4 mi E of Otero-Pueblo Co. Line, 3 June 1980, Freeman 483 (KSC). Pueblo Co.: 0.8 mi W of Otero-Pueblo Co. Line, 3 June 1980, Freeman 484 (KSC); 3.1 mi S of Hwy 165 along I-25, 4 June 1980, Freeman 487 (KSC).

5. Penstemon buckleyi Pennell

Penstemon amplexicaule Buckley, Proc. Acad. Nat. Sci. Philadelphia 13: 461. 1862. non Moench. 1794. Penstemon buckleyi Penn., Proc. Acad. Nat. Sci. Philadelphia 73: 486. 1921. Type: "About 60 miles N.E. of Camp Colorado (Texas). June. 1861." According to Pennell (1921), the type locality was probably in Stephens County, Texas; type collected by S.B. Buckley. (Holotype: PH, not seen).

Stout herbaceous perennial. Stems erect or ascending, 1.5-5.5(8.2) dm tall, glabrous and glaucous, 1-5 from a thick crown or short-branched woody caudex surmounting a taproot. Leaves entire, thick, firm, glabrous and glaucous; basal leaves oblanceolate to spatulate, 1.9-11.6(15) cm long overall, 0.3-2.2(3.1) cm wide, acute to obtuse and often mucronate, petiolate, the petioles usually winged; lower cauline leaves lanceolate to

lance-ovate, upper cauline leaves lance-ovate to ovate, 2-9.5 cm long, 1-3 cm wide, clasping to cordate-clasping, lower cauline leaves frequently crowded and longer than the internodes. Thyrse (4)10-35(57) cm long, with (2)4-20(35) verticillasters, usually very elongate, scarcely to distinctly interrupted, narrow, cylindrical and not secund, individual cymes (2)3-5(11) flowered, peduncles usually absent or if present less than 2 mm long, pedicels glabrous, 1-15 mm long; bracts lance-ovate to ovate or orbiculate, much-reduced above, the lower ones to 7 cm long and 3.1 cm wide, short-acuminate to acute, bases clasping to cordate-clasping and overlapping, the lower bracts concealing the pedicels. Calyx glabrous and glaucous, sepals lance-ovate to ovate, 3.5-6 mm long, 1.5-2.5 mm wide, acuminate to acute, margins broadly scarious and occasionally suberose, green or tinged lavender or purple; corolla (12)14-20 mm long, tubular-salverform, scarcely bilabiate, pale pink or lavender to very pale blue, glabrous externally and internally, throat 4-6 mm wide, slightly ampliate, scarcely ventricose anteriorly, lined internally on the anterior surface with prominent reddish or reddish-purple guidelines, the guidelines occasionally passing onto the lobes of the lower lip, lobes of the upper lip spreading or only slightly reflexed, lobes of the lower lip spreading, the limb usually appearing relatively flat; staminode 7-9 mm long from its point of attachment, included or reaching the orifice, broadly flattened distally, the tip abruptly recurved, densely to moderately bearded with golden-yellow hairs for 1/2 its length, the hairs 1.5 mm long; fertile stamens included or the longer pair reaching the orifice, anther-sacs 0.8-1.2 mm long, purple, lined with white or tan along the sutures, externally minutely papillose, divergent, dehiscing nearly to the apices and across the connective, not becoming explanate; style 9-11 mm long, glabrous. Capsule 12-18(20) mm long. Seeds 2.5-3.5 mm long, angular,

finely reticulate, brown to dark brown. $n = 8$.

Sandy soil, particularly in dunes. Northcentral Kansas west to Kiowa and Prowers Counties, Colorado; south through western Oklahoma to central Texas and southeastern New Mexico.

Penstemon buckleyi is quite similar to P. angustifolius var. caudatus and this morphological similarity has long caused taxonomic difficulties distinguishing the two taxa, particularly in the herbarium. However, field studies indicate the two taxa are distinct and virtually allopatric in their ranges.

Penstemon buckleyi is morphologically distinguished from P. angustifolius var. caudatus by its slightly smaller flowers, bracts that are more ovate and normally lacking a long-acuminate tip, and a more elongate inflorescence that is frequently interrupted. Probably the most distinguishing character, however, is flower color. In all populations of Penstemon buckleyi examined in Kansas, Oklahoma, and Texas, flower color tended to be quite consistent within populations, while interpopulational variation was most frequently lavender but ranged from pale pink to very pale blue. This variation is far less than that exhibited by populations of P. angustifolius var. caudatus examined in New Mexico, Oklahoma, and Colorado. In this taxon it is normal to find populations with flower colors ranging from pink to deep blue. Blue to deep blue colors were never observed in populations of P. buckleyi. Reticulation on the surface of the fruit was used by Pennell (1935) to separate these two entities, however, it appears to vary greatly from plant to plant, and it is best used only as a character of secondary importance.

Penstemon buckleyi and P. angustifolius var. caudatus are undoubtedly closely related and it is probable that the former species arose from the

latter, possibly following the Pleistocene. Differentiation of the two taxa may have taken place as the Wisconsin Glacier receded from the northern Great Plains. Habitats differing markedly from those of the present high plains took shape during the Pleistocene in the form of extensive eolian and fluvial deposits along the Arkansas, Cimarron, and Canadian Rivers in the southwestern Great Plains. Penstemon buckleyi may have had its inception as plants with slightly different ecological adaptations from those of P. angustifolius var. caudatus were selected for in the sandy habitats along these rivers. In Kansas, these sand dunes and to a lesser extent, coarse loess deposits, along the Arkansas and Cimarron Rivers also acted as corridors to the sandy habitats associated with Cretaceous Dakota Sandstone deposits of the Smoky Hills, an area now inhabited by P. buckleyi.

REPRESENTATIVE SPECIMENS:

UNITED STATES:

COLORADO: Kiowa Co.: 2 mi N Eads, 25 May 1973, Stephens 64716 (KANU). Prowers Co.: Near Lamar, 5 June 1892, annon. 1804 (CS).

KANSAS: Barber Co.: Sec. 34, T30S, R12W, 2 June 1979, Freeman & Freeman 92 (KSC); 5.2 mi S Sawyer, 27 April 1980, Freeman & Wetter 381 (KSC). Chase Co.: N of Cottonwood Falls, 15 May 1938, Cook s.n. (FHKSC). Clark Co.: 6 mi W Englewood, 10 July 1929, Rydberg & Imler 830 (KANU, NY). Cloud Co.: 1930, Fraser 480 (KSC). Comanche Co.: 6 mi W Barber Co. Line along Hwy 160, McGregor 12877 (KANU, NY). Edwards Co.: 3 mi E Kinsley, 14 May 1975, Stephens 84018 (KANU). Ellsworth Co.: Horsethief Canyon on E side Kanopolis Reservoir, 18 June 1981, Freeman 1010 (KSC). Finney Co.: Buffalo Park State Game Refuge S of Garden City, 2 June 1980, Freeman 472 (KSC). Gove Co.: Near Park, 1941, Weber 87 (KSC). Gray Co.: 1 September 1897, Hitchcock s.n. (KSC). Hamilton Co.: Along Arkansas River, 15 June 1912, Wilson & Miller s.n. (KANU). Harper Co.: 3 mi W & 6 mi N Attica, 18 May 1972, McGregor 24219 (KANU). Harvey Co.: Sand Prairie Nat. History Reservation 13 mi W North Newton, 18 May 1966, Hulbert 4316 (KSC). Kearney Co.: 11.1 mi SW Lakin, 9 June 1979, Freeman 142 (KSC). Kingman Co.: 7 mi W & 2 mi N Kingman, 18 May 1972, McGregor 24222 (KANU). Kiowa Co.: 0.8 mi E Greensburg, 23 May 1980, Freeman 445 (KSC); 2 mi E Greensburg, 2 May 1936, Bondy 367 (OKL, FHKSC, OKLA-2, MO). Lincoln Co.: 10 mi SW Lincoln, 26 June 1953, McGregor 7436 (KANU). Meade Co.: SE ¼ sec. 1, T32S, R26W, 2 June 1979, Freeman & Freeman 98 (KSC); SE ¼ sec. 1, T32S, R26W, 23 May 1980,

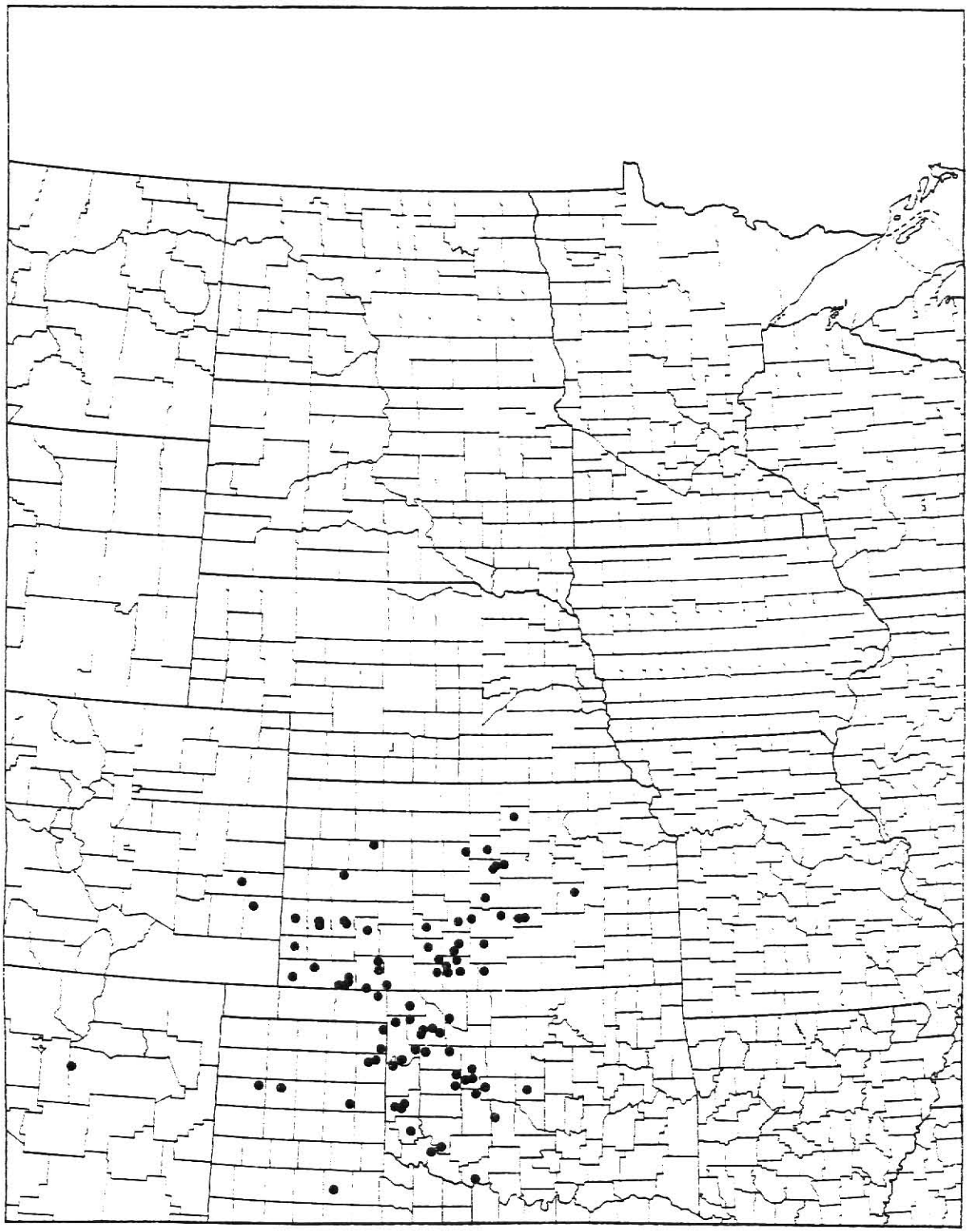
Freeman 443 (KSC). Morton Co.: 12 mi SE Richfield in Cimarron Valley, 20 September 1912, Rose 17113 (NY). Pratt Co.: Sawyer, 26 April 1935, Runyon 49 (IND, KSC, RM, FHKSC); 5 mi E Pratt, 4 May 1943, Horr E 471 (SDC, KSP, KANU-2, NY, RM, OKLA, OKL, IND-2). Reno Co.: 5 mi N & 3 mi E Stafford, 4 May 1963, Harris 23 (FHKSC). Rice Co.: August 1895, Hitchcock s.n. (KSC). Russell Co.: 8 mi S Lucas, 30 April 1976, McGregor 28916 (KANU, NY). Saline Co.: SW of Brookville, 25 April 1930, Hancin 187 (KSC). Scott Co.: Horse Thief Canyon in Scott Co. State Park, 5 May 1963, Russell 42 (FHKSC). Seward Co.: 3 mi SW Cimarron River along Hwy 54, 22 May 1980, Freeman 441 (KSC); 12 mi E Liberal, 11 July 1929, Rydberg & Imler 861 (KANU, NY). Stafford Co.: 8.5 mi W Stafford, 14 May 1975, Stephens 84002 (KANU). Stanton Co.: August 1895, Hitchcock s.n. (KSC). Stevens Co.: August 1895, Hitchcock s.n. (KSC).

NEW MEXICO: San Miguel Co.: E of Pecos, 8-19 May 1902, Earle 679 (NY).

OKLAHOMA: Beaver Co.: Near Knowles, 5 May 1913, Stevens 323 (MO, NY, OKLA, OKL). Beckham Co.: W of Sayre, 24-25 May 1920, Pennell 10560 (MO, NY, OKLA). Blaine Co.: 2.5 mi E & 3.5 mi N Hydro, 26 April 1952, Patterson 35 (OKLA). Caddo Co.: Hinton, 26 April 1936, Demaree 12324 (FHKSC, MO, NY, OKLA, OKL); Caddo Canyon, 15 April 1934, Goodman 2092 (MO, NY, RM, OKL). Canadian Co.: Canadian River Valley along US 66, 12 May 1951, Goodman 5472 (OKL). Cotton Co.: Along Red River, 14 June 1941, Pottz 103 (OKL). Custer Co.: 6 mi E Thomas, 27 April 1964, Means 1016 (OKLA). Dewey Co.: 4.5 mi S Vici, 28 April 1974, Stephens 74728 (KANU, OKL). Ellis Co.: 21.5 mi N Shattuck, 8 May 1974, Stephens 75079 (KANU). Grady Co.: Verden, 30 April 1939, Brooks s.n. (OKL). Greer Co.: Quartz Mt. State Park NE of Magnum, 25 April 1980, Freeman & Wetter 358 (KSC). Harper Co.: 12 mi S Buffalo, 18 May 1973, Goodman & Lawson 8298 (KANU, OKL). Jackson Co.: 5 mi SE Headrick, 16 April 1954, Booker 21 (OKLA). Kiowa Co.: W edge Kiowa Co. along US 62, 30 April 1944, Hopkins, Nelson, & Nelson 212 (MO, OKL, OKLA, RM). Oklahoma Co.: Near Oklahoma City, 18 April 1941, Hyde 8039 (OKL). Roger Mills Co.: Antelope Hills, 26 May 1935, Goodman 2607 (MO). Woods Co.: N of Cimarron River near Waynoka, 18 May 1947, Goodman & Waterfall 4232 (NY, OKLA, OKL). Woodward Co.: Entrance to Boiling Springs State Park, 5 April 1962, Waterfall 16961 (KSC, OKLA).

TEXAS: Andrews Co.: 8.4 mi S Andrews, 16 April 1965, Reed 8 (TTC). Callahan Co.: 5 mi E Cross Plains, 29 May 1961, Cumbie 190 (TTC). Garza Co.: 13 mi E Post, 11 April 1966, Hutchins 1043 (TTC, OKLA). Gray Co.: 6 mi N McLean, 21 April 1946, McFarland 49 (OKL). Hemphill Co.: 7 mi NE Canadian, 4 June 1957, Rowell 5301 (TTC-3). Howard Co.: Big Spring, 17 May 1928, Palmer 34010 (NY). Kent Co.: Near Salt Fork of Brazos River, 25 September 1960, Cumbie 55 (TTC). Lipscomb Co.: 7.5 mi E Follett, 9 May 1974, Stephens 75149 (KANU). Motley Co.: 5 mi W Matador, 20 May 1980, Freeman 421 (KSC). Oldham Co.: S of Channing near Canadian River, 29 April 1972, Higgins 5103 (NY). Potter Co.: 35 mi N Amarillo, 1 May 1968, Crook & Crook 559 (OKL). Taylor Co.: Near Abilene, 7 June 1900, Eggert s.n. (MO). Winkler Co.: 10 mi NE Kermit, 6 May 1961, Rowell, Cornett, & Crum 8207 (TTC). Yoakum Co.: 8 mi S Plains, 8 April 1944, Reed s.n. (TTC-3).

Figure 59. Great Plains Distribution of Penstemon buckleyi



6. Penstemon cobaea Nuttall

Pentstemon cobaea Nutt., Trans. Amer. Philos. Soc. 2(5): 182. 1837. Penstemon cobaea (subsp.) typicus Penn., Acad. Nat. Sci. Philadelphia Monogr. 1. 249. 1935. Type: "In the sterile and denuded portions of the prairies of Red river, in calcareous soil. Flowering in May.", collected by Nuttall, type labeled "Pentstemon Cobaea Red River" and possibly from the vicinity of Choctaw County, Oklahoma, fide Pennell (1935). (Holotype: BM; Isotype: PH; Phototypes: DS, GH, NY!).

Penstemon hansonii A. Nels., Univ. Wyoming Publ. Sci. Bot. 1: 129. 1926. Type: "The type is H.C. Hanson's Arizona no. 709, which he reports as infrequent on over-grazed south slopes, near Flagstaff, July 23, 1923." (Holotype: RM!; Isotype: PH; Phototype: NY!).

Robust herbaceous perennial. Stems erect or assurgent, (1.5)2.5-6.5(10) dm tall, retrorsely puberulent below and glandular-pubescent near the inflorescence, 1-3(4) stems arising from a frequently massive, woody, creeping rootstock. Leaves subentire or undulate to sharply serrate, glabrous to puberulent or occasionally pubescent, thick; basal leaves frequently absent or withering, when present (ob)lanceolate to spatulate, 3.5-18(26.4) cm long overall, 0.8-5.5(7.6) cm wide, acute to rounded, subsessile to petiolate, the petioles frequently winged; cauline leaves lanceolate to ovate, 3.5-12(15) cm long, 1-4.5(5.4) cm wide, acute, the lower ones sessile, becoming cordate-clasping above. Thyrse 10-30(52) cm long, with 3-6(8) distinct to indistinct verticillasters, individual cymes 2-6 flowered, peduncles and pedicels densely glandular-pubescent, peduncles appressed or erect, to 3.9 cm long, pedicels 1-13 mm long; bracts mostly ovate, the lower ones to 7.8 cm long and 7.4 cm wide, acute, glabrous to glandular-pubescent. Calyx densely glandular-pubescent and viscid, sepals lanceolate to lance-ovate, (8)10-16 mm long, 2.5-4.5 mm wide, acute, entire, herbaceous throughout or with narrowly scarious margins near the base, usually reddish-purple at the tip; corolla 35-55 mm long, strongly bilabiate, white or pink to pale or deep violet-purple, glandular-pubescent and viscid externally, throat (15)18-25

mm broad, abruptly much-inflated and ventricose-ampliate, glandular internally, constricted very slightly at the orifice, lined internally with prominent magenta or violet guidelines, the guidelines passing well onto the lobes of the lower and upper lips, palate glandular-pubescent but not pilose, lobes of the upper lip arched-projecting, lobes of the lower lip spreading to reflexed; staminode 23-30 mm long from its point of attachment, included or slightly exserted, tip flattened and recurved, bearded nearly the entire length with golder-yellow hairs, hairs at the tip tortuous and 3.5 mm long, medial hairs shorter and stiff, retrorse; fertile stamens included, anther-sacs 1.3-1.6 mm long, light brown to brown, glabrous, divaricate, dehiscent throughout and across the connective, becoming explanate; style 18-34 mm long, glabrous. Capsule 13-18 mm long. Seeds 2.5-3.5 mm long, angular, finely reticulate, black. $n = 8$.

Calcareous or gypsiferous loams or sand-loams in open prairies, eroded pastures, and hills. Southern Nebraska south of the Platte River through Kansas, southwestern Missouri, Arkansas, Oklahoma, and in Texas east of the 101st meridian. Harrington (1954) also cites a specimen from Baca County, Colorado (not seen). Frequently taken into cultivation in gardens, the species is known to escape occasionally and has been reported in Ohio (Pennell, 1935) and Arizona. Flowering from early April in Texas through June in Nebraska.

Our plants in the Great Plains are referable to var. cobaea. In the White River valley and Ozark region of southern Missouri and northern Arkansas, southwestern Arkansas, and southeastern Oklahoma, nomenclaturally typical Penstemon cobaea is replaced by var. purpureus Pennell. This variety differs from the var. cobaea in having a corolla which is dark violet-purple. Pennell (1922) states var. purpureus also differs in having

a less inflated corolla, longer leaves, and herbage tending to be darker green, however, these characters appear to be inconsistent. While the corolla color of the typical variety is subject to much variation, ranging from white to pale violet-purple, none of the populations examined in the Great Plains attain the deep purple color exhibited by var. purpureus.

Easily recognized in the field, the two varieties are virtually indistinguishable on a herbarium sheet due to the fading of corolla color upon pressing of the dark-flowered plants.

REPRESENTATIVE SPECIMENS:

UNITED STATES:

KANSAS: Allen Co.: 2 mi N Iola near Deer Creek, 7 June 1979, Freeman 120 (KSC). Anderson Co.: 1.5 mi N Welda, 2 June 1950, McGregor 4263 (KANU). Barber Co.: 5 mi SW Medicine Lodge, 6 July 1929, Rydberg & Imler 691 (NY, KANU). Barton Co.: 3.5 mi N Susank, 5 June 1974, Brooks 6077 (KANU). Bourbon Co.: Ft. Scott, July 1892, Hitchcock s.n. (KSC). Brown Co.: Everest, 1939, Olson 4 (KSC). Butler Co.: Flint Hills Prairie 5.75 mi E Cassoday, 28 May 1981, Freeman & Freeman 936 (KSC). Chase Co.: 12.2 mi S Council Grove, 6 June 1979, Freeman 114 (KSC). Chautauqua Co.: 0.5 mi W Waunetta, 20 May 1967, Stephens 10968 (OKLA, NY, KANU). Clay Co.: July 1895, Hitchcock s.n. (KSC). Cloud Co.: Concordia, 17 June 1897, Hitchcock s.n. (KSC). Coffey Co.: 1 mi NE Waverly, 1 June 1966, Henderson 66-416 (KANU). Cowley Co.: 1 mi W Cambridge, 8 June 1979, Freeman 131 (KSC); 2 mi S & 2 mi E Arkansas City, 18 May 1967, Barker 3552 (NDA, NY, KANU). Crawford Co.: 0.75 mi W Greenbush, 28 May 1972, Holland 3022 (KSP). Dickinson Co.: 12.7 mi W Junction City, 10 June 1979, Freeman 154 (KSC). Douglas Co.: 2 mi SW Lawrence, 1 June 1940, McGregor 66 (KSC, KANU). Edwards Co.: May 1933, Finch s.n. (KSC). Elk Co.: 3 mi W Grenola, 8 June 1955, McGregor 10353 (KANU). Ellis Co.: 14 mi N Hays, 29 June 1935, Runyon 140 (RM, OKLA, OKL, FHKSC, IND). Ellsworth Co.: 0.9 mi W CK Ranch & 2 mi S Hwy 40, 20 October 1979, Freeman 327 (KSC). Finney Co.: 10 mi W & 6 mi N Kalvesta, 2 June 1967, Stephens 11302 (KANU). Franklin Co.: June 1901, Smyth s.n. (KSC). Geary Co.: N ½ sec. 1, T12S, R6E, 21 May 1979, Freeman 50 (KSC). Greenwood Co.: N of Madison, 7 June 1979, Freeman 117 (KSC); Flint Hills Prairie 6.25 mi E Cassoday, 21 May 1981, Freeman & Freeman 957 (KSC). Harper Co.: 3 mi E Danville, 31 May 1968, Birkholz 2222 (NDA, KANU). Harvey Co.: 8.5 mi E Newton, 3 June 1961, Harms 1634 (KANU). Jackson Co.: Pottawatomie Indian Reservation W of Mayetta, June 1941, Schultz A106 (KSC). Jefferson Co.: 4.5 mi SE Williamston, 27 July 1950, Latham 557 (KANU). Jewell Co.: 5 mi S & 4.5 mi W Mankato, 2 June 1936, Osborn 928R (KSC). Johnson Co.: 1.25 mi SW Stanley, 6 June 1957, Wagenknecht 3688 (KANU). Kingman Co.: 23 August 1896, Hitchcock s.n. (KSC). Kiowa Co.: 1 mi SW Belvidere, 13 June 1951, Horr & McGregor 3761 (NY, KANU). Labette Co.:

3 mi W Valeda, 23 May 1967, Stephens 11018 (KANU). Lincoln Co.: 2 mi E jct Hwy 181 & 18 along Hwy 18, 10 June 1979, Freeman 150 (KSC). Linn Co.: Mound City, 9 June 1928, Taylor s.n. (KSP-2). Lyon Co.: 3 mi W Allen, 3 June 1960, McGregor 15618 (NY, KANU). Marion Co.: 3 mi W Marion, 23 May 1956, Hulbert 2550 (KSC, KANU). Marshall Co.: 10 December 1896, Hitchcock s.n. (KSC). McPherson Co.: McPherson, July 1892, Hitchcock s.n. (KSC). Miami Co.: 8 mi W Osawatomie, 30 May 1966, Henderson 66-401 (KSC, KANU). Mitchell Co.: S of Simpson, 28 May 1942, Gates 21414 (FHKSC). Montgomery Co.: 3.5 mi S Cherryvale, 3 June 1966, Barker 2198 (NY, KANU). Morris Co.: Council Grove Reservoir 2 mi N Council Grove, 6 June 1979, Freeman 112 (KSC). Nemaha Co.: Nemaha Co. State Lake, 26 June 1974, Brooks 6877 (KANU). Neosho Co.: 7 mi E Chanute, 28 May 1966, Holland 1284 (KSP). Osage Co.: 5 June 1899, Brown s.n. (KSC). Osborne Co.: 1 mi NW Bloomington, 1 June 1979, Freeman 77 (KSC); Near Osborne City, 2 June 1894, Shear 70 (RM, NEB, NY). Ottawa Co.: Ottawa Co. State Park, 21 May 1948, McGregor 1458 (KSC, KANU). Pottawatomie Co.: Tuttle Creek State Park N of Manhattan, 31 May 1979, Freeman 64 (KSC); Tuttle Creek State Park N of Manhattan, 31 May 1979, Freeman 65 (KSC). Pratt Co.: 2 mi SE Pratt, 10 May 1977, McGregor 30141 (KANU). Rawlins Co.: 9 mi W Atwood, 21 June 1957, Hulbert 2984 (KSC). Reno Co.: 5 mi N Hutchinson, McGregor 7328 (KANU). Republic Co.: NE ¼ sec. 1, T3S, R3W, 4 June 1960, Morley 23 (NY, KANU). Rice Co.: 3 mi E & 6 mi N Little River, 5 June 1974, Brooks 6128 (KANU). Riley Co.: 1.5 mi S Manhattan, 23 May 1979, Freeman 51 (KSC); 1.5 mi S Manhattan, 31 May 1979, Freeman 67 (KSC); 1.5 mi S Manhattan, 31 May 1979, Freeman 68 (KSC); 0.5 mi NE jct Denison Ave & Kimball Ave along Kimball in Manhattan, 6 May 1981, Freeman 916 (KSC); Konza Prairie Research Natural Area, 17 June 1977, Freeman 7780 (KSC). Rooks Co.: 6 mi SW Stockton, 25 May 1973, McGregor 24950 (KANU). Rush Co.: 6 mi E Rush Center, 19 June 1957, Lathrop 3850 (KANU). Russell Co.: 3.5 mi N Russell, 1 June 1979, Freeman 88 (KSC). Saline Co.: 10 mi E Salina, 4 June 1963, Nagel 147 (FHKSC). Sedgwick Co.: Wichita, May 1892, Miller s.n. (KSC). Shawnee Co.: 2 mi E Dover, 4 June 1951, Horr 3722 (OKLA, IND). Sheridan Co.: 4 mi S Hoxie, 23 June 1976, Hauser & Brooks 3006 (KANU). Smith Co.: 1.1 mi W Cedar, 13 June 1980, Freeman 602 (KSC). Sumner Co.: 0.5 mi S New Haven, 20 May 1961, McGregor 16892 (KANU). Wabaunsee Co.: 2.8 mi SE Wabaunsee, 21 May 1981, Freeman & Freeman 934 (KSC). Wallace Co.: Ft. Wallace, 1867, Bell s.n. (RM). Washington Co.: NW of Linn, 1933, Dodd 84 (KSC). Wilson Co.: 3 mi NW Neodesha, 3 June 1950, McGregor 4294 (KANU). Woodson Co.: 14 mi SE Yates Center, 9 June 1960, Hulbert 3949 (KANU). Wyandotte Co.: S 136th St, Kansas City, 1 June 1964, Brawner s.n. (KSP).

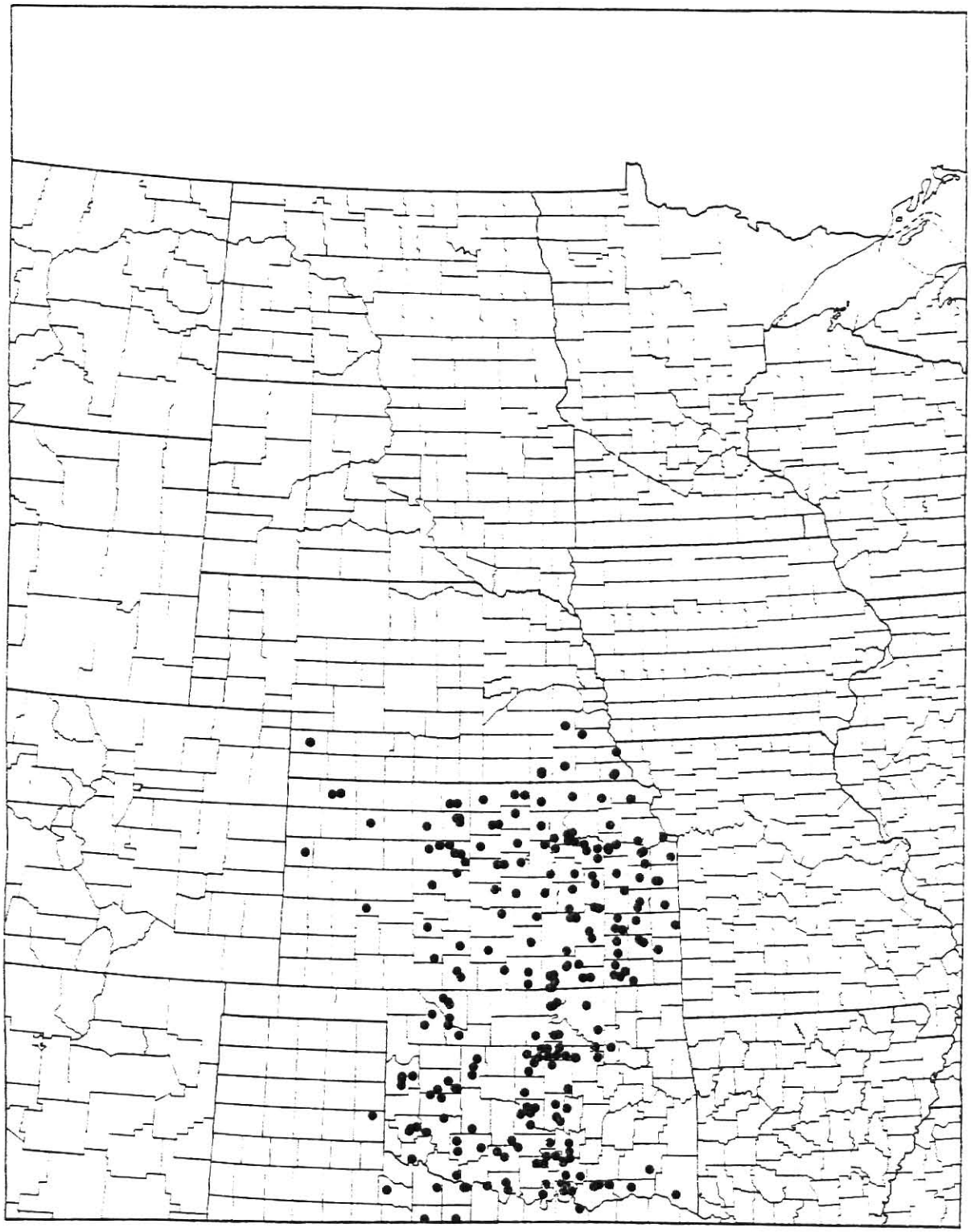
NEBRASKA: Chase Co.: 21 July 1941, Tolstead 411606 (NEB). Gage Co.: 1882, Knight s.n. (NEB). Jefferson Co.: Fairbury, 31 May 1886, annon. 29 (NEB). Lancaster Co.: Lincoln, 20 June 1885, Webber 5563 (NEB). Nemaha Co.: Peru, 22 June 1935, Clark s.n. (SDU). Otoe Co.: Palmyra, 28 June 1894, Turrell 130 (NEB). Richardson Co.: Salem, 25 June 1951, Kiener 27150 (NEB, KANU, OKL). Webster Co.: 5 mi S Red Cloud, 6 June 1975, Nagel s.n. (*KNSC).

OKLAHOMA: Blaine Co.: 8 mi S Watonga, 25 May 1935, Goodman 2566 (OKL, MO). Bryan Co.: 2.5 mi N & 1.5 mi E Cade, 16 May 1962, Taylor & Taylor 685 (OKLA, OKL). Caddo Co.: 8 mi W Apache, 11 May 1968, Stephens 20306 (KANU). Carter Co.: Lake Murray, 9 May 1942, Tenney 176 (OKL). Choctaw Co.: 6 mi W & 3 mi N Hugo, 12 May 1941, Rose 36 (OKLA). Cleveland Co.: Lake Thunderbird E of Norman, 18 May 1980, Freeman 401 (KSC); 3 mi SE Norman, 30 May

1944, Hopkins, Nelson, & Nelson 636 (OKLA, NY, OKL, MO, RM). Comanche Co.: Wichita Nat. Forest, 9 May 1937, Eskew 1716 (OKLA, OKL). Creek Co.: Sapulpa, 2 June 1924, Williams s.n. (KANU). Custer Co.: Weatherford, 25 May 1920, Pennell 10572 (OKLA, NY, MO). Garvin Co.: 14.9 mi N Sulphur, 19 May 1980, Freeman 405 (KSC). Grady Co.: 4 mi NE Cox City, 14 June 1964, Pearce 1246 (OKL, KSC). Greer Co.: 11.9 mi N jct US 62 & OK 34, 17 May 1975, Barber 805 (OKLA, OKL). Jackson Co.: 6 mi E Eldorado, 18 May 1971, Harkins 77 (OKLA). Jefferson Co.: 0.9 mi E & 3 mi N Oscar, 20 May 1980, Freeman 415 (KSC); 15.5 mi E Waurika, 25 April 1980, Freeman & Wetter 342 (KSC). Johnson Co.: 2.5 mi N Ravia, 29 July 1967, McWilliam P6707 (OKL-2). Kay Co.: 4.4 mi W Kaw City, 30 May 1935, Stratton 3929 (OKLA). Kiowa Co.: Granite Mts. S of Lake Altus, 14 May 1950, Waterfall 9450 (OKLA, KANU). Lincoln Co.: 6 mi SE Perkins, 3 May 1936, Payton 80 (OKLA). Logan Co.: 1.5 mi W Langstone, 5 May 1938, Wade 119 (OKLA). Love Co.: 4 mi W & 6 mi N Marietta, 17 June 1968, Russel & Mapp P6830 (OKL). McClain Co.: Johnson's Pasture, 25 June 1964, Thomas s.n. (OKL-2). McCurtain Co.: Near Idabel, 21 May 1916, Houghton 3717 (NY, OKL). Major Co.: Glass Mts., 18 May 1947, Goodman & Waterfall 4225 (OKL, OKLA). Marshall Co.: 3 mi E & 0.25 mi S Kingston, 19 May 1980, Freeman 411 (KSC). Murray Co.: 2 mi E Big Canyon, 19 May 1980, Freeman 407 (KSC). Noble Co.: 1.5 mi W Lela, 10 May 1964, Graves 69 (OKLA). Oklahoma Co.: Oklahoma City, 16 May 1937, Waterfall 564 (OKL, OKLA). Osage Co.: W of Skiatook along Quapaw Creek, 18 May 1980, Freeman 392 (KSC). Pawnee Co.: 2 mi W Pawnee, 6 June 1937, McLean 29 (OKL). Payne Co.: 17 mi SE Stillwater, 14 May 1939, Simpson 86 (OKLA). Pontotoc Co.: 2.5 mi S Ada, 14 May 1947, Robbins 2459 (NY, OKL). Pottawatomie Co.: 1 mi E Sacred Heart, 4 May 1968, Semtner 166 (OKLA). Pushmataha Co.: Near Stink, 16 April 1938, Hopkins 2858 (OKL-2). Roger Mills Co.: 7 mi S Roll, 27 May 1959, Wiedeman 252 (OKL, OKLA). Seminole Co.: 6 mi NW Seminole, 12 May 1940, Nelson 62 (OKL). Stephens Co.: 8 mi N & 4 mi W Duncan, 27 May 1960, Waterfall 15914 (OKL). Tillman Co.: N edge of Grandview, 25 April 1980, Freeman & Wetter 348 (KSC). Tulsa Co.: Tulsa, 4 June 1957, Clark 267 (OKL, OKLA). Washita Co.: 3 mi NE Foss, 16 May 1938, Pennell 21413 (NY). Woods Co.: Cora, 21 May 1913, Stevens 539 (MO, NY, OKL, OKLA). Woodward Co.: 5 mi E Woodward, 29 May 1952, Waterfall 10721 (OKLA).

TEXAS: Archer Co.: 2 mi W Archer City, 14 May 1968, Stephens 20627 (KANU). Austin Co.: Industry, 1844, Lindheimer s.n. (MO). Baylor Co.: 4 mi SW & 6 mi NW Seymour, 9 May 1966, Patterson s.n. (TTC). Bee Co.: Beeville, 29 March 1937, Cutler 909 (MO). Bell Co.: 9.3 mi W Belton, 23 April 1954, York & York 54216 (KANU, NEB, OKL). Bexar Co.: 15 mi S San Antonio, April 1949, Burr 524 (KANU). Brown Co.: 15 mi SW Brownwood, 26 April 1966, Faubion 17 (OKL). Burleson Co.: 6 mi W Caldwell, 28 April 1958, Sperry 3168 (TTC). Burnett Co.: 2 mi N Briggs, 20 April 1946, Whitehouse 15369 (NY). Clay Co.: 1 mi W Byers, 13 May 1968, Stephens 20544 (KANU). Collingsworth Co.: 6 mi S Shamrock, 20 May 1966, Rowell 11003 (TTC, OKLA). Comanche Co.: N of Comanche, 8 May 1900, Eggert s.n. (MO-2). Dallas Co.: May-June, Reverchon s.n. (MO-3, NEB, NY-2, KANU); Urbandale, 2 May 1942, Lundell & Lundell 10410 (MO). Denton Co.: 3 mi S Denton, 19 April 1940, Lundell & Lundell 8428 (NY). Erath Co.: 2 mi S Stephenville, 28 April 1966, Lee s.n. (NDA). Fayette Co.: LaGrange, 2 May 1935, Tharp s.n. (TTC). Foard Co.: 26 mi E Paducah, 20 May 1980, Freeman 417 (KSC). Grayson Co.: Denison, 22-25 July 1880, Letterman s.n. (MO). Hamilton Co.: Near Star, 28 April 1959, Correll & Johnston 21097 (MO). Harris Co.: Houston, May 1843, Lindheimer

Figure 60. Great Plains Distribution of *Penstemon cobaea* var. *cobaea*



s.n. (MO-2, NY). Hays Co.: Kyle, 8 April 1949, Johnson 497 (KANU, NY). Hood Co.: Granbury, 6 May 1900, Eggert s.n. (MO). Kerr Co.: Kerrville, 23 April 1953, Beamer s.n. (KANU). Knox Co.: 10 mi WNW Benjamin, 19 May 1962, Davis 1030 (OKL). McLennan Co.: Waco, 13 April 1906, Johnson 75 (MO). Mills Co.: 7.3 mi S Goldthwaite, 27 April 1970, Flyr 1378 (MO). Nolan Co.: 12 mi N Blackwell, 6 May 1980, Brooks 14577 & McGregor (KANU). Parker Co.: M.A.N. (MO). Tarrant Co.: 12 May 1912, Ruth 101 (MO-2, RM-2, SDC, KSC, NDA, NY-3). Travis Co.: Austin, 13 May 1918, Young 125 (MO, NY-2). Taylor Co.: 3 mi S Camp Barkeley, 30 April 1943, Tolstead 7102A (MO). Uvalde Co.: Frio River near Uvalde, 20 April 1931, Tharp s.n. (MO, NY). Waller Co.: Hempstead, 20 April 1872, Hall 408 (MO, NY-2). Washington Co.: 2 mi SW Gayhill, 13 April 1950, Gould & Celerier 5455 (NY). Wichita Co.: Red River above Burkburnett, 21 July 1921, Tharp 522 (NY). Wilbarger Co.: 6.2 mi W Electra, 12 May 1945, Whitehouse 9798 (NY). Young Co.: Ft. Belknap, 1855, Vollum s.n. (NY).

7. Penstemon digitalis Nuttall ex Sims

Pentstemon digitalis Nutt. ex Sims, Bot. Mag. 52: pl. 2587. 1825. Chelone digitalis (Nutt.) Sweet, Brit. Fl. Gard. pl. 120. 1825. Pentastemon digitalis α albidus Trautv., Bull. Acad. Imp. Sci. Saint-Petersbourg 5: 345. 1839. Pentstemon laevigatus Solander var. digitalis (Nutt.) A. Gray, Syn. Fl. N. Amer. 2(1): 268. 1878. Penstemon laevigatus Solander subsp. digitalis (Nutt.) Bennett, Phytologia 9(2): 57. 1963. Type: "Communicated by Robert Barclay,.....to whom the seeds were sent by Professor Nuttall, in March 1824, under the name which we have adopted. Native of the Arkansas territory." Nuttall later independently described the species in Trans. Amer. Philos. Soc. 2(5): 181. 1837. (Type: not seen).

Pentstemon nuttallii Beck, Amer. J. Sci. 14: 120. 1828. Type: "Illinois or Missouri." (Type: not seen).

Pentstemon glaucophyllus Sheele, Linnaea 21: 763. 1848. Type: "Illinois." (Type: not seen).

Penstemon digitalis f. baueri Steyermark, Rhodora 43: 663. 1941. Type: "Wooded southwest-facing limestone bluffs along Maries River, T43N, R10W, sect. 18, 3 mi. northeast of Westphalia, Osage Co., Missouri, July 1, 1939, Julian A. Steyermark 27665". (Holotype: F, not seen).

Robust herbaceous perennial. Stems mostly erect, 2.5-9 dm tall, glabrous and shiny or somewhat glaucous, frequently anthocyanic near the base, 1-3 stems arising from a thick caudex surmounting a short taproot. Leaves entire to obscurely or sharply serrate or denticulate, glabrous; basal leaves lanceolate to (ob)ovate or spatulate, 3-18(22) cm long overall,

0.4-3.8(6) cm wide, acute to obtuse or rounded, subpetiolate to distinctly petiolate; cauline leaves linear-lanceolate to ovate, 2.6-17 cm long, 0.4-4.8 cm wide, acuminate to acute, sessile to distinctly clasping, lower cauline leaves commonly crowded and large, upper caulines leaves widely spaced and much reduced, the upper half of the stem appearing rather naked except for the inflorescence. Thyrse 7-26(34) cm long, with (2)3-6 verticillasters, individual cymes 3 to many flowered, peduncles glabrous, or those immediately below the pedicels sparingly glandular-pubescent, much-branched and ascending or spreading, to 9.3 cm long, pedicels glandular-pubescent, 1-8 mm long; bracts normally greatly reduced, the lower ones to 10.5 cm long and 4 cm wide. Calyx glandular-pubescent, sepals lance-ovate to ovate, 4-8 mm long, 2-3 mm wide, acuminate to acute, entire or occasionally suberose, noticeably scarious along the margins; corolla (18)20-30 mm long, only slightly bilabiate, white, glandular-pubescent externally, throat 8-12 mm broad, abruptly inflated and slightly ampliate, lined internally with faint reddish-purple guidelines, the guidelines reaching the bases of the lobes of the lower lip, barely 2-ridged anteriorly within, palate sparsely to moderately bearded with white eglandular hairs, lobes of the upper lip spreading, lobes of the lower lip moderately projecting; staminode 13-17 mm long from its point of attachment, reaching the orifice, the tip recurved and flattened, terminal 6-8 mm sparsely to moderately bearded with stiff yellow or dirty-yellow hairs to 1 mm long; fertile stamens included or reaching the orifice, anther-sacs 1.4-1.7 mm long, dark brown or black, lined with white along the sutures, the external surface minutely papillose, anther-sacs usually pubescent with few to many white hairs, sutures slightly to moderately papillose, widely divergent, dehiscing nearly to the apices, not becoming explanate; style 13-18 mm long, glabrous. Capsule 8-14 mm long.

Seeds 1-1.3 mm long, slightly rounded to angular, finely reticulate, tan to dark brown. n = 48.

Loamy to sandy loam soil in prairies, meadows, and open woodlands. Maine and Quebec west to Ontario and South Dakota; south to Alabama and Louisiana. Flowering from mid-April to July, depending on latitude.

Pennell (1935) indicated that P. digitalis is probably native to the Mississippi River basin and that as a result of man's activity, the species has extended its range, especially to the northeast and east. The adventive nature of this species closely parallels that of Penstemon tubaeflorus, another polyploid species of the Great Plains.

Penstemon digitalis has been variously treated in the past. Initially recognized as a species, it was given varietal status under P. laevigatus Solander by Asa Gray (1878). Bennett (1963b) combined P. laevigatus Solander, P. digitalis Nutt., P. calycosus Small, P. alluviorum Penn., and P. deamii Penn., into a single species under the oldest name, P. laevigatus, and he recognized the other taxa as subspecies (except P. deamii which he considered a variety of subsp. alluviorum).

Chromosome counts for P. laevigatus, P. digitalis, and P. calycosus indicate all three taxa to be dodecaploids (2n = 96). Counts are presently not available for P. alluviorum or P. deamii. However, in light of these data, serious consideration should be given to Bennett's (1963b) treatment of the group as at least three of the taxa concerned show indications of a common ancestry, based on cytology. No morphological examination of these taxa was undertaken (excluding P. digitalis), but Pennell's (1935) treatment indicates close morphological similarities among the taxa. While cytological and morphological similarities do not predispose one to treat these taxa as Bennett has, they do make such a treatment much more credible.

In the Great Plains, Penstemon digitalis is a quite distinct taxon and thus has been maintained here as a species. However, further field studies in the eastern United States may support the validity of including this entity in an expanded concept of P. laevigatus.

A form having three leaves at a node rather than two leaves has been described by Steyermark as f. baueri. Similar leaf aberrations have been observed by the author in P. cobaea and P. albidus.

REPRESENTATIVE SPECIMENS:

UNITED STATES:

ARKANSAS: Ashley Co.: Mist, 8 May 1943, Demaree 24392 (OKL, KANU). Clay Co.: 25 May 1893, Eggert s.n. (MO). Drew Co.: Monticello, 7 May 1945, Demaree 25396 (OKL, KANU). Faulkner Co.: 10 mi E Conway, 9 May 1953, Lane 133 (OKL). Fulton Co.: Mammoth Spring, 8 June 1923, Pennell 11544 (KSC). Marion Co.: Bull Shoals, 17 June 1950, Demaree 29116 (OKL-2). Miller Co.: Kiblah, 11 May 1959, Demaree 40827 (OKL, KANU). Pike Co.: Langley, 14 May 1955, Demaree 36804 (OKL, KANU). Polk Co.: 0.5 mi E Oklahoma State Line on US 270 & 59, 18 July 1964, McWilliam 2019 (OKL, KANU, KSC). Prairie Co.: DeValls Bluff, 15 June 1941, Demaree 22187 (OKL). Ripley Co.: Cross Plains, 16 June 1946, Demaree 15627 (KANU). Scott Co.: Along Ritz Rd near Fourche River, 21 May 1966, McWilliam P6674 (OKL). Washington Co.: Farmington, 7 May 1927, Demaree 2992 (FHKSC). White Co.: Near Beebe, 8 May 1965, McWilliam P6593 (OKL).

CONNECTICUT: Hartford Co.: Southington, 5 June 1897, Sheldon s.n. (NEB).

ILLINOIS: Champaign Co.: Homer, September 1907, Coons s.n. (NEB). Clinton Co.: Along Hwy 50 on W edge Carlyle, 9 June 1966, Henderson s.n. (KANU). Cook Co.: Stony Island, Chicago, 16 July 1903, Shull s.n. (OKL). Lawrence Co.: Along Embarrass River 1.5 mi E Lawrenceville, 9 June 1966, Henderson 66-445 (KANU). Piatt Co.: Near Monticello, 8 June 1952, Jones 19602 (NEB). Tazwell Co.: Fon du lac Twp., Sec. 2, 24 July 1952, Chase 12829 (KSC, KANU, OKL).

INDIANA: Brown Co.: Near Salt Creek, 13 June 1945, Springer 30 (NEB). Jennings Co.: Vernon, 18-19 June 1923, Pennell 11759 (NEB). Marion Co.: Indianapolis, 30 May 1936, Friesner 9626 (FHKSC, OKL).

IOWA: Appanoose Co.: 27 June 1899, Fitzpatrick s.n. (RM, NY). Davis Co.: 1 mi W Floris, 26 June 1939, Hayden 9529 (NY). Iowa Co.: N of Homestead, 26 May 1907, Shimek s.n. (WET). Johnson Co.: Lake MacBride, June 1938, Loufek s.n. (NY). Muscatine Co.: Lindle Lake, Sec. 12, T77N, R3W, 30 June 1945, Conard & Anderson s.n. (NY). Warren Co.: 1 mi E Carlisle, 14 June 1957, Van Bruggen 1988 (SDU).

KANSAS: Anderson Co.: 8 mi N Lone Elm, 2 June 1966, Croat 1581 (KANU, NY). Atchison Co.: 5 mi S Atchison, 5 June 1951, Nordhus 146 (KSC). Bourbon Co.: 5 mi S Bronson, 26 May 1969, Stephens 30929 (NY, KANU). Brown Co.: Everest, 1938, Olson 1 (KSC). Butler Co: 8 mi S Cassoday, 7 June 1966, Stephens 4493 (KANU). Cherokee Co.: 2.4 mi S & 1 mi SE Galena, 11 June 1970, Bare 2332 (KANU); 1896, Hitchcock 780 (NY, RM, KSC). Clay Co.: Near Clay Center, 5 June 1939, Gates s.n. (KSC). Coffey Co.: 5.2 mi N Aliceville, 7 June 1970, Magrath 5392A (KANU). Crawford Co.: Crawford Co. State Park, June 1938, Ross s.n. (KSP, KSC). Douglas Co.: 3 mi S & 0.75 mi E Lawrence, 16 June 1969, Johnson 2090 (KANU, NY). Franklin Co.: 3.5 mi W Rantoul, 28 May 1969, Stephens 31057 (KANU). Greenwood Co.: 3.5 mi E Fall River, 7 June 1979, Freeman 128 (KSC). Jefferson Co.: 8 mi NW Oskaloosa, 27 May 1970, McGregor 22212 (KANU). Johnson Co.: Near Olathe, 6 June 1975, Dickinson 24 (KSP). Labette Co.: 1 mi W Bartlett, 23 May 1967, Stephens 11034 (KANU, NY, OKLA). Leavenworth Co.: 5 mi NW Tongonoxie State Lake, 19 June 1969, Stephens 32260 & Brooks (KANU). Lincoln Co.: 2 mi W Lincoln, 10 June 1979, Freeman 152 (KSC). Linn Co.: 3 mi W Mound City, 5 June 1976, Hulbert 4566 (KSC). Miami Co.: 8.2 mi E Franklin Co. Line, 30 May 1980, Freeman & Wetter 467 (KSC); 3 mi W Osawatomie, 21 May 1946, Horr & McGregor E501 (SDC, KSP, RM, KANU-2, OKLA, OKL, NY); 1.5 mi W Osawatomie, 20 June 1936, Horr E546 (SDC, RM, OKLA, NY, OKL). Montgomery Co.: 1 mi W Tyro, 23 May 1967, Stephens 10991 (KANU). Neosho Co.: 2 mi N Erie, 7 June 1979, Freeman 123 (KSC); 2 mi N & 0.5 mi W Erie, 7 June 1979, Freeman 124 (KSC). Ottawa Co.: 8 mi E Tescott, 4 June 1974, Stephens 77038 (KANU). Pottawatomie Co.: E edge Tuttle Creek State Park along State 13, 6 October 1979, Freeman 321 (KSC); E edge Tuttle Creek State Park along State 13, 16 May 1980, Freeman 388 (KSC). Republic Co.: SE ¼, SE ¼ sec. 26, T1S, R4W, 12 May 1961, Morley 1249 (KANU). Riley Co.: Along Hwy 24 1.7 mi S jct Hwy 24 & 177, 31 May 1981, Freeman 971 (KSC). Shawnee Co.: 5 mi N Dover, 20 May 1949, Volle 114 (KANU). Wilson Co.: 4.5 mi E Fall River, 7 June 1979, Freeman 127 (KSC). Wyandotte Co.: 1 mi S & 2 mi E Piper, 3 June 1973, Brooks 4379 (KANU).

KENTUCKY: Bath Co.: 3 mi W Salt Lick, 31 May 1945, McFarland 93 (OKL).

LOUISIANA: Ouchita Parish: 6 mi SW Monroe, 4 May 1941, Smith s.n. (OKL).

MASSACHUSETTS: Hampden Co.: Springfield, 28 June 1928, Lyman s.n. (KSC).

MINNESOTA: Pine Co.: 6 mi N Hinckley, 6 July 1939, Butters & Moore 10889 (NY).

MISSOURI: Barry Co.: Eagle Rock, 9 June 1897, Bush 129 (KSC). Bates Co.: 0.1 mi W jct County Rd B & O, 30 May 1980, Freeman & Wetter 462 (KSC). Boone Co.: E of Columbia, 21 May 1936, Rickett 1347 (FHKSC, OKL). Caldwell Co.: 3 mi W Hamilton, 4 June 1953, Tolstead 12753 (NEB-2). Cass Co.: 2 mi N Peculiar, 17 June 1966, Henderson 66-474 (KSC, KANU). Christian Co.: Christian Center, 10 June 1923, Pennell 11640 (RM). Franklin Co.: Pacific, 11 June 1886, Eggert s.n. (RM). Henry Co.: 5 mi S Clinton, 5 June 1953, Tolstead 12811 (NEB). Howell Co.: Willow Springs, 9 June 1923, Pennell 11610 (KSC). Jackson Co.: Independence, 30 May 1894, Bush 340 (KSC, NY). Jasper Co.: 1 mi E Galena, KS, 7 May 1977, Ikenberry 79-77 (KSP). Johnson Co.: 2 mi W Warrensburg, 30 May 1980, Freeman & Wetter 452 (KSC); 1 mi NW

Warrensburg, 30 May 1980, Freeman & Wetter 454 (KSC). Laclede Co.: 4 mi S Lebanon, 9 June 1938, Ownbey & Ownbey 1601 (RM, OKL, NY). Lafayette Co.: Wellington, 16 June 1930, Bush 11749 (KSC, NY). Lawrence Co.: June 1879, Flint s.n. (NY). Lewis Co.: 3 mi S Clark Co. Line along Hwy 61, 11 June 1937, Peck s.n. (RM). Lincoln Co.: Whiteside, 30 June 1915, Davis 4458 (NDA). Macon Co.: Ethel, 11 June 1915, Bush 7583 (NY). Newton Co.: Neosho, 2 June 1933, Drushel 8845 (NDA). Oregon Co.: Thayer, 7-8 June 1923, Pennell 11513 (OKL). Polk Co.: 3 mi N Bolivar, 1 June 1968, Sutherland 1614 (KANU, NEB). St. Claire Co.: 4.4 mi N Lowrey City, 30 May 1980, Freeman & Wetter 456 (KSC). St. Louis Co.: Allenton, 12 June 1923, Pennell 11677 (NEB). St. Louis City: St. Louis, July 1838, Riehl 143 (NY).

NEBRASKA: Cuming Co.: Mt. Hope Cemetary near West Point, 13 June 1970, Einemann s.n. (NEB). Richardson Co.: Along Nemaha River SE of Preston, 25 June 1975, Shildneck C-7599 (KANU). York Co.: June 1893, Hopper s.n. (NEB).

NEW JERSEY: Middlesex Co.: Woodbridge, 10 June 1892, Lighthipe 3248 (KSC).

NEW YORK: Dutchess Co.: 6 mi S Pine Plains, 3 July 1967, Hess 1261 (OKL). Tompkins Co.: SW slope Turkey Hill in Ithaca Twp., 1 July 1947, Freitag 115 (SDC). Warren Co.: S of Brayton near Lake George, 3 July 1943, House 29294 (OKL).

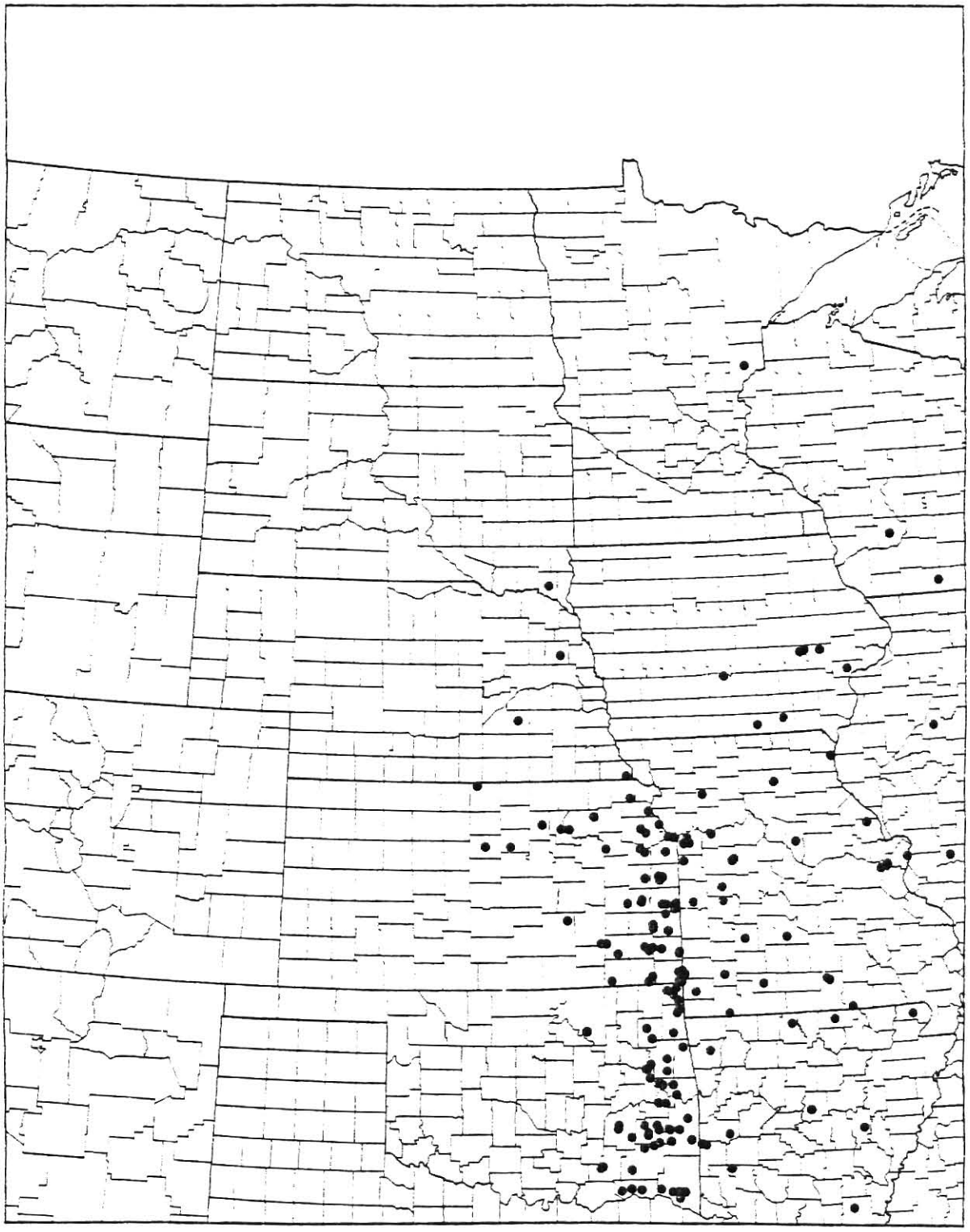
NORTH CAROLINA: Orange Co.: S side Morgan Creek near Chapel Hill, 14 August 1969, Leonard 3031 (OKL, KANU).

OHIO: Hamilton Co.: Westwood, Cincinnati, 30 July 1906, Cleburne s.n. (NEB). Jackson Co.: Along Hwy 93, 3 June 1967, Cribben 198 (OKL). Stark Co.: Canton, Stoddart s.n. (KSC).

OKLAHOMA: Adair Co.: 1 mi S & 5 mi W Watts, 10 June 1947, Waterfall 7011 (OKL, OKLA). Atoka Co.: 1 mi NW Atoka, 29 May 1961, Waterfall 16030 (KSC, OKLA). Bryan Co.: 2 mi W Unger, Nelson & Holland 6011 (OKL, OKLA). Cherokee Co.: Near Grand River, 22 May 1949, Goodman 5073 (OKL, KANU, NY). Choctaw Co.: 4 mi E Hugo, 19 May 1944, Hopkins, Nelson, & Nelson 317 (OKL, RM, OKLA). Delaware Co.: Near Dripping Springs, 7 May 1938, Hopkins 3266 (OKL, KANU). Haskell Co.: 2 mi E Keota, 2 June 1949, Waterfall 8761 (OKL, OKLA). Latimer Co.: 4 mi S Red Oak, 28 May 1968, Means 3413 (OKLA); 8 June 1940, Bebb 5491 (OKLA, OKL). LeFlore Co.: Rich Mt., 21 May 1944, Hopkins, Nelson, & Nelson 573 (OKL, RM, OKLA). McCurtain Co.: Valliant, 16 May 1936, Demaree 12610 (OKL, FHKSC, NY). Mayes Co.: 2.6 mi S Locust Grove, 29 May 1968, Perino & Pierson 264 (OKL). Muskogee Co.: 3 mi E & 0.75 mi N Ft. Gibson, 2 June 1958, Wallis 7059 (OKL, KANU). Osage Co.: 6 mi S Hominy, 30 May 1951, Waterfall 9944 (OKLA). Ottawa Co.: 0.5 mi NE Quapaw, 12 June 1958, Wallis 7274 (OKL, KANU). Pittsburg Co.: McAlester, 27 May 1920, Pennell 10589 (NY, OKLA). Pushmataha Co.: 7 mi N Clayton, 20 May 1939, Hopkins & Van Valkenburgh 4319 (OKL). Sequoyah Co.: 6 mi NE Gore, 31 May 1958, Wallis 7020 (OKL, KANU, OKLA).

PENNSYLVANIA: Butler Co.: Near Conoquenessing, 20 June 1937, Bright 15463 (FHKSC). Chester Co.: Near Valley Forge, 22 June 1935, Bright 10453 (FHKSC). Union Co.: 6 mi N Milton, 21 June 1953, Sargent 6336 (OKL).

Figure 61. Great Plains Distribution of *Penstemon digitalis*



SOUTH DAKOTA: Clay Co.: Glenwood Twp., Sec. 13, 9 July 1959, Vernard s.n. (SDC).

TENNESSEE: Shelby Co.: Memphis, 27 May 1944, Taylor 5627 (SDC).

TEXAS: Bowie Co.: Near Texarkana, 29 August 1898, Heller & Heller s.n. (RM, NEB, NY). Dallas Co.: Dallas, 1 May 1902, Reverchon 3220 (NY). Franklin Co.: 3 mi E Mount Vernon, 3 May 1945, Lundell 13700 (NY).

VERMONT: Rutland Co.: Chittenden, 1 July 1923, Dutton s.n. (KSC).

WEST VIRGINIA: Randolph Co.: 2 mi E Helvetia, 22 June 1941, Hutton 255 (KSC, OKL). Wetzel Co.: Near Littleton, 11 June 1961, Haught 7100 (KANU).

WISCONSIN: Rock Co.: 0.6 mi E Swan Creek, 12 July 1972, Musselman & Musselman 4611 (OKL). Sauk Co.: Sec. 10, T11N, R5E, 27 June 1965, Wilson 23 (SDU).

8. Penstemon eriantherus Pursh

Pentstemon erianthera Pursh, Fl. Amer. Sept. 2: 737. 1814. Chelone erianthera (Pursh) Steud., Nom. Bot. ed. 1. 186. 1821. Type: "P. erianthera. Fras. Catal. 1813. In upper Louisiana.", collected by Bradbury along the Missouri River in the present state of South Dakota, fide Pennell (1935). (Holotype: PH; Isotype: BM, not seen).

Penstemon cristatum Nutt., in Fras. Catal. 2. 1813. nomen nudum. Pentstemon cristatam Nutt., Gen. N. Amer. Pl. 2: 52. 1818. Chelone cristata (Nutt.) Spreng., Syst. Veg. 2: 813. 1825. Type: "On the arid denuded argillaceous hills from the confluence of Teeton river and the Missouri to the Mountains." (Holotype: PH, not seen).

Pentstemon saliens Rydb., Mem. New York Bot. Gard. 1: 344. 1900. Penstemon eriantherus (subsp.) saliens (Rydb.) Penn., Contr. U.S. Natl. Herb. 20: 343. 1920. Type: "Montana: Columbia Falls, Mrs. J.J. Kennedy, 53." (Holotype: NY!).

Penstemon eriantherus Pursh var. grandis Pennell et Keck, Bull. Torrey Bot. Club 65: 251. 1938. Type: "F.W. Pennell & F.B. Cotner 20511, from black soil over limestone, 5800-6000 ft. alt., divide between Rocky and Bridger Mts., east of Bozeman." (Holotype: PH; Isotypes: MO!, RM!).

Herbaceous perennial. Stems erect or ascending, 1-4(4.5) dm tall, villose-canescent throughout or merely canescent below, stems 5(10) arising from a woody caudex surmounting a taproot. Leaves entire to salient-serrate, moderately to densely pubescent; basal leaves (ob)lanceolate to spatulate,

3.5-8(11) cm long overall, 0.5-3(3.7) cm wide, acute to obtuse, subpetiolate or tapering to a petiolate base; cauline leaves (ob)lanceolate to oblong or spatulate, 2.5-9 cm long, 0.4-1.8(2.5) cm wide, acute, sessile and scarcely clasping. Thyrse 4-13(27) cm long, with (2)3-7(9) verticillasters, compact, leafy-bracted, individual cymes 3-6 flowered, peduncles and pedicels villose-canescent and viscid, peduncles to 1.2 cm long, pedicels 0.3-1 cm long; bracts lanceolate to oblong, pubescent, the lower ones to 5.5 cm long and 1.5 cm wide. Calyx viscid-pubescent, sepals lanceolate, (6)8-12(13) mm long, 1.5-3 mm wide, acuminate to acute, herbaceous throughout with entire margins; corolla (20)22-35(42) mm long, strongly bilabiate, lavender to pale purple or pinkish, viscid-pubescent externally, throat 8-14 mm broad, abruptly inflated, ventricose-ampliate, lined internally with deep reddish-purple nectar guides on the anterior and posterior surfaces, the guidelines passing well onto the upper and lower lips of the limb, eglandular to glandular-pubescent internally and on the lateral lobes of the lower lip, palate densely pilose with straw-yellow hairs, lobes of the upper lip arched-projecting, lobes of the lower lip spreading or projecting; staminode 15-18 mm long from its point of attachment, prominently exserted, distally expanded and recurved, bearded on the terminal 13-15 mm with golden-yellow hairs, hairs at the tip tortuous and to 4 mm long, medial hairs shorter and stiff, retrorse; fertile stamens included, anther-sacs (1.1)1.2-1.6(1.8) mm long, minutely papillose along the sutures, tan, dehiscing the entire length and across the connective, becoming explanate in var. eriantherus; style 16-20 mm long, ovary and occasionally the proximal 1/4 to 1/2 of the style sparingly glandular-pubescent. Capsule (6)9-12(13) mm long. Seeds 2-2.8 mm long, dark brown to black, angular, finely reticulate. $n = 8$.

Dry sandy or gravelly soil in open prairies, slopes, sides of buttes,

and into the lower elevations of the mountains in the northwestern part of its range. Western and southcentral North Dakota south to northwestern Nebraska and Weld and Larimer Counties in Colorado. West to southeastern British Columbia, central Washington, and central Oregon.

Penstemon eriantherus is an exceedingly variable species throughout its range, with plants differing in a number of characters, including corolla size and color, leaf size and shape, pubescence, bearding of the staminode, size of the anther-sacs, and degree of anther-sac explanation. Such variability has resulted in the naming of a number of subspecies and varieties, several of which are here included in synonymy, as they appear to fit within the range of variability of the nomenclaturally typical plants. Our plants in the Great Plains are referable to var. eriantherus which is also found in northwestern Montana, southeastern British Columbia, and into Washington (Cronquist, 1959).

REPRESENTATIVE SPECIMENS:

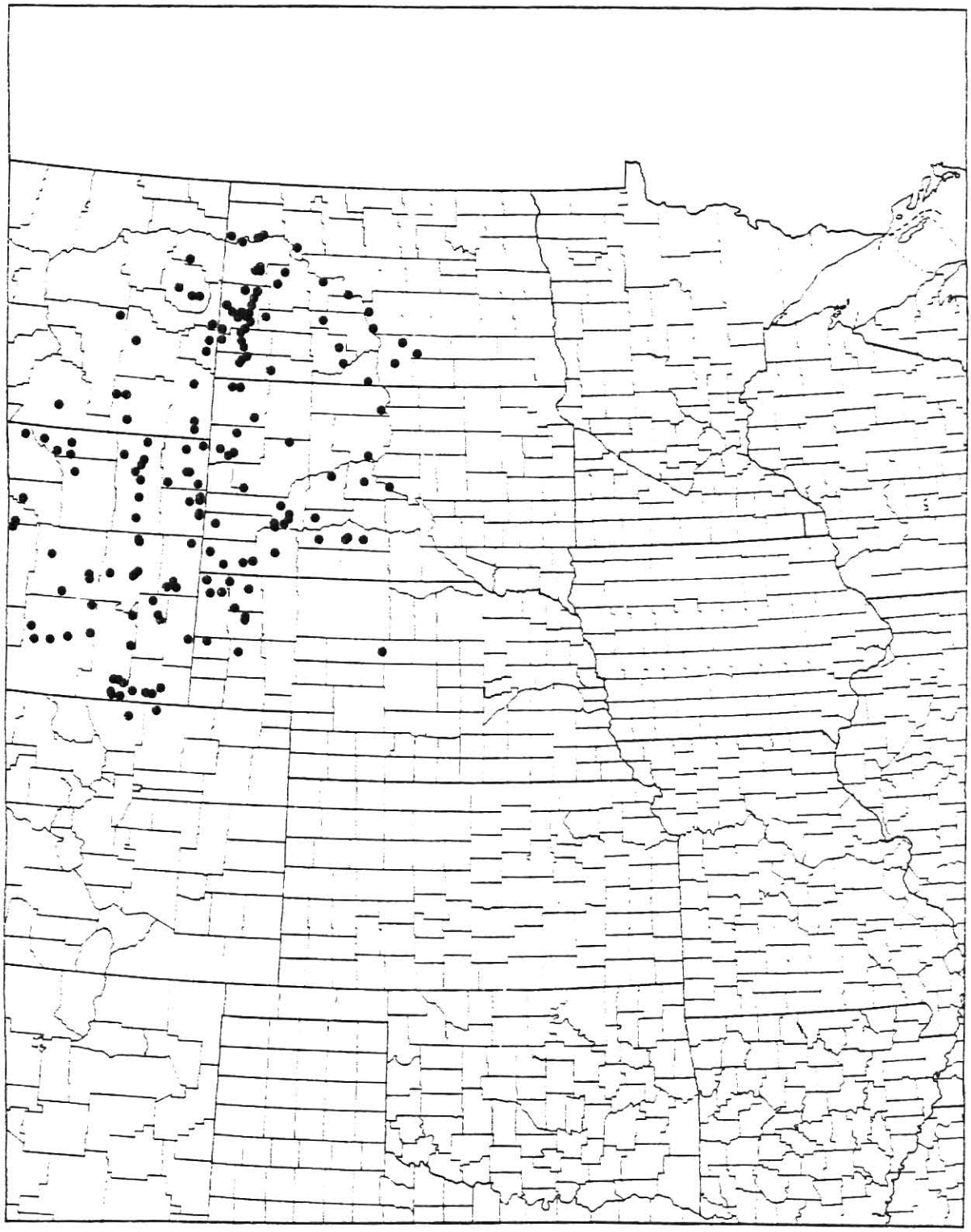
UNITED STATES:

COLORADO: Larimer Co.: Granite Canyor Rd, 22 June 1941, Keck 1949 (CS). Weld Co.: E of Cheyenne, WY, 13 June 1918, Osterhout 5736 (RM, OKL).

IDAHO: Butte Co.: Lost River Range E of Pass Creek Summit, 8 July 1971, Holmgren & Marttala 5322 (KANU).

MONTANA: Big Horn Co.: Sec. 24, T9S, R39E, 25 May 1977, Brink & Mayer 1263 (RM). Broadwater Co.: Divide on White Sulphur Springs-Townsend Hwy, 2 July 1945, Hitchcock & Muhlick 11879 (MO, NY, RM). Carbon Co.: 5 mi S Red Lodge, 17 July 1969, Seiler 635 (KANU, NDA). Carter Co.: 5 mi S Ekalaka, 25 June 1968, Stephens 23237 & Brooks (KANU). Cascade Co.: Great Falls, 10 June 1892, Williams s.n. (NY). Custer Co.: Custer Flat well, 7 June 1944, Woolfolk W-172 (NY). Dawson Co.: 18 mi E Glendive, 15 June 1974, Stephens 77898 (KANU). Deer Lodge Co.: 7 mi S Phillipsburg, 3 July 1950, Call & Call 447 (NY). Fallon Co.: 10 mi N Baker, 26 June 1968, Stephens 23314 & Brooks (KANU). Fergus Co.: 28 mi S Lewiston, 2 July 1947, Hitchcock 16021 (NY). Flathead Co.: Kalispell, 2 June 1900, Wilcox 369 (NY). Gallatin Co.: Bridger Mts., 11 June 1897, Rydberg & Bessey 4914 (NEB-2, RM-2, NY); 2 mi up Bridger Canyon, 1 September 1937, Pennell &

Figure 62. Great Plains Distribution of *Penstemon eriantherus* var. *eriantherus*



Cotner 21356 (RM, NY). Glacier Co.: Midvale, 24 June 1903, Umbach 140 (NY). Granite Co.: 30 mi E Missoula, 20 June 1944, Hitchcock & Muhlick 9116 (NY, RM). Jefferson Co.: 5 mi SW Whitehall, 26 June 1956, Booth 56904 (RM). Lewis and Clark Co.: 3 mi SW Gibson Lake dam, 4 July 1948, Hitchcock 18023a (NY-2, NDA, RM). Madison Co.: Tobacco Mts., 13 July 1909, Butler 5043 (NY). Meagher Co.: 5 mi NE Ringling, 1 July 1947, Hitchcock 15972 (NY). Missoula Co.: N Patte Rd, 21 May 1939, Connor & Clark 12 (MO, RM). Park Co.: 9 mi NW Wilsall, 24 June 1921, Suksdorf 242 (MO, NY). Powder River Co.: 22 mi W Broadus, 24 June 1974, Stephens 78775 (KANU). Powell Co.: 2 mi S Halmville, 28 June 1945, Hitchcock & Muhlick 11661 (RM, MO, NY); 6 mi W Ovando, 25 June 1945, Hitchcock & Muhlick 11528 (RM, NY, MO). Richland Co.: 14 mi Lambert, 16 June 1974, Stephens 77987 (KANU). Rosebud Co.: 1 mi N Angela, 22 June 1974, Stephens 78570 (KANU). Stillwater Co.: July 1920, Kemp 42 (NY). Wheatland Co.: 10 mi N Harlowton, 2 July 1947, Hitchcock 16011 (NY). Wibaux Co.: 23 mi S Wibaux, 26 June 1968, Stephens 23344 & Brooks (KANU).

NEBRASKA: Box Butte Co.: Hemingford, 30 July 1951, Kiener 27437 (NY, NDA, NEB). Dawes Co.: 5 mi SE Sioux Co. Line along Hwy 71 & 2, 7 June 1980, Freeman 530 (KSC). Morrill Co.: SW of Vance, 11 June 1931, Pennell 15085 (NY). Scotts Bluff Co.: N of Mitchell, 19 June 1930, Osterhout 7207 (RM-2). Sioux Co.: 3 mi N Harrison, 23 June 1979, Freeman 182 (KSC); 8 mi W Montrose, 23 June 1979, Freeman 183 (KSC). Thomas Co.: Halsey, July 1911, Pool s.n. (NEB).

NORTH DAKOTA: Adams Co.: 3 mi S Reeder, 21 June 1970, Stephens 40405 & Brooks (KANU). Billings Co.: Medora, 7 July 1953, Stevens 1447 (NDA, KANU). Bowman Co.: 1 mi E & 4 mi N Bowman, 21 June 1970, Stephens 40353 & Brooks (KANU). Burleigh Co.: 6 mi S & 2 mi E Bismarck, 14 June 1970, Johnson 224 (NDA). Dunn Co.: 9 mi W & 1 mi N Killdeer, 25 June 1979, Freeman 214 (KSC). Emmons Co.: Linton Cemetary 1.5 mi NW of Linton, 24 June 1973, Williams 1583 (KANU, NDA-2). Golden Valley Co.: 1 mi E Sentinel Butte, 17 June 1970, Zaczkowski 2878 (NDA). Grant Co.: 15 mi S Raleigh, 16 June 1970, Stephens 39893 & Brooks (KANU). Logan Co.: Shell Butte 13.5 mi S & 3 mi W Napoleon, 7 June 1972, Williams 979 (KANU, NDA). McKenzie Co.: Along Little Missouri River in N Roosevelt Park, 11 June 1938, Stevens 354 (NY, NDA). Mercer Co.: 4 mi S & 2 mi E Stanton, 3 June 1976, Larson 5483 (NDA). Morton Co.: Glen Ullin, 25 July 1912, Bergman 2464 (NDA). Mountrail Co.: 3 mi NW Newton, 12 June 1969, Hegstad 166 (NDA). Sioux Co.: 6 mi E & 2.5 mi S Selfridge, 27 June 1967, Stephens 12392 & Brooks (KANU). Slope Co.: 4 mi W & 12 mi N Amidon, 24 June 1979, Freeman 209 (KSC). Stark Co.: Dickinson, 19 June 1912, Waldron 96 (RM, NDA-2). Williams Co.: 4 mi N Buford, 8 June 1971, Hegstad 7980 (NDA).

SOUTH DAKOTA: Butte Co.: 6.5 mi E Belle Fourche, 15 June 1970, Stephens 39812 & Brooks (KANU). Corson Co.: Across Missouri River from Mobridge, 7 June 1960, Van Bruggen 4808 (SDU). Custer Co.: Entrance to Jewel Cave Nat. Monument along Hwy 16, 7 June 1980, Freeman 534 (KSC). Dewey Co.: 12.5 mi E & 11.5 mi SE Eagle Butte, 25 June 1967, Stephens 12272 & Brooks (KANU-2, NY, NDA). Fall River Co.: 24.6 mi S Hot Springs, 7 June 1980, Freeman 532 (KSC). Haakon Co.: 9 mi N & 11 mi E Billsburg, 24 June 1967, Stephens 12193 & Brooks (KANU). Harding Co.: 14 mi SW Reva, 21 June 1970, Stephens 40462 & Brooks (KANU). Hughes Co.: Near Pierre, 1892, Adams s.n. (SDC). Jackson Co.: 0.5 mi from Cedar Pass in Badlands Nat. Monument, 10

June 1957, Lindstrom 74 (SDU). Meade Co.: 7 mi E Maurine, 15 June 1970, Stephens 39870 & Brooks (KANU). Mellette Co.: 10 mi W Cedar Butte, 14 July 1971, Stephens 49342 (KANU). Pennington Co.: 8 mi S Wall, 7 September 1937, Pennell 21379 (NY). Shannon Co.: Sec. 4, T3S, R13E, 12 June 1973, Van Bruggen 6182 (SDU). Stanley Co.: Saddle Pass, 2 June 1914, Over 6116 (SDU). Washabaugh Co.: Sec. 17, T42N, R35W, 11 June 1959, Buntley 12 (SDC).

WYOMING: Albany Co.: 14 mi N Colorado Line along Hwy 287, 11 June 1980, Freeman 576 (KSC); E of Laramie, 22 June 1943, Porter 3211 (RM, OKLA, MO); Laramie, 14 June 1900, Nelson 7273 (RM, NEB, NY). Big Horn Co.: 10-15 mi E Kane, 19 June 1936, Williams & Williams 3012 (RM, NY, MO). Campbell Co.: 15.8 mi N Gillette, 10 June 1980, Freeman 548 (KSC); S of Gillette along Belle Fourche River, 10 June 1980, Freeman 553 (KSC); 12.9 mi N Converse Co. Line, 10 June 1980, Freeman 555 (KSC). Carbon Co.: Along Platte River at Ft. Steele, 26 May 1947, Porter 4174 (MO, RM). Converse Co.: 10.5 mi S Campbell Co. Line along Hwy 59, 10 June 1980, Freeman 557 (KSC); 13.2 mi NE Douglas, 10 June 1980, Freeman 559 (KSC). Crook Co.: 5.6 mi N Weston Co. Line along Hwy 16, 7 June 1980, Freeman 539 (KSC); 12 mi SE Alzada, 12 June 1975, Churchill 5716 (NY, NEB, KANU). Fremont Co.: SE Thermopolis & E Wind River Canyon, 15 June 1961, Fisser 409 (RM). Goshen Co.: 3 mi SW Torrington, 12 June 1931, Pennell 15095 (NY). Hot Springs Co.: SE Thermopolis & E Wind River Canyon, 21 June 1961, Fisser 510 (RM). Johnson Co.: 10 mi W Buffalo, 29 June 1953, Porter 6256 (RM, MO). Laramie Co.: Along Hwy 85, 8.4 mi NE jct Hwy 85 & I-25, 11 June 1980, Freeman 570 (KSC). Natrona Co.: North Platte River valley 1 mi S Casper, 5 July 1933, Hermann 4526 (MO). Niobrara Co.: 27 mi S Newcastle, 6 June 1956, Porter 6918a (NY, RM). Park Co.: E approach to Dead Indian Hill, 11 July 1950, Porter 5433 (RM, NY). Platte Co.: Glendo State Park, 10 June 1980, Freeman 561 (KSC); Guernsey State Park, 11 June 1980, Freeman 564 (KSC). Sheridan Co.: Goose Canyon in Big Horn Mts., 21 May 1935, Rollins 440 (NY, MO). Washakie Co.: W of Worland, 9 May 1962, Nichols 317 (RM). Weston Co.: 1.5 mi NW Osage, 7 June 1980, Freeman 538 (KSC). Yellowstone National Park: Mammoth Hot Springs, Yellowstone Nat. Park, 1901, Scheuber 331 (NY).

9. Penstemon fendleri Torrey & Gray

Pentstemon fendleri T. & G., Pacif. R.R. Rep. 2(4): 168. pl. 5. 1855. Pentstemon acuminatus var. fendleri (T. & G.) Jones, Contr. W. Bot. 12: 61. 1908. Type: "On the Pecos and Llano Estacado; March, April.", collected by W.L. Dieffenderfer on Pope's Expedition, fide Pennell (1935). (Holotype: GH, not seen).

Herbaceous perennial. Stems mostly erect, (1.5)2-5.5(6) dm tall, glabrous and glaucous, 1-2(4) stems arising from a woody subterranean caudex surmounting a taproot. Leaves entire, firm, glabrous and glaucous; basal leaves oblanceolate or spatulate, 2-10 cm long overall, 0.4-2.4 cm wide,

acute to obtuse and occasionally mucronate, subsessile or short-petiolate, the petioles often winged; cauline leaves lanceolate to ovate or often trullate midway up the stem, (1.4)2.3-9.5 cm long, (0.4)0.6-3.1 cm wide, scarcely clasping below to distinctly clasping above, lower cauline leaves normally crowded, upper cauline leaves widely spaced, the upper half of the stem with leaves normally much shorter than the internodes. Thyrse (5)11-27 cm long, with (3)4-10 remote verticillasters, elongate, distinctly interrupted, narrow, cylindrical and not secund, individual cymes 2-3(5) flowered, peduncles usually absent or if present less than 2 mm long, pedicels glabrous, 1-12(28) mm long; bracts much-reduced above and resembling the cauline leaves below, trullate to ovate, the lower ones to 7 cm long and 3.8 cm wide, short-acuminate to acute, bases clasping to distinctly cordate-clasping, the lower bracts usually concealing the pedicels. Calyx glabrous and glaucous, sepals lance-ovate to ovate, 4.5-7 mm long, 1.5-3.5 mm wide, acuminate to acute, margins broadly scarious and frequently suberose to erose, green or tinged lavender to purple; corolla 14-23(28) mm long, tubular-salverform, scarcely bilabiate, purple to violet or pale blue, externally glabrous, tube slender, slightly decurved in mature open flowers and distinctly decurved in mature unopened corollas just prior to anthesis, throat 4-6 mm broad, barely ampliate, lined internally on the anterior surface and to a lesser extent on the posterior surface with prominent violet or reddish-purple guidelines, the guidelines passing slightly onto the lobes of the lips, lobes of the upper lip arched-spreading or reflexed, lobes of the lower lip projecting to spreading, palate glabrous or sparsely bearded with white eglandular hairs; staminode 8-11 mm long from its point of attachment, reaching the orifice, broadly flattened distally, the tip abruptly recurved and bearded with golden-yellow hairs to 1.5 mm long; fertile stamens

included or the longer pair reaching the orifice, anther-sacs 1-1.3 mm long, purple, lined with white or tan along the sutures, externally minutely papillose, divergent, dehiscing nearly to the apices and across the connective, not becoming explanate; style 11-15 mm long, glabrous. Capsule 10-15 mm long. Seeds 2.5-3.5 mm long, angular, finely reticulate, brown to dark brown. n = 8.

Sandy to gravelly soil on prairies, or at low elevations in the mountains of New Mexico. Southwestern Kansas southwest across New Mexico to southeastern Arizona, southeast to Oklahoma (Caddo and Comanche Counties) and south through Texas west of the 99th parallel to Chihuaha, Mexico. Flowering from late March in southern Texas to June in Kansas. One specimen, Henry 117 (KSC), collected in the vicinity of Hugoton in Stevens County, Kansas, was collected in full anthesis in July.

Penstemon fendleri is a common spring flowering species in the panhandle of Texas, southwestern Oklahoma, and northeastern New Mexico where it is frequently found on gypsiferous or calciferous soils. In northcentral and northeastern New Mexico, P. fendleri is sympatric with P. secundiflorus Benth., a closely related species of Section Coerulei. In this area of sympatry, Nisbet and Jackson (1960) indicate there may be some introgressive hybridization between the two species.

REPRESENTATIVE SPECIMENS:

UNITED STATES:

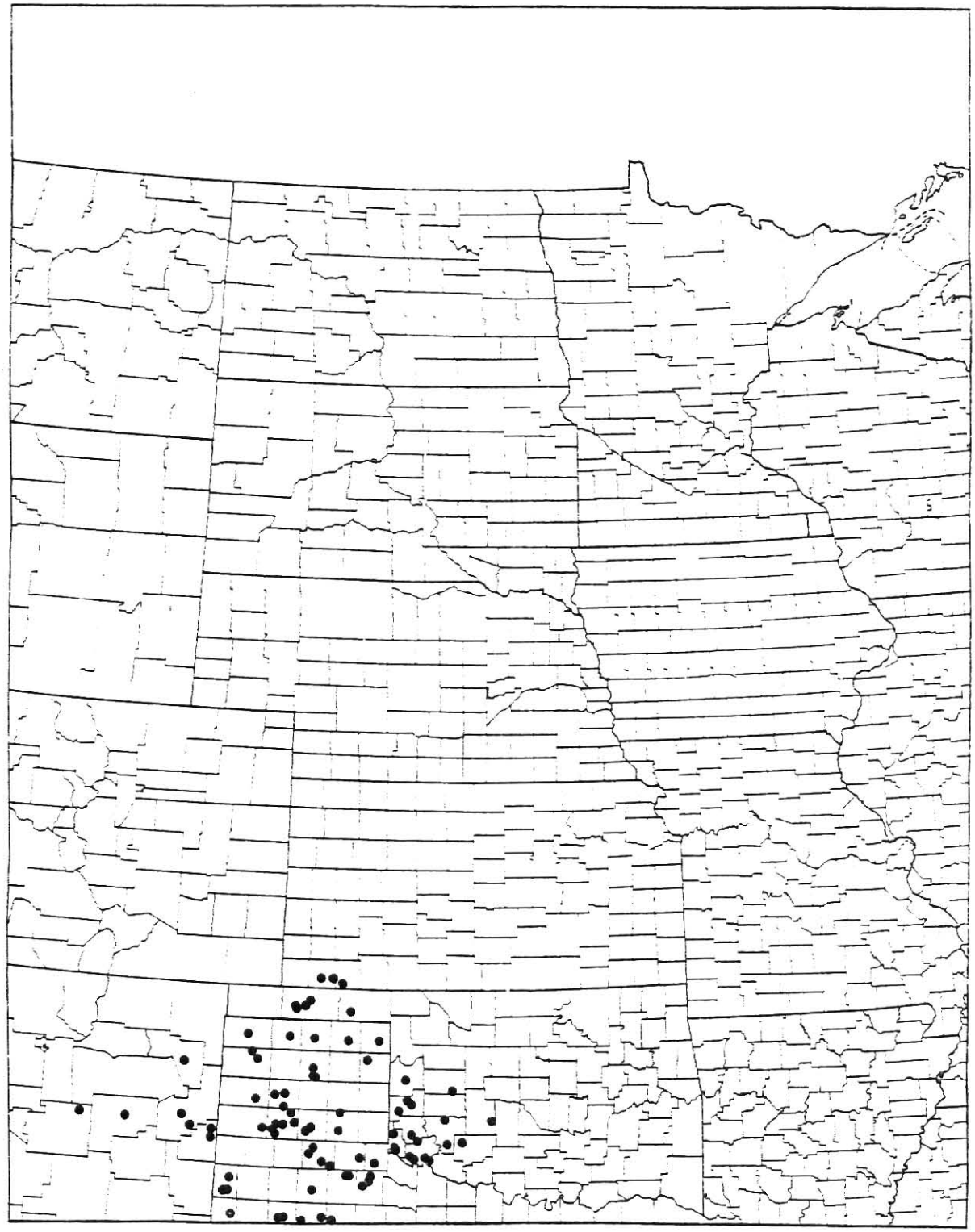
KANSAS: Seward Co.: 3 mi W of Liberal, 30 April 1972, Harris 23 (FHKSC). Stevens Co.: 3 mi W of Stevens-Seward Co. Line on Hwy 51, 28 May 1957, McGregor 12926 (KANU).

NEW MEXICO: Curry Co.: 8.6 mi S of Broadview, 21 May 1980, Freeman 424 (KSC). Dona Ana Co.: Near Las Cruces, 1926, Child 521 (MO). Grant Co.: Fort Bayard, 3 August 1895, Mulford 631 (MO). Guadalupe Co.: Santa Rosa, 21 May 1931, Nelson 11336 (RM). Harding Co.: 34.3 mi NW of Harding Co. Line along Hwy 39, 21 May 1980, Freeman 430 (KSC). Hidalgo Co.: 20 mi S of Animas, 21 April 1968, Hess 1822 (OKL). Luna Co.: Florida Mts., 12 mi SW of Deming, 20 April 1973, Holmgren & Holmgren 6880 (KANU). Sierra Co.: Hillsboro, 6 May 1905, Metcalfe 1577 (MO-2). Torrance Co.: 12 mi E Cline's Corner, 4 July 1965, Crook 40 (OKL). Quay Co.: 5.2 mi W of Quay Co. Line along Hwy 18 & 88, 21 May 1980, Freeman 425 (KSC); 9.8 mi S of Tucumcari, 21 May 1980, Freeman 427 (KSC).

OKLAHOMA: Beaver Co.: 15 mi SW of Beaver City, 8 May 1913, Stevens 352 (OKLA, MO, OKL). Beckman Co.: 1 mi E & 8 mi S of Erick, 30 April 1960, Horn 37 (OKLA). Caddo Co.: Valley of Washita River along Hwy 9, 30 April 1944, Hopkins, Nelson, & Nelson 232 (MO, OKL, NY, RM). Comanche Co.: Wichita National Forest, 19 May 1937, Eskew 1594 (OKLA, OKL, IND). Custer Co.: S edge Clinton, 4 May 1980, Brooks 14495 & McGregor (KANU). Greer Co.: 1 mi W of Mangum, 16 April 1960, Hatchett 18 (OKLA). Harmon Co.: 3.7 mi S & 1 mi W of Hollis, 26 April 1980, Freeman & Wetter 359 (KSC). Jackson Co.: 5 mi SE of Eldorado, 25 April 1980, Freeman & Wetter 353 (KSC); N edge of Eldorado, 25 April 1980, Freeman & Wetter 355 (KSC). Kiowa Co.: 3 mi W of Gotebo, 6 May 1956, Goodman 6271 (OKL). Roger Mills Co.: 9 May 1939, Engleman 2011 (OKL). Texas Co.: Near Guymon, 17 May 1941, Hopkins & Van Valkenburgh 5768 (NY, OKL, RM).

TEXAS: Palo Duro Canyon, 26 April 1980, Freeman & Wetter 378 (KSC); Palo Duro Canyon 15 mi S of Claude, 24 April 1965, Rowell 10780 (OKL, OKLA, TTC-2). Bailey Co.: Muleshoe Wildlife Refuge 20 mi S of Muleshoe, 11 May 1965, Rosson 633 (OKLA, TTC). Brewster Co.: Alpine on College Hill, 28 March 1936, Sperry T108 (NEB, TTC). Briscoe Co.: 0.3 mi E of jct Farm Rd 599 & Hwy 86, 26 April 1980, Freeman & Wetter 377 (KSC). Childress Co.: 2 mi W of Childress, 9 April 1966, Whitten 34 (TTC). Cochran Co.: 6 mi W of Whiteface, 1 May 1960, Gould 9119 (TTC). Coke Co.: 6 mi E Bronte, 6 May 1980, Brooks 14587 & McGregor (KANU). Cottle Co.: 10 mi S of Childress, 26 April 1980, Freeman & Wetter 364 (KSC); 4.4 mi N of jct Hwys 83 & 62, & Farm Rd 1440, 26 April 1980, Freeman & Wetter 370 (KSC). Crosby Co.: 6 mi E of Crosbyton, 25 April 1964, Gaines 25 (OKLA). Dallam Co.: 3 May 1938, McLaughlin 132 (OKLA). Deaf Smith Co.: S of Dawn, 15 April 1967, Waller 1293 (TTC). Dickens Co.: 7 mi E of Crosbyton, 25 April 1964, McKee s.n. (OKLA). Donley Co.: 2 mi S Claredon, 5 May 1980, Brooks 14523 & McGregor (KANU). Ector Co.: 3 mi W of Odessa, 8 April 1966, McCracken 29 (TTC). Fisher Co.: 5 mi N of Rotan, 19 April 1964, Gibson s.n. (OKL). Floyd Co.: E of Floydada, 30 April 1925, Small & Wherry 12160 (NY). Garza Co.: Post, 21 May 1920, Pennell 10533 (MO, NY). Hall Co.: W of Estelline, 24 May 1904, Reverchon s.n. (MO). Hansford Co.: 1 mi E & 1 mi S of Gruver, 13 May 1955, Cutter 12 (OKL). Hartley Co.: 3.8 mi SE of Dalhart, 13 June 1975, Semple & Semple 1470 (MO). Hemphill Co.: Canadian, 15 May 1938, Bondy s.n. (FHKSC, MO, RM). Hutchinson Co.: In Borger, 26 April 1980, Freeman & Wetter 380 (KSC). Jeff Davis Co.: Limpia Canyon, 26 April 1902, Tracy & Earle 289 (MO, NEB, NY). Kent Co.: 11 mi SW of Clairemont, 4 May 1963, Pritchard s.n. (OKLA). Lipscomb Co.: 16 mi SE of Darrouzett, 6 May 1960, Wallis 8454 (KANU). Lubbock Co.: 4 mi SE of Lubbock, 4 May 1966, Hawkins

Figure 63. Great Plains Distribution of Penstemon fendleri



31 (TTC). Martin Co.: 15.9 mi N of Midland, 26 March 1972, Churchill 9 (MO, NEB). Menard Co.: Menard, 11 May 1917, Palmer 11881 (MO). Mitchell Co.: 7 mi S of Colorado City, 25 April 1965, Stinson 31 (OKLA). Motley Co.: 2 mi W of jct Farm Rds 94 & 1440, 26 April 1980, Freeman & Wetter 374 (KSC); 1 mi W of jct Farm Rds 656 & 94, 26 April 1980, Freeman & Wetter 375 (KSC). Nolan Co.: Near Sweetwater, 15 May 1928, Palmer 33974 (MO, NY). Ochiltree Co.: Lake Fryer, Wolf Creek Rec. Park, 13 May 1945, Jespersen & Jespersen 2669 (MO, NEB, NY, RM). Oldham Co.: 5 mi N of Vega, 21 May 1974, Stephens 76099 (KANU). Pecos Co.: Between Ft. Stockton and Marathon, 27 March 1972, Higgins 5011 (NY). Potter Co.: 16 mi N of Amarillo, 22 April 1935, Goodman 2437 (MO, NY-2, OKL, RM). Presidio Co.: Cemetary E of Marfa, 24 April 1944, Hickley 2940 (NY). Randall Co.: 11 mi SE of Amarillo, 26 April 1963, McNabb 68 (OKLA). Runnels Co.: 8.3 mi NE of Winters, 11 April 1948, Cory 54308 (IND, NEB, KANU). Scurry Co.: 4.5 mi SE of Snyder, 6 April 1963, Winter 21 (OKL). Sherman Co.: 14 mi E & 5.5 mi S of Stratford, 10 May 1974, Stephens 75309 (KANU). Sutton Co.: 9 mi NE of Sonora, 16 April 1947, Reed 49 (NY). Swisher Co.: Tulia, 21 May 1920, Pennell 10538 (MO, NY). Taylor Co.: Camp Barkeley, 8 April 1943, Tolstead 6954 (MO, NY). Tom Green Co.: San Angelo, 18-19 May 1920, Pennell 10486 (MO, NY). Wichita Co.: 1.1 mi W of Electra, 27 April 1945, Whitehouse 9726 (NY).

10. *Penstemon glaber* Pursh

Stout herbaceous perennial. Stems assurgent, (1)5-6.5(8) dm tall, glabrous to puberulent or pubescent, one to many arising from a well developed and often much-branched suffrutescent caudex surmounting a taproot. Leaves entire, glabrous to puberulent or pubescent, thick; basal leaves frequently wanting or smaller than the cauline leaves, (ob)lanceolate to obovate, 2-8(15.5) cm long overall, 0.5-2(4.5) cm wide, acute to obtuse and occasionally mucronate, subsessile to petiolate, the petioles usually winged; cauline leaves linear-lanceolate to lanceolate, 3-12(15) cm long, (0.7)1.2-3.5(4.8) cm wide, acute to obtuse, sessile below to broadly clasping above. Thyrse 8-26(30) cm long, with (5)8-12 verticillasters, congested, secund, leafy-bracted at the base, individual cymes typically 2-4 flowered, peduncles and pedicels glabrous or sparingly puberulent, peduncles to 7.1 cm long, pedicels 4-14 mm long; bracts lanceolate to lance-ovate, the lower ones to 10 cm long and 3.6 cm wide, acute. Calyx glabrous to puberulent, sepals lance-ovate to ovate or orbiculate, 2-7(10) mm long, 1.5-3(4) mm

wide, broadly rounded at the apex or with an abruptly short-acuminate to long-acuminate tip, margins usually broadly scarious and distinctly erose; corolla 26-35(40) mm long, strongly bilabiate, posteriorly deep blue to bluish-purple or occasionally pink, anteriorly light blue or white, glabrous externally, throat 8-13(18) mm wide, moderately inflated and ventricose-ampliate anteriorly, pale internally and lined on the anterior surface with pale or deep reddish-purple nectar guides, the guidelines occasionally passing onto the lobes of the lower lip, palate glabrous to pubescent or villose with white eglandular hairs, especially near the base of the lobes of the lower lip, lobes of the upper lip arched-projecting, lobes of the lower lip spreading to strongly reflexed; staminode (15)18-22 mm long from its point of attachment, included or slightly exserted, distally expanded and slightly recurved, the tip rounded or distinctly bifurcate, glabrous or the terminal 2 mm sparingly bearded with pale yellow hairs to 1.5 mm long; fertile stamens included or the longer pair reaching the orifice, anther-sacs 1.9-2.5(2.8) mm long, white to tan, sparingly to moderately hirsute or rarely glabrous, papillate along the sutures, divergent, dehiscent nearly to the apices but not across the connective, not becoming explanate, occasionally somewhat twisted; style 18-20 mm long, glabrous. Capsule 10-15 mm long, thin and quite pliable. Seeds 2.5-3.2 mm long, angular-elongate, finely reticulate, dark brown. $\underline{n} = 8$.

Penstemon glaber exhibits considerable morphological variation throughout its range. Several varieties may be distinguished by the following characters.

1. Sepals 2-4 mm long, lance-ovate to orbiculate and broadly rounded or with an abruptly short-acuminate tip; corolla glabrous or pubescent internally on the anterior surface; staminode rounded at the tip . . . . . 10a. var. glaber

1. Sepals 4-7(10) mm long, ovate and usually with a long-acuminate tip; corolla glabrous to pubescent or villose internally on the anterior surface; staminode rounded to distinctly bifurcate at the tip.
   2. Staminode rounded or obscurely bifurcate at the tip; corolla 24-35 mm long; stems glabrous to pubescent . . . . . 10b. var. alpinus
   2. Staminode usually distinctly bifurcate at the tip; corolla 30-40 mm long; stems puberulent to pubescent . . . . 10c. var. brandegei

10a. Penstemon glaber Pursh var. glaber

Pentstemon glabra Pursh, Fl. Amer. Sept. 739. 1814. Type: "In Upper Louisiana", description based on a collection made by Bradbury on his trip up the Missouri River in 1811 and collected in South Dakota, fide Pennell (1935). (Holotype: PH, not seen).

Penstemon erianthera Nutt., in Fras. Catal. 2. 1813. nomen nudum. Pentstemon erianthera Nutt., Gen. N. Amer. Pl. 2: 52. 1818. Type: "In arid soils near the confluence of Shian (Cheyenne) river (with the Missouri River)." (Holotype: not located by Pennell).

Pentstemon gordoni Hook., Bot. Mag. 73: tab. 4319. 1847. Type: Grown from seeds collected by, "Mr. Gordon in the valley of the Platte River, on the east side of the Rocky Mountains." (Holotype: K; Phototype: NY!).

Penstemon glaber f. pubicaulis Pennell, Contr. U.S. Natl. Herb. 20: 348. 1920. Type: No type was designated by Pennell in publishing this name, however, Pennell cites only one specimen as fitting his description. Therefore, Pennell's form is lectotypified using the specimen cited in his 1920 publication. Lectotype: Nelson 8541, collected on Dome Lake road, Sheridan County, Wyoming, 29 July 1901. (Lectotype: RM!).

Sandy to gravelly soil on high plains and in the foothills of the Rocky Mountains. Southwestern North Dakota and northcentral South Dakota west to northwestern Wyoming; south to the panhandle of Nebraska and southeastern and southcentral Wyoming. Flowering from early July to early September.

In southeastern and eastcentral Wyoming, two varieties of P. glaber

(var. glaber and var. alpinus) exist sympatrically and it is in this area that morphological intergradants are observed. Puberulent-stemmed specimens of the normally glabrous P. glaber var. glaber occur very sporadically in this area of sympatry and undoubtedly represent introgression between var. glaber and var. alpinus. Such puberulent-stemmed forms of var. glaber may be referred to as f. pubicaulis Pennell.

REPRESENTATIVE SPECIMENS:

UNITED STATES:

MONTANA: Powder River Co.: 31 mi SW Broadus in Butte Creek Valley, 21 June 1949, Considine s.n. (NY).

NEBRASKA: Banner Co.: Lawrence Fork, 8 July 1891, Rydberg 276 (KSC, NEB, NY). Box Butte Co.: Alliance, 14 July 1889, Webber 4915 (NEB). Dawes Co.: Belmont, July 1889, Webber 4960 (NEB-2, MO). Morrill Co.: Chimney Rock near Baynard, 12 July 1935, Hapeman s.n. (NY, RM). Scotts Bluff Co.: Scotts Bluff Nat. Monument, 22 June 1966, Stephens 5394 (KANU, OKLA). Sioux Co.: 5 mi NW Harrison, 12 August 1967, Stephens 16312 & Brooks (KANU).

NORTH DAKOTA: Oliver Co.: Fort Clark, June 1853, Hayden s.n. (MO, NY). Stark Co.: Dickinson, 6 July 1922, Blume s.n. (NDA).

SOUTH DAKOTA: Butte Co.: N edge of Belle Fourche along Hwy 85, 24 June 1979, Freeman 201 (KSC); 1 mi N Shepherds' Monument along Hwy 85, 24 June 1979, Freeman 204 (KSC). Corson Co.: 3 mi W Mobridge, 28 June 1968, McGregor & Bare 1201 (KANU, NDA). Custer Co.: Near the Needles, 5 July 1937, Tolstead 3776 (KSC, RM). Dewey Co.: 12.5 mi E & 11.5 mi SE Eagle Butte, 25 June 1967, Stephens 12273 & Brooks (KANU, NY, OKLA). Fall River Co.: 14 mi S Hot Springs, 25 June 1966, Stephens 5766 (KANU). Harding Co.: Buffalo, 21 July 1958, Alberson s.n. (SDC). Lawrence Co.: 2.1 mi W Savoy along Hwy 14A, 24 June 1979, Freeman 197 (KSC); 1.5 mi E Savoy along Hwy 14A, 24 June 1979, Freeman 198 (KSC); Deadwood, 14 July 1913, Rydberg 84 (NEB, SDC, SDU). McPherson Co.: Webbs Ranch, 8 September 1892, Griffiths & Schlosser 410 (SDC). Meade Co.: 1 mi N Sturgis, 25 June 1928, McIntosh s.n. (SDU). Pennington Co.: Nasby, 25 July 1912, Rydberg 1510 (NY, SDU); 1 mi E & 3 mi S Deerfield, 6 August 1969, Stephens 35445 & Brooks (KANU, NDA, NY). Shannon Co.: Between Wounded Knee & Porcupine Creek, 21 June 1938, Benson 638 (NEB).

WYOMING: Albany Co.: 20 mi N Laramie, 15 July 1942, Porter 3131 (RM); * 1 mi S & 18 mi NE Bosler, 10 August 1973, Stephens 70701 (KANU). Big Horn Co.: Head of Middle Fork of Powder River, 18 July 1901, Goodding 285 (MO, NEB, NY, RM); 10-15 mi E Kane, 19 June 1936, Williams & Williams 3009 (MO, NY, RM). Campbell Co.: Along Hwy 59 12.9 mi N Converse Co. Line, 10 June 1980, Freeman 555 (KSC). Carbon Co.: Along Hwy 487 25.1 mi S Natrona Co.

Line, 28 June 1974, Nelson & Nelson 1521 (RM). Converse Co.: 7 mi SW Esterbrook, 6 August 1975, Hammel 103 (RM); * 6 mi S Douglas, 10 July 1951, Porter 5726 (MO, NY, RM). Crook Co.: 10 mi E & 2 mi N Moorcroft, 7 June 1980, Freeman 541 (KSC); 1.25 mi E entrance to Devil's Tower Nat. Monument, 3 September 1962, Crosswhite & Crosswhite s.n. (RM); Sundance Mt., 3 July 1896, Nelson 2146 (MO, NY, RM). Fremont Co.: Birds Eye, 24 June 1910, Nelson 9352 (MO, NY, RM). Hot Springs Co.: SW of Thermopolis and W of Wind River Canyon on N flank of Owl Creek Range, 28 June 1961, Fisser 557 (RM). Johnson Co.: Along Hwy 16 10 mi W Buffalo, 29 June 1953, Porter 6254 (NY, RM). Natrona Co.: 5 mi S Casper, 8 July 1933, Hermann 4656 (MO, RM). Niobrara Co.: 22 mi N & 3 mi W Lusk, 22 June 1968, Stephens 23085 & Brooks (KANU). Park Co.: Carter Mt. near Cody, 14 July 1915, Marston 24X (RM). Platte Co.: Oregon Trail near Warm Springs 3 mi W Guernsey, 15 June 1949, Porter 4911 (RM). Sheridan Co.: Big Horn Mts. W of Dayton, 25 May 1934, Rollins 477 (MO, NY). Sweetwater Co.: Table Rock, 5 July 1940, Wehmeyer, Martin, & Loveland 5432 (NY). Washakie Co.: Tensleep Canyon in Big Horn Mts., 17 June 1934, Nelson & Nelson 1091 (MO, NDA, NY, RM). Weston Co.: Newcastle, 19 July 1942, Degener & Peiler 16226 (MO, NY-2).

* indicates specimens referable to f. pubicaulis Pennell

10b. Penstemon glaber var. alpinus (Torrey) A. Gray

Pentstemon alpina Torr., Ann. Lyceum Nat. Hist. New York 1: 35. 1824. Chelone alpina (Torr.) Spreng., Syst. Veg. 4: Cur. Post. 235. 1827. Pentstemon glaber γ alpinus (Torr.) A. Gray, Proc. Amer. Acad. Arts 6: 60. 1862-63. Type: "Hab. with the preceding (On James (= Pikes) Peak, * * * 10,000 feet above the level of the ocean, near the region of perpetual snow.)", collected by Dr. Edwin James in July, 1820, in Colorado. (Holotype: NY!).

Pentstemon riparius A. Nels., Bull. Torrey Bot. Club 25: 379. 1898. Penstemon alpinus f. riparius (A. Nels.) Penn., Contr. U.S. Natl. Herb. 20: 349. 1920. Type: "Collected at Laramie by Mr. Elias Nelson, June 18, 1897, and fruited specimens later in the season. Type specimen in Herb. Univ. of Wyoming, no. 3185.", from Albany County, Wyoming. (Holotype: RM!; Isotype: NY!).

Pentstemon oreophilus Rydb., Bull. Torrey Bot. Club 31: 642. 1905. Type: "Eldorado to Baltimore, 1903, Tweedy 5711", collected in Gilpin County, Colorado. (Holotype: NY!; Isotype: RM!).

Sandy or gravelly soil primarily on the eastern slope of the Rocky Mountains, ascending to ca 11,000 ft. In the northern part of its range, descending to the high plains where it introgresses with P. glaber var. glaber. Southeastern Wyoming south to southcentral Colorado. Flowering from early June to late August.

Penstemon glaber var. alpinus is variable, particularly with respect to size, length of the corolla, and pubescence of stems, leaves, palate of the corolla, and anther-sacs. Plants from the northern half of the range frequently have pubescent to puberulent stems and leaves, and may be referred to as f. riparius (A. Nels.) Penn. Plants from the southern half of the range are normally glabrous or glabrate. Plants referable to f. riparius frequently occur in mixed populations with glabrous-stemmed plants.

REPRESENTATIVE SPECIMENS:

UNITED STATES:

COLORADO: * Boulder Co.: 1 mi E Gold Hill, 10 July 1949, Beamer 16 (RM). * Clear Creek Co.: Near Empire, 19 July 1892, Patterson 256 (NY-3, OKL). Custer Co.: 13 mi N San Isabel, 3 August 1968, Stephens 26792 & Brooks (KANU). Denver Co.: Along South Platte River at Valverde, 15 June 1915, Pennell 5842 (NY, RM). Douglas Co.: 5 mi W of Sedalia, 23 June 1937, Beetle & Snyder 50 (RM). El Paso Co.: Colorado Springs, July 1893, Saunders s.n. (NEB-3, SDC). * Gilpin Co.: Eldora to Baltimore, 20 June - 10 July 1903, Tweedy 5710 (NY, RM); Tolland, 19 July 1917, Clokey 2832 (RM, NY). Huerfano Co.: 8 mi NE Walsenburg, 10 June 1968, Stephens 22213 & Brooks (KANU). * Jefferson Co.: 20 mi W Denver along I-70, 26 July 1980, Freeman 737 (KSC). * Larimer Co.: Horsetooth Mt., 18 June 1896, Cowen 4201 (CS, NEB, NY, RM); Stove Prairie Hill, 13 July 1898, Cowen 1808 (NY, RM, CS). Park Co.: Kenosha Pass, 13 July 1950, Ripley & Barneby 10446a (NY). Pueblo Co.: 6 mi S Beulah, 6 August 1970, Stephens 42850 & Brooks (KANU). Sagauche Co.: Marshall Pass, 20 August 1901, Baker 869 (NY). Teller Co.: Divide to Cripple Creek, 3 July 1920, Clokey 3866 (RM, NY). Weld Co.: Twin Bridges on the South Platte River, 15 June 1926, Osterhout 6525 (OKL, RM).

WYOMING: * Albany Co.: Dunn's Ranch, 16 July 1900, Nelson 7616 (KANU, NEB, NY, RM); Chug Creek, 29 June 1900, Nelson 7309 (NEB-2, NY, RM). * Carbon Co.: Arlington, 10 July 1924, Nelson 10147 (NY, RM); Near McFadden, 29 June 1949, Porter 4916 (MO, NY, OKL, RM). Goshen Co.: 12 mi W Lagrange, 21 June 1968, Stephens 22933 & Brooks (KANU). * Laramie Co.: Cheyenne, 12 July 1889, Bodin s.n. (KSC). * Natrona Co.: N side Casper Mt., 23 June 1968, Tresler 397 (RM). Platte Co.: 10 mi S Wheatland, 1 July 1935, Ownbey 782 (NY, RM).

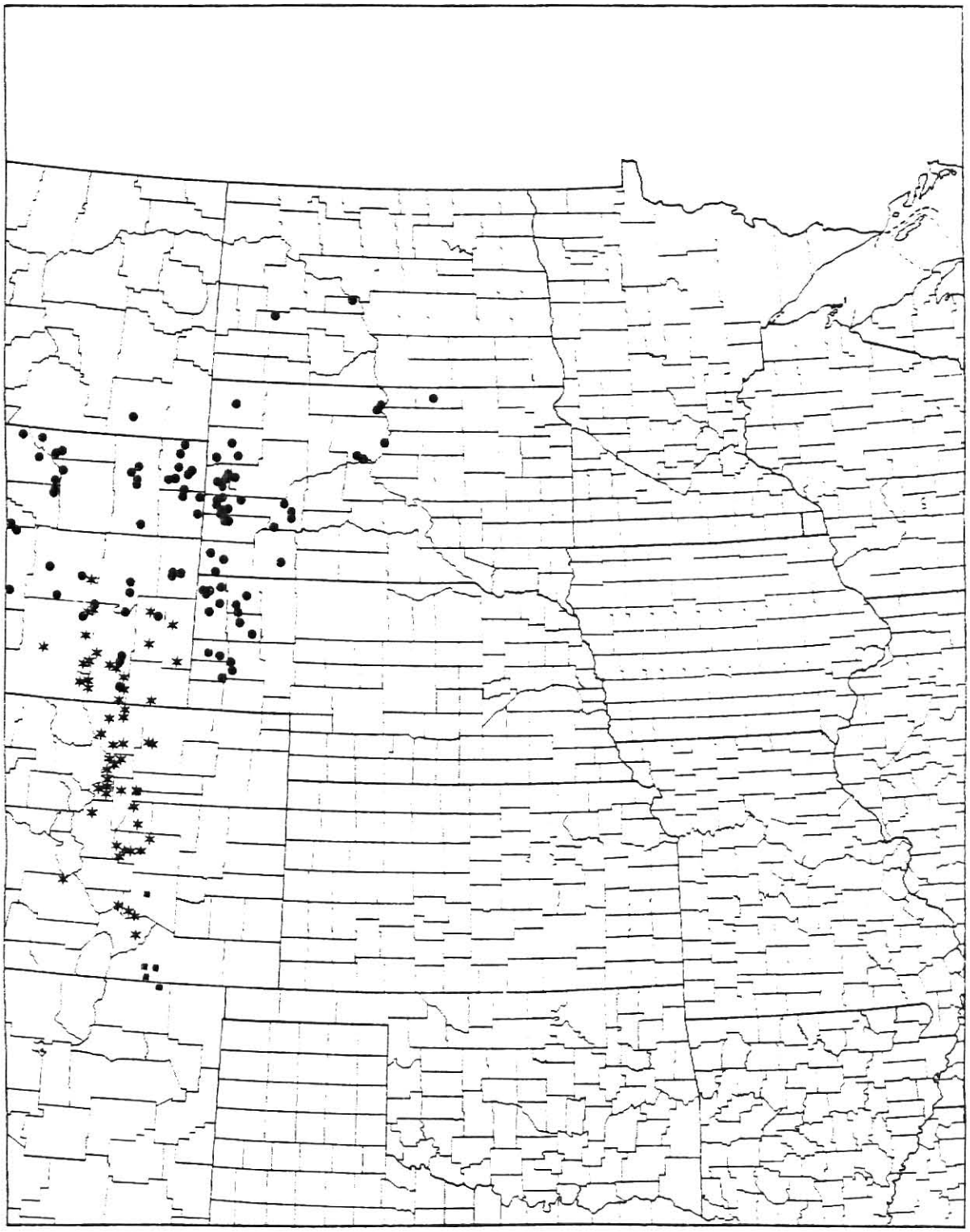
* indicates counties from which specimens referable to f. riparius (A. Nels.) Penn. have been seen

Figure 64. Great Plains Distribution of Penstemon glaber

•= var. glaber

*= var. alpinus

▪= var. brandegei



10c. Penstemon glaber var. brandegei (Porter ex Rydberg) Freeman comb. nov.

Pentstemon cyananthus Hook. var. brandegei Porter in Port. & Coult., Syn. Fl. Colo. 91. 1874. Pentstemon brandegei Porter ex Rydb., Mem. New York Bot. Gard. 1: 343. 1900. Penstemon alpinus Torr. subsp. brandegei (Porter ex Rydb.) C. Wm. T. Penland in Harrington, Man. Pl. Colo. 496, 641. 1954. Type: "Sierra Mojado, Brandegee." (Isotype: MO, not seen).

Sandy or gravelly soil on the eastern slope of the Southern Rocky Mountains at low elevations in the mountains and in the foothills; descending to the high plains. Southcentral Colorado south to northeastern New Mexico. Flowering from early June to early August.

Penstemon glaber var. brandegei barely enters the southwestern Great Plains. Nisbet & Jackson (1960) cite specimens from Colfax and Union Counties in New Mexico (not seen) and the taxon may be encountered sporadically on the high plains in southcentral Colorado. Penland, writing in Harrington (1954), and Nisbet & Jackson (1960) indicate the variety hybridizes readily with var. alpinus, a fact attested to by morphological intermediates commonly encountered in southcentral Colorado.

REPRESENTATIVE SPECIMENS:

UNITED STATES:

COLORADO: Las Animas Co.: 5 mi N Trinidad, 27 June 1944, Harrington & Smith 156 (CS). Pueblo Co.: Pueblo, 16 June 1897, Berg 1970 (CS-2).

NEW MEXICO: Colfax Co.: Summit of Johnson Mesa 7 mi above Yankee, NE of Raton, 8 August 1970, Weber & Arp 14179 (NEB).

11. Penstemon gracilis Nuttall

Pentstemon gracile Nutt., Gen. N. Amer. Pl. 2: 52. 1818. Chelone gracilis (Nutt.) Spreng., Syst. Veg. 2: 813. 1825. Pentastemon digitalis ε gracilis Trautv., Bull. Aca. Imp. Sci. Saint-Petersbourg 5: 345. 1839. Pentstemon pubescens β gracilis A. Gray, Proc. Amer. Acad. Arts 6: 69. 1862-63. Type: "From the Arikarees to Fort Mandan, in depressed soils." (Holotype: PH, not seen).

Pentstemon glaucum R. Grah., Edinburgh New Philos. J. 7: 348. 1829. Pentastemon digitalis β glaucus Trautv., Bull Acad. Imp. Sci. Saint-Petersbourg 5: 345. 1839. Type: "The seeds of this species, which flowered at the Botanic Gardens during the greater part of the summer, were received from Mr. Drummond after his return from the second journey to British North America." (Type: not seen).

Penstemon gracilis var. gracilis f. scogganii Boivin, Phytologia 22(5): 331. 1972. Type: "Boivin & Laishley 13092, Reserve Forestiere Whiteshell, falaise au bord du Lily Pond a l'ouest du lac Caddy, fleurs blanches, croissant avec la forme typique, 26 juin 1959 (DAO)." (Holotype: not seen).

Slender herbaceous perennial. Stems erect or assurgent, (1.5)2-5 dm tall, commonly anthocyanic above, retrorsely puberulent below and glandular-pubescent near the inflorescence, stems 1-4(6) arising from a short, typically slender herbaceous caudex surmounting a taproot. Leaves subentire to obscurely or sharply serrate, glabrous to sparingly puberulent, seldom densely puberulent; basal leaves (ob)lanceolate to ovate, 2.5-7.5 cm long overall, 0.4-1.5 cm wide, acute to obtuse, subsessile or petiolate, the petioles usually winged; cauline leaves linear to lanceolate, 2.5-8(9) cm long, (0.2)0.4-1(1.5) cm wide, acuminate to acute and somewhat clasping; bracts linear-lanceolate and resembling the upper cauline leaves, the lower ones to 8 cm long and 0.8 cm wide. Thyrse (3)5-17(21) cm long, with (2)3-5(7) verticillasters, narrow, interrupted to congested, individual cymes 2-6 flowered, peduncles appressed or erect, glandular-pubescent, to 4.5(6.5) cm long, pedicels glandular-pubescent, to 1 cm long. Calyx glandular-pubescent, sepals lanceolate to lance-ovate, 4-6 mm long, 1.5-2 mm wide, acuminate to acute, entire, herbaceous throughout or with scarious margins toward the base; corolla (14)15-22 mm long, bilabiate, pale lavender to mauve externally and lighter within, glandular-pubescent externally, tube slender, throat 4-6 mm broad, slightly inflated and flattened, barely ampliate, lined internally with purple or mauve nectar guides, the guidelines reaching the

bases of the lobes of the lower lip or passing slightly onto the lobes, strongly 2-ridged anteriorly within, palate slightly up-arched and bearded with whitish eglandular hairs extending back to 1/2 the length of the throat, lobes of the upper lip spreading to reflexed, lobes of the lower lip projecting and extending beyond the upper lip; staminode 11-12 mm long from its point of attachment, reaching the orifice or barely exserted, slightly expanded distally, the terminal 7-9 mm densely bearded with stiff golden-yellow hairs to 1.5 mm long; fertile stamens included, anther-sacs 1-1.3 mm long, deep purple, glabrous, papillose along the sutures, divergent, dehiscing nearly to the apices and across the connective, not becoming explanate; style 9-12 mm long, glabrous. Capsule 6-8 mm long. Seeds 0.6-0.8 mm long, rounded to slightly angular, finely reticulate, dark brown. $n = 8$.

Sandy or gravelly soil in prairies, valleys, and at lower elevations on the eastern slope of the Rocky Mountains. Southwestern Ontario west to Alberta and northeastern British Columbia; south to Wisconsin, northern Iowa, and southern Nebraska; along the eastern slope of the Rocky Mountains from British Columbia through Montana, Wyoming, Colorado, and northern New Mexico. Most abundant in the northern Great Plains. Flowering from late May to early August depending on latitude and elevation.

Throughout most of its range, Penstemon gracilis has leaves which are glabrous or nearly so on the adaxial surface. However, Pennell (1935) recognized certain plants from the Driftless Area of Wisconsin as differing from the nomenclaturally typical P. gracilis by having leaves which were puberulent on the adaxial surface. Pennell designated these puberulent plants as Penstemon wisconsinensis, which he subsequently lowered tc subspecific rank as P. gracilis subsp. wisconsinensis (Pennell) Pennell.

During this study, an examination of the many collections from North Dakota revealed a number of plants with puberulent leaves, similar to subsp. wisconsinensis of Wisconsin. Frequently, these puberulent-leaved plants occurred along with glabrous-leaved specimens on sheets where several plants were mounted and thus assumedto have come from the same population. These puberulent-leaved plants were all from north or east of the Missouri River, including Barnes, Benson, Eddy, Pembia, Pierce, Ramsey, Wells, and Williams Counties in North Dakota. From no other states (excluding Wisconsin) were specimens found which had puberulent leaves.

Pennell (1935), in reducing P. wisconsinensis to a subspecies of P. gracilis, stated, "The constancy of its indument should be checked again from more ample material than I have now at my disposal." Little material from Wisconsin was examined in this study, so it cannot be said whether populations of P. gracilis from Wisconsin also consist of mixtures of puberulent and glabrous leaved plants. If, however, the situation in Wisconsin is similar to that observed in North Dakota, puberulent-leaved plants of Penstemon gracilis probably represent no more than an expression of a freely varying character-state.

White flowered forms of nomenclaturally typical P. gracilis may be referred to as f. scogganii, however, such color morphs appear to be quite rare as none were observed in the extensive material examined in the course of this study.

REPRESENTATIVE SPECIMENS:

UNITED STATES:

COLORADO: Boulder Co.: Boulder, 19 June 1921, Bethel & Clokey 4286 (IND, MO, NY, RM). Douglas Co.: Larkspur, 10 July 1917, Johnston & Hedgcock 436 (MO, NY). El Paso Co.: Palmer Lake, 22 July 1895, Osterhout s.n. (CS, RM).

Huerfano Co.: Wahatoya Creek, 7 July 1900, Rydberg & Vreeland 5640 (NY). Larimer Co.: Horsetooth Reservoir W of Ft. Collins, 12 June 1980, Freeman 594 (KSC). Las Animas Co.: 1 mi S of Morley, 4 July 1937, Rollins 1817 (MO, NY). Teller Co.: Manitou Expt. Forest, 24 July 1957, Harrington 41 (CS).

IOWA: Lyon Co.: Gitche Manito State Park, 22 June 1937, Hayden 9032 (NY).

MINNESOTA: Anoka Co.: 1926, Stoesz s.n. (NDA). Becker Co.: 1 mi W of Osage, 30 June 1970, Seiler 1911 (KANU, NDA). Big Stone Co.: S of Ortonsville, 14 July 1940, Gleason 9414 (NY). Clay Co.: 6 mi E & 1 mi S of Glyndon, 16 June 1969, Barker 5342 (NDA). Crow Wing Co.: Brainerd, June 1892, Sheldon s.n. (NY, RM). Douglas Co.: 3 mi N and 0.25 mi W of Melby, 12 June 1976, Sperling 275 (NDA). Goodhue Co.: West Redwing, 15 June 1937, Tolstead 22 (NEB). Hennepin Co.: June 1890, Sandberg 4921 (MO-2, NY). Hubbard Co.: 2 mi S of Park Rapids, 27 June 1974, Holland 3303-B (KSP). Lac Qui Parle Co.: Appleton Twsp., 19 June 1974, Barchenger 93 (NDA). Norman Co.: 10 mi S Fertile, 13 June 1941, Moore & Thatcher 14340 (KSC). Otter Tail Co.: Richdale, 14 June 1911, Chandonnet s.n. (NY, RM). Ramsey Co.: St. Anthony, 25 June 1888, Schuette 88 (NY). Rock Co.: 9 mi W of Luverne, 14 June 1941, Johnson 292 (NY). St. Louis Co.: Skyline Parkway, Duluth, 9 July 1938, Lakela 2556 (NDA, FHKSC).

MONTANA: Carter Co.: 7.5 mi S of Ekalaka, 25 June 1968, Stephens 23223 & Brooks (KANU). Custer Co.: 14 mi E of Miles City, 10 July 1973, Stephens 67083 (KANU). Dawson Co.: 19 mi E of Glendive, 27 June 1968, Stephens 23501 & Brooks (KANU). McCone Co.: 23 mi N of Circle, 21 June 1974, Stephens 78462 (KANU). Powder River Co.: 38 mi W of Broadus, 29 June 1968, Stephens 23778 & Brooks (KANU). Roosevelt Co.: Near Wolf Point, 2 July 1925, Degener 1676 (NY). Sheridan Co.: Bjorgen's Lake near Westby, 29 June 1927, Larsen 149 (MO).

NEBRASKA: Antelope Co.: Neligh, 1895, Coney s.n. (NEB). Blaine Co.: 0.25 mi SE of Bessey Forest, 15 June 1968, Koch 4705 (NEB). Box Butte Co.: Alliance, 5 July 1906, Churchill s.n. (NEB). Brown Co.: 5 mi SE of Wood Lake, 15 June 1968, Koch 4750 (KANU, NEB). Buffalo Co.: Near Poole, 23 June 1935, Hapeman s.n. (*KNSC, MO, NY, OKLA). Cherry Co.: Hwy S-16B between Kennedy & Brownlee, 22 June 1979, Freeman 167 (KSC); 1.2 mi E of Nenzel, 22 June 1979, Freeman 172 (KSC); 1.2 mi E of Nenzel, 6 June 1980, Freeman 526 (KSC). Custer Co.: 12 mi W, 2 mi S, and 1 mi SW of Merna, 11 June 1977, Churchill 9249 (KANU, MO, NDA). Dawes Co.: E of Chadron, 17 June 1953, Kiener 29317 (NEB, OKL). Deuel Co.: 26 June 1891, Rydberg 279 (NEB-2, NY, SDC). Franklin Co.: Franklin, 24 April 1894, Laybourn 84 (MO). Garfield Co.: 16 mi E of Burwell, 11 July 1968, Stephens 24309 & Brooks (KANU). Hall Co.: 1 mi N of Cairo, 30 May 1963, Lemaire 2437 (KSC, NEB). Holt Co.: Swan Lake, 16 June 1968, Koch 4800 (NEB, OKL, OKLA). Lancaster Co.: 7 mi W and 2 mi N of Lincoln, 16 June 1949, Voigt s.n. (NEB). Kearney Co.: Minden, June 1898, Hapeman s.n. (IND, *KNSC). Rock Co.: 1.5 mi W of Newport, 4 June 1970, Stephens 38867 & Brooks (KANU). Sheridan Co.: 14 mi N of Rushville, 30 June 1966, Stephens 6195 (KANU, NY). Sioux Co.: 6 mi NW of Ft. Robinson, 20 June 1970, McGregor 22308 (KANU). Thomas Co.: 15.5 mi SW of Thedford, 22 June 1979, Freeman 163 (KSC); 15 mi SW of Thedford, 22 June 1979, Freeman 164 (KSC). Wheeler Co.: 3 mi E of Ericson, 23 June 1971, Stephens 48703 (KANU).

NEW MEXICO: Colfax Co.: Philmont Scout Ranch near Cimarron, 28 June 1968, Hartman 2184 (RM). Mora Co.: Morphy Lake, 24 July 1972, Higgins 5845 (NY).

NORTH DAKOTA: Adams Co.: 4 mi S Reeder, 21 June 1970, Stephens 40415 & Brooks (KANU). Barnes Co.: * 20 mi N Valley City, 25 June 1970, Seiler 1834 (KANU, NDA); 5.5 mi E & 1 mi S Dazey, 7 July 1972, Godfread 4198 (NDA). Benson Co.: 6 mi W Knox, 24 June 1968, Bare 1003 & Brooks (KANU, NDA); *20 mi N of Valley City, 25 June 1970, Seiler 1834 (NDA). Billings Co.: 10 mi S & 0.5 mi W of Medora, 21 June 1969, Zaczkowski 487 (NDA). Bottineau Co.: 20 mi W of Bottineau, 22 July 1969, Ward 886 (NDA). Bowman Co.: 6 mi S & 6 mi W Rhame, 16 June 1970, Zaczkowski 2746 (NDA). Burke Co.: 2 mi SE Powers Lake, 22 June 1970, Hegstad 4924 (NDA). Burleigh Co.: 6 mi S & 2.8 mi E of Sterling, 25 June 1979, Freeman 221 (KSC). Cass Co.: Fargo, 26 June 1891, Lee 534 (NDA). Dickey Co.: Kulm, 22 June 1959, Stevens s.n. (NDA). Divide Co.: 0.5 mi E Westby, 26 June 1970, Hegstad 5311 (KANU, NDA). Dunn Co.: 7 mi W & 1.5 mi N of Killdeer, 25 June 1979, Freeman 215 (KSC); 10 mi W & 0.5 mi N of Killdeer, 25 June 1979, Freeman 213 (KSC). Eddy Co.: 24 mi E New Rockford, 2 July 1969, Seiler 231 (NDA); * 1 mi E of New Rockford, 4 July 1969, Seiler 254 (NDA). Emmons Co.: Lake Oahe Beaver Creek Public Use Area, 25 June 1979, Freeman 223 (KSC); 9.1 mi N of South Dakota border, 26 June 1979, Freeman 226 (KSC). Golden Valley Co.: 8 mi S & 1 mi W Golva, 12 June 1969, Zaczkowski 399 (NDA). Grand Forks Co.: Turtle Creek State Park, 28 June 1952, Bartlett & Grayson 333 (NY). Grant Co.: Cannon Ball Valley at Wade, 25 June 1907, Bell 94 (NDA, RM). Griggs Co.: Cooperstown, 29 July 1965, Stevens s.n. (NDA). Kidder Co.: 13 mi S Dawson, 16 June 1970, Stephens 39945 & Brooks (KANU). LaMoure Co.: Adrian, 27 June 1912, Bergman 1793 (MO, NDA). Logan Co.: 4 mi W Burnstad, 19 June 1973, Larson 2098 (NDA). McHenry Co.: 4 mi N of Towner, 24 June 1968, Bare & McGregor 1015 (KANU, NDA). McKenzie Co.: 8.5 mi S Watford City, 20 June 1970, Stephens 40235 & Brooks (KANU). McLean Co.: 0.9 mi W of jct Hwy 83 & 41, 25 June 1979, Freeman 219 (KSC). Mercer Co.: 0.4 mi W Golden Valley, 25 June 1979, Freeman 218 (KSC). Morton Co.: 13 mi W Mandan, 10 July 1969, Stephens 33617 & Brooks (KANU, NDA). Mountrail Co.: 9 mi S & 1 mi E Powers Lake, 14 July 1969, Hegstad 813 (NDA). Oliver Co.: Ft. Clark, 25 June 1975, Larson 5204 (KANU, *KNSC, NDA). Pembina Co.: 5 mi W Cavalier, 17 June 1969, Barker 5373 (NDA); * Icelandic State Park, 17 July 1969, Ward 862 (MO, NDA). Pierce Co.: * SW of Esmond, 15 July 1964, Stevens s.n. (NDA). Ramsey Co.: Webster, 27 June 1911, Tufte 191 (RM); * Church's Ferry, 2 July 1891, Stockbridge 533 (NDA, NY). Renville Co.: 3 mi N & 14 mi W Mohall, 10 June 1976, Larson & Lind 5568 (NDA). Richland Co.: 1.5 mi E McLeod, 17 June 1970, Seiler 1608 (KANU, MO, NDA). Rolette Co.: Rolla, 1905, Lovell s.n. (NDA). Sargent Co.: 2 mi S & 4 mi E Oakes, 24 June 1971, Seiler 3259 (KANU, NDA). Sioux Co.: 1 mi W & 8 mi N Ft. Yates, 11 July 1969, Stephens 33694 & Brooks (KANU, NY). Slope Co.: 22 mi S Belfield, 27 June 1969, Zaczkowski 548 (NDA). Stark Co.: 5 mi W & 2 mi S Dickinson, 13 July 1969, Barker 5725 (NDA). Steele Co.: Luverne, 7 July 1966, Stevens s.n. (NDA). Stutsman Co.: 5 mi N Streeter, 5 July 1969, Stephens 33321 & Brooks (KANU, NDA); * 11 mi W & 0.5 mi N Edmunds, 2 July 1971, Godfread 1052 (NDA). Towner Co.: Maza, 26 June 1900, Kildahl 11 (KANU, RM). Ward Co.: 4 mi N Foxholm, 2 July 1967, Stephens 12902 & Brooks (KANU). Wells Co.: *8 mi W New Rockford, 4 July 1970, Seiler 2074 (NDA). Williams Co.: 1 mi NE McGregor Wildlife Area, 3 August 1969, Hegstad 4205 (NDA); * S Wildrose, 26 June 1970, Hegstad 5152 (NDA).

SOUTH DAKOTA: Aurora Co.: 4 mi E & 11 mi N White Lake, 24 June 1971, Stephens 48758 (KANU, OKL). Beadle Co.: 3 June 1890, Douglas s.n. (MO). Brookings Co.: 1.5 mi W White, 28 June 1971, Stephens 49008 (KANU, NY). Brown Co.: 17 mi N & 9 mi W Aberdeen, 26 June 1971, Stephens 48884 (KANU, OKL). Brule Co.: Chamberlain, 4 July 1892, Wilcox s.n. (SDC-2). Campbell Co.: 2 mi S Herreid, 26 June 1979, Freeman 227 (KSC). Codington Co.: McKilligans Lake, 22 June 1958, Dugle 619 (SDU). Corson Co.: 1 mi S Mahto, 26 June 1967, Stephens 12344 & Brooks (KANU). Custer Co.: Black Hills National Forest, 23 June 1979, Freeman 185 (KSC). Day Co.: NE edge Enemy Swim Lake, 30 June 1966, Croat 2262 (KANU). Dewey Co.: T15N, R30E, 28 June 1971, Van Bruggen 6023 (SDU). Edmunds Co.: 3.5 mi E Ipswich, 26 June 1971, Stephens 48869 (KANU). Fall River Co.: Hot Springs, 15 June 1892, Rydberg 921 (NY). Faulk Co.: 6 mi E & 7 mi N Faulkton, 30 July 1967, Stephens 15270 & Brooks (KANU). Hand Co.: 16 mi N & 0.5 mi E Miller, 25 June 1971, Stephens 48831 (KANU, NY). Harding Co.: 1.4 mi S Ludlow, 24 June 1979, Freeman 205 (KSC). Hughes Co.: 8 mi N, 3 mi W Pierre, 3 July 1969, Stephens 33038 & Brooks (KANU). Jackson Co.: Cedar Pass, 5 June 1914, Over 5187 (SDU). Jerauld Co.: W of Wessington Springs, 22 June 1968, Bare & McGregor 838 (KANU). Lawrence Co.: Lead City, 6 July 1892, Rydberg 921 (NEB, NY, SDC); Deadwood, 9 July 1913, Carr 35 (MO, NY, SDC, SDU). Lyman Co.: 1.5 mi S Iona, 22 June 1967, Stephens 12008 (KANU, NY, OKLA). McPherson Co.: 4.5 mi E Eureka, 29 July 1967, Stephens 15219 & Brooks (KANU). Marshall Co.: 6 mi NW Veblen, 16 June 1959, Ailts 128 (SDU). Meade Co.: 3 mi S Faith, 8 June 1972, Boke 498 (OKL). Mellette Co.: 2.5 mi E Norris, 6 June 1970, Stephens 39142 & Brooks (KANU). Minnehaha Co.: 2 mi S Garretson, 15 June 1969, Stephens 31904 & Brooks (KANU, NY). Pennington Co.: 2 mi W Deerfield, 15 July 1924, McIntosh 481 (SDU, RM). Potter Co.: 16 mi W & 7 mi S Gettysburg, 3 July 1969, Stephens 33101 & Brooks (KANU). Roberts Co.: Big Stone Lake, 10 July 1959, Ailts 265 (SDU). Spink Co.: 3 mi S & 0.5 mi W Redfield, 25 June 1971, Stephens 48841 (KANU). Stanley Co.: Fort Pierre, 19 June 1839, Geyer 127 (MO, NY). Sully Co.: 18 mi W & 10 mi S Onida, 3 July 1969, Stephens 33060 & Brooks (KANU). Todd Co.: 4 mi S Mission, 29 June 1968, Bare & McGregor 1260 (KANU). Tripp Co.: 2 mi W Rahn Lake, 26 June 1979, Freeman 228 (KSC). Walworth Co.: LeBeau, 9 September 1892, Griffiths & Schlosser 509 (SDC). Washabaugh Co.: Cottonwood Canyon, 6 July 1911, Visher 2001 (NY, SDU).

WISCONSIN: Trempealeau Co.: Trempealeau, 31 July 1888, Holzinger s.n. (KSC).

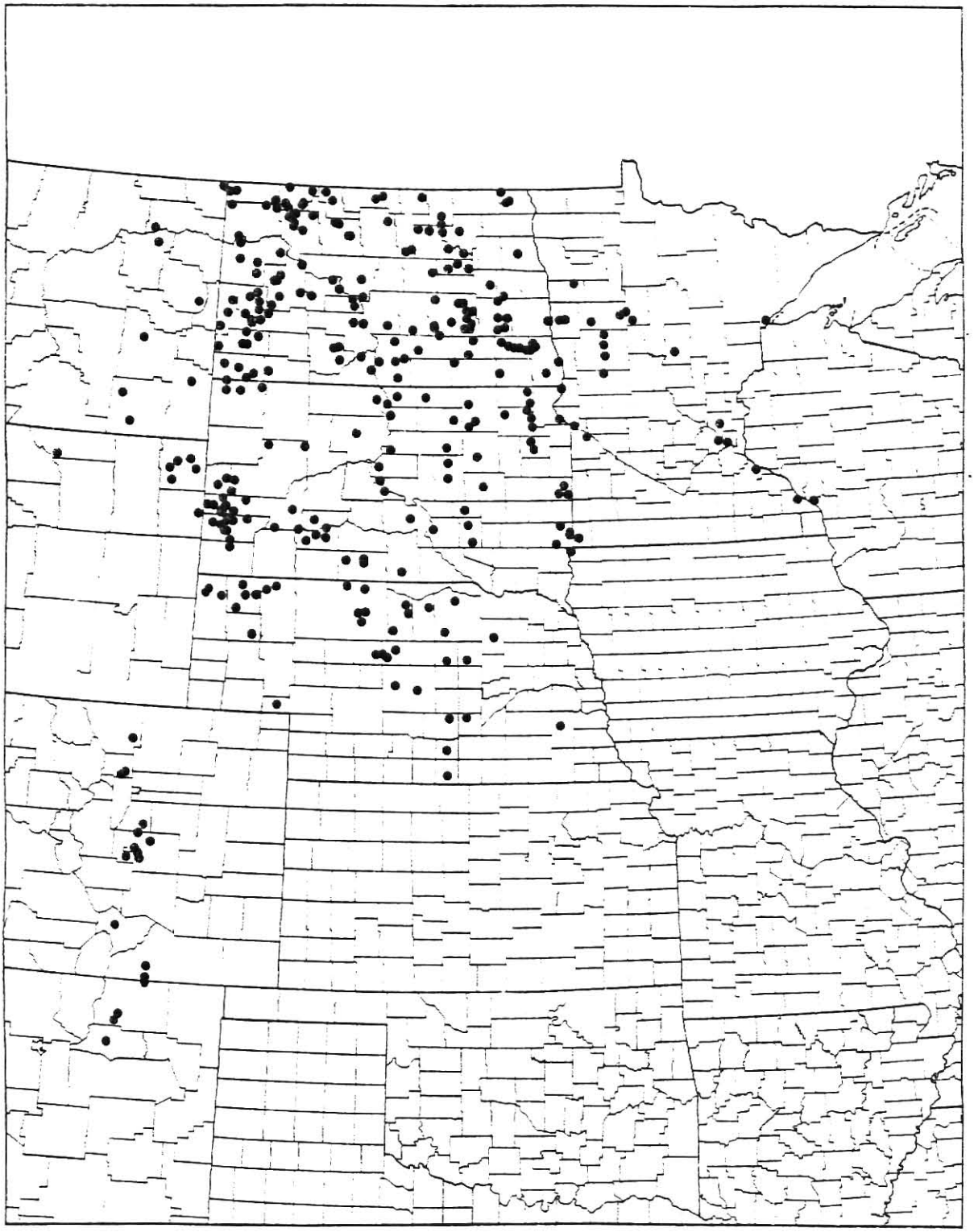
WYOMING: Crook Co.: 3.7 mi N Keyhole State Park, 8 June 1980, Freeman 544 (KSC). Sheridan Co.: Little Goose Creek, 16 July 1896, Nelson 2375 (RM). Weston Co.: Newcastle, 6 June 1896, Bates s.n. (RM).

CANADA:

ALBERTA: Pendant-d'Oreille, 8 mi NE Dune fixee, 28 June 1958, Boivin & Perron 12300 (OKL).

* indicates pubescent-stemmed specimens

Figure 65. Great Plains Distribution of Penstemon gracilis var. gracilis



12. Penstemon grandiflorus Nuttall

Penstemon grandiflorum Nutt., in Fras. Catal. 2. 1813. Chelone grandiflora (Nutt.) Spreng., Syst. Veg. 2: 813. 1825. Type: "collected a considerable distance up the Missourie. P. grandiflorum is nearly the commonest species in that country, and it was first met with near the confluence of the river Platte, from whence it continues to the Andes" (Holotype: not located by Pennell).

Pentstemon bradburii Pursh, Fl. Amer. Sept. 738. 1814. Chelone bradburii (Pursh) Steud., Nom. Bot. ed. 1. 186. 1821. Type: Description apparently based on a collection made by Bradbury on his trip up the Missouri River in 1811, but source of material omitted by Pursh in the description. Holotype labeled "Pentstemon Bradburii" by Lambert and seen by Pursh. Isotype labeled "Louisiana, J. Bradbury. 1811-12." (Holotype: PH; Isotype: BM, not seen).

Stout herbaceous perennial. Stems mostly erect, (4)5-9.5(12) dm tall, glabrous and glaucous, 1-2(3) stems arising from a woody and seldom branched subterranean caudex surmounting a taproot. Leaves entire, thick, firm, glabrous and glaucous; basal leaves spatulate or obovate and petiolate, 3-16 cm long overall, 0.6-5 cm wide, acute to obtuse; cauline leaves spatulate to orbicular, 1.8-9(11) cm long, 1.5-5 cm wide, scarcely clasping below to cordate-clasping above. Thyrse 12-30(40) cm long, with 3-7(9) verticillasters, interrupted, narrow, leafy-bracted below, individual cymes 2-3 flowered, peduncles and pedicels glabrous and usually anthocyanic, peduncles absent or to 1 mm long, pedicels 3-12 mm long; bracts ovate to orbicular, the lower ones to 5 cm long and 4 cm wide, acute to short-acuminate, bases cordate-clasping and usually overlapping, concealing the peduncles and most pedicels. Calyx glabrous and glaucous, sepals lanceolate to lance-ovate, 7-11 mm long, 2.5-4 mm wide, acute to acuminate, entire, herbaceous throughout or with narrow scarious margins toward the base; corolla 35-48 mm long, distinctly bilabiate, pink to bluish-lavender or pale blue, glabrous internally and externally, throat 15-18 mm broad, abruptly inflated and ventricose posteriorly, moderately ampliate, lined internally

on the anterior surface with magenta nectar guides, lobes of the upper lip spreading to reflexed, lobes of the lower lip projecting or spreading; staminode 16-19 mm long from its point of attachment, included or reaching the orifice, strongly flattened distally, the tip abruptly recurved and bearded with golden-yellow hairs to 0.5 mm long; fertile stamens included, anther-sacs 1.4-1.7 mm long, purple or tan, lined with white along the sutures, widely divergent, dehiscing the full length and across the connective, not becoming explanate, minutely papillose along the sutures; style 19-21 mm long, glabrous. Capsule 16-20(25) mm long. Seeds 2.5-4 mm long, angular, finely reticulate, brown to dark brown. $\underline{n} = 8$.

Sandy to loamy soil in prairies. Wisconsin, west to central North Dakota and northeastern Wyoming; south to Gillespie County, Texas.

Penstemon grandiflorus exhibits an irregular distribution throughout its range. It is encountered most commonly in the central Great Plains but is also represented by a number of widely disjunct populations, especially in Oklahoma and Texas. To explain the irregular occurrence of the species, Pennell (1935), suggested that it had a more southern distribution during the Wisconsin Stage of the Pleistocene Epoch, being distributed from Kansas to Texas. With the recession of the Wisconsin Glacier, arenaceous glacial outwash and eolian sands deposited periglacially provided habitats suitable for the species in the central and northern Great Plains, as well as in the northwestern Central Lowlands. These habitats were subsequently inhabited by the species. Isolated populations in the southern portion of the species range probably represent relicts of the species earlier more southern range. The virtual absence of the species in the James River Valley of eastern South Dakota and North Dakota and northcentral Iowa and southcentral Minnesota suggests the species has been slow to invade those areas occupied by ice

during the Wisconsin Stage, as these areas were covered by the James River Lobe and the Des Moines Lobe of the Wisconsin Glacier.

The correct name of the species has been the subject of controversy in the past, as have many other names associated with Fraser's Catalogue. This controversy has at times led to spirited verbal jousting between pro factions supporting the validity of certain names in the catalogue (Cronquist et al., 1956; Cronquist, 1957; Reveal, 1968), and con factions opposed to the acceptance of any Fraser's Catalogue names (Shinner, 1955; Shinners, 1959). An examination of specimens annotated by F.S. Crosswhite indicated vacilation on the part of the examiner, as some specimens bear annotation labels with the name P. grandiflorus Nutt., while others have been annotated P. grandiflorus Nutt. ex Fras. & Fras. or P. bradburii Pursh. Having read the arguments both for and against acceptance of the various names that appear in Fraser's Catalogue, this author concurs with Reveal (1968) that Penstemon grandiflorus is validly published and should be accepted as the proper name for the species in question.

REPRESENTATIVE SPECIMENS:

UNITED STATES:

COLORADO: Baca Co.: 14 June 1945, Eriksen s.n. (CS). Sedgwick Co.: 0.1 mi S I-76 at Julesburg, 5 June 1980, Freeman 514 (KSC). Washington Co.: Sec. 21, T5N, R52W, 6 June 1959, Dahl 80 (CS). Yuma Co.: 2 mi N Wray, 6 June 1954, Harrington 7444 (CS).

ILLINOIS: Henderson Co.: Along Mississippi River at Oquawaka, June, Patterson s.n. (NY).

INDIANA: Elkhart Co.: Along Hwy 120 3 mi E Bristol, 16 June 1945, Deam 63301 (IND).

IOWA: Bremer Co.: Along Cedar River in N Waverly, 29 May 1978, Freeman 7869 (WET). Cherokee Co.: 9 mi S Cherokee, 9 June 1938, Hayden 11438 (NY). Dubuque Co.: Dubuque, Watson s.n. (NY). Lyon Co.: NW corner of county, 25 August 1924, Shimek s.n. (NY). Mills Co.: 5.7 mi S Pottawattamie Co.

Line along I-29, 28 June 1980, Freeman & Freeman 609 (KSC); 3 mi N Pacific Junction, 4 June 1968, Adams & Sutherland 1675 (KANU, *KNSC, NEB). Monona Co.: N of Turin, 28 May 1938, Goodman 3024 (NY). Muscatine Co.: S of Muscatine, 1935, Estle & Brown s.n. (NY). Polk Co.: Polk City cemetary, 14 June 1957, Van Bruggen 1979 (SDU). Pottawattamie Co.: Fairmont Park, Council Bluffs, 26 May 1897, Cleburne s.n. (NEB-2).

KANSAS: Chase Co.: N of Cottonwood Falls, June 1939, Cook s.n. (FHKSC). Clark Co.: S of Ashland, 15 Jay 1937, Cook s.n. (OKLA). Clay Co.: July 1895, Hitchcock s.n. (KSC). Cloud Co.: 5 mi SW Aurora, 26 May 1977, McGregor 30268 (KANU). Cowley Co.: 1.4 mi N Eaton, 8 June 1979, Freeman 132 (KSC). Ellsworth Co.: 1.2 mi S I-70 along Hwy 156, 3 June 1979, Freeman & Freeman 102 (KSC). Geary Co.: Sec. 3, T12S, R7E, 21 May 1979, Freeman 48 (KSC); Sec. 31, T11S, R7E, 21 May 1979, Freeman 49 (KSC). Johnson Co.: 1 mi W & 3 mi N Stanley, 25 May 1976, Hauser & Brooks 2892 (KANU). Kiowa Co.: 3.3 mi W Greensburg, 23 May 1980, Freeman 444 (KSC). Lincoln Co.: 100 yds E Russell Co. Line along Hwy 18, 23 May 1980, Freeman 450 (KSC). Marion Co.: 1 mi S Florence, 11 June 1976, Stephens 89187 (KANU). Pawnee Co.: 3 mi W Larned, 7 June 1975, Stephens 84898 (KANU). Pottawatomie Co.: E side Tuttle Creek Reservoir 1.5 mi N Carnahan Cove, 20 May 1979, Freeman & Freeman 40 (KSC); E side Tuttle Creek Reservoir 1 mi N Carnahan Cove, 20 May 1979, Freeman & Freeman 41 (KSC). Riley Co.: 3 mi S & 2.5 mi E Manhattan, 17 May 1979, Freeman 39 (KSC); 1.5 mi N I-70 along Deep Creek Rd, 20 May 1979, Freeman 42 (KSC); South Pasture of Konza Prairie Research Natural Area, 21 May 1979, Freeman 47 (KSC); Sand hills, 18 May 1895, Norton 378 (KSC, MO, NY, RM); SW ¼ sec. 6, T10S, R8E, 6 May 1981, Freeman 917 (KSC); Konza Prairie Research Natural Area, 17 June 1977, Freeman 7780 (KSC). Russell Co.: Jct Hwy 176 & 18 N of Lucas, 10 June 1979, Freeman 149 (KSC). Saline Co.: NE of Salina, 18 May 1930, Hancin 245 (KSC). Shawnee Co.: 2 mi E Dover, 13 June 1956, Lathrop 2463 (KANU). Wabaunsee Co.: S of Wabaunsee, 22 May 1927, Maus 212 (KSC). Washington Co.: 1 mi W Linn, 27 May 1951, McGregor 4825 (KANU, NY).

MINNESOTA: Anoka Co.: Near Moore Lake, 25 June 1925, Stoesz s.n. (NDA). Becker Co.: Detroit, 17 June 1911, Waldron s.n. (NDA). Big Stone Co.: Big Stone Lake, Ortonville, 12 June 1898, Moyer s.n. (NY). Chippewa Co.: June 1894, Moyer s.n. (RM). Clay Co.: Muskoda, 19 June 1940, Stevens 446 (KANU, MO, NDA, NY, RM). Dakota Co.: Elk Lake, June 1894, Sheldon s.n. (RM-2, NY). Douglas Co.: 3 mi N & 0.25 mi W Melby, 12 June 1976, Sperling 274 (NDS). Goodhue Co.: Cannon Falls, July 1891, Sandberg 335 (NDA). Hennepin Co.: Ft. Snelling, 14 June 1890, Mearns 499 (NY). Lincoln Co.: 1 mi E Lake Benton, 11 June 1944, Moore & Hall 16428 (NDA). Otter Tail Co.: Luce, 21 June 1913, Chandonnet s.n. (IND). Polk Co.: 1 mi S & 0.5 mi W Fertile, 22 July 1970, Seiler 2405 (NDA). Ramsey Co.: Falls of St. Anthony, July 1832, Houghton 69 (NY). Traverse Co.: Sec. 9, Folsom Township, 17 June 1974, Barchenger 242 (NDA).

MISSOURI: Atchison Co.: Watson, 1 June 1894, Bush 476 (KSC, NY). Pettis Co.: Sedalia, 24 June 1895, Cooper s.n. (KSC).

NEBRASKA: Antelope Co.: 3 mi W Royal, 8 July 1972, Wells 87 (SDU). Blaine Co.: 1.7 mi N Brewster, 26 June 1979, Freeman 235 (KSC). Boone Co.: 1.5 mi S Petersburg, 20 June 1967, Stephens 11812 & Brooks (KANU). Boyd Co.:

1 mi S Bristow, 22 June 1965, McGregor 19390 (KANU). Brown Co.: 9.4 mi NW Long Pine, 26 June 1979, Freeman 232 (KSC). Buffalo Co.: 4 mi S & 2 mi W Ravenna, 2 August 1975, Luce s.n. (*KNSC). Butler Co.: 3 mi E & 0.5 mi S Linwood, 28 May 1974, Churchill 3124 (NEB). Cass Co.: Weeping Water, 10 May 1895, Bentz s.n. (*KNSC). Cedar Co.: 2 mi SE St. James, 7 June 1974, Sutherland 3766 & Churchill (NEB). Cherry Co.: Merritt Reservoir ca 40 mi SW of Valentine, 22 June 1979, Freeman 169 (KSC). Cuming Co.: 3 mi S, 3 mi E, & 1 mi N of Pilger, 8 June 1973, Churchill 986 (KANU, NEB-2). Custer Co.: NE city limits Broken Bow, 21 June 1979, Freeman 158 (KSC); 4.1 mi W Victoria Springs State Park, 21 June 1979, Freeman 159 (KSC). Dawes Co.: 12 mi SE Chadron, 22 June 1979, Freeman 176 (KSC). Dixon Co.: Ponca, 16 June 1893, Clements 2537 (NEB, SDC). Dodge Co.: 1 mi E Hooper, 2 June 1970, Stephens 38591 & Brooks (KANU). Franklin Co.: Franklin, 9 June 1929, Hapeman s.n. (OKLA). Garfield Co.: 3.1 mi W Burwell, 26 June 1979, Freeman 237 (KSC). Hall Co.: 2 mi W Grand Island, 4 July 1962, Lemaire 2298 (KSC). Hamilton Co.: Few miles W Big Blue River to Ft. Kearney, 10 July 1849, Fendler 86 (MO). Holt Co.: 6 mi E & 21 mi N Atkinson, 3 June 1970, Stephens 38750 & Brooks (KANU). Howard Co.: 4 mi N Cairo, 27 June 1979, Freeman 239 (KSC). Jefferson Co.: 5 mi S Fairbury, 24 May 1974, Churchill 3054 (NEB, NDA). Kearney Co.: 13 June 1891, Rydberg 277 (NEB, NY, RM). Keya Paha Co.: 1 mi S South Dakota State Line, 26 June 1979, Freeman 232 (KSC). Knox Co.: 3.5 mi S Niobrara, 28 May 1969, Magrath, Hays, Taylor, & Taylor 3959 (KANU, NY). Lancaster Co.: 3 mi W Emerald, 4 June 1973, Churchill 926 (KANU, NEB); Lincoln, 8 June 1886, Webber 5562 (MO, NEB-2, NY). Loup Co.: NW of Almeria, 26 June 1979, Freeman 236 (KSC). McPherson Co.: 2 mi N Tryon, 5 June 1980, Freeman 520 (KSC). Madison Co.: Norfolk, 11 June 1893, Bessey s.n. (NEB). Nance Co.: 1.5 mi N & 3 mi E Meadow along Loup River, 11 June 1936, Osborn 1123R (MO). Otoe Co.: S of Palmyra, 1 August 1894, Turrell 77 (NEB). Pierce Co.: 1 mi E & 1.5 mi N Hadar, 2 June 1970, Stephens 38634 & Brooks (KANU). Platte Co.: SW of Columbus, 8 June 1931, Pennell 15034 (MO). Rock Co.: 1.5 mi W Newport, 4 June 1970, Stephens 38876 & Brooks (KANU). Sarpy Co.: 9 mi S Gretna along Platte River, 22 May 1968, Stephens 20920 (KANU). Saunders Co.: 4 mi S Valparaiso, 28 June 1966, Croat 2128 (KANU, MO). Sheridan Co.: 0.6 mi E Clinton, 6 June 1980, Freeman 527 (KSC). Sherman Co.: 9 mi N Loup City, 26 June 1979, Freeman 238 (KSC). Sioux Co.: 10.5 mi S Agate, 6 June 1968, Stephens 31519 & Brooks (KANU, NY). Stanton Co.: 3.6 mi S & 0.5 mi E Stanton, 1 June 1974, Churchill 3340 (NEB). Thomas Co.: Nebraska National Forest, 22 June 1979, Freeman 161 (KSC).

NORTH DAKOTA: Barnes Co.: Oriska, 30 June 1927, Durbin s.n. (NDA). Burleigh Co.: 7 mi S Bismarck, 9 June 1969, Johnson 98 (NDA). Emmons Co.: 1.5 mi NE Beaver Creek Public Use Area on Lake Oahe, 25 June 1979, Freeman 222 (KSC). Grand Forks Co.: 12 June 1934, Schonberger s.n. (NDA). Grant Co.: Along Cannonball River at Janesburg, 31 August 1907, Bell 1381 (NDA). McLean Co.: Along Hwy 83 0.9 mi NW jct Hwy 83 & 41, 25 June 1979, Freeman 220 (KSC). Mercer Co.: 0.4 mi W Golden Valley, 25 June 1979, Freeman 217 (KSC). Morton Co.: Mandan, 21 August 1891, Lee 528 (NDA, RM-2). Oliver Co.: Yucca Creek S of Center, 1 August 1963, Stevens s.n. (NDA). Ranson Co.: 1 mi W McLeod, 7 June 1971, Seiler 2970 (KANU, NDA). Richland Co.: 1.5 mi E McLeod, 17 June 1970, Seiler 1607 (KANU, MO, NDA). Sioux Co.: 1 mi W & 15 mi N Ft. Yates, 11 July 1969, Stephens 33681 & Brooks (KANU). Walsh Co.: Park River, July 1938, Fox 55 (NEB).

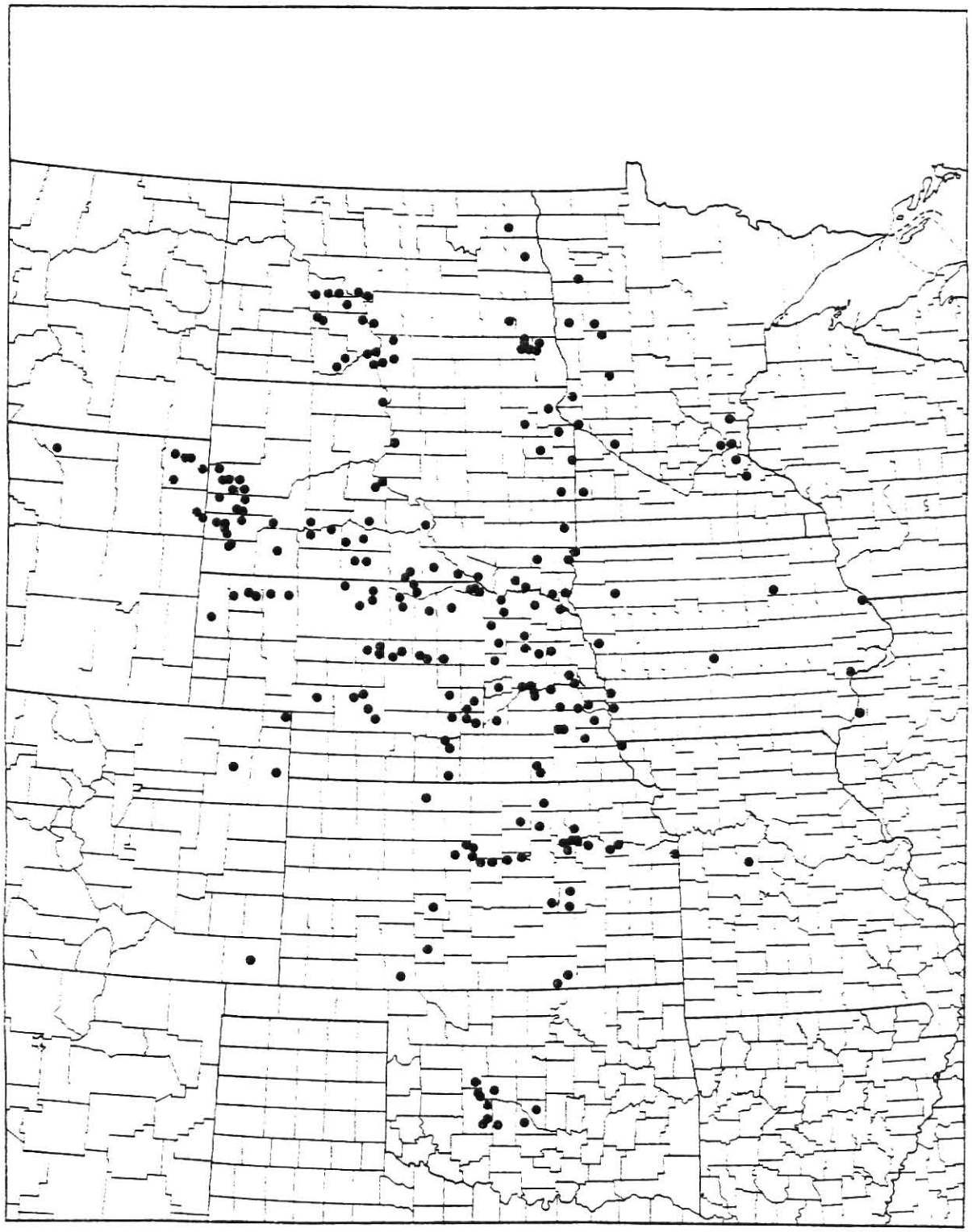
OKLAHOMA: Blaine Co.: W of Geary, 15 May 1926, Myers 355 (OKL). Caddo Co.: Rim of Devil's Canyon, 13 May 1944, Hopkins, Nelson, & Nelson 305 (MO, OKL, OKLA, RM). Canadian Co.: Sec. 3, T11N, R10W, 14 May 1960, Taylor 167 (OKL). Cleveland Co.: 120th Ave SE in Norman, 18 May 1980, Freeman 398 (KSC). Grady Co.: 18 mi S Chickasha, 16 May 1942, Waterfall 3646 (NY-2, OKL, OKLA). McClain Co.: 10 mi S Blanchard, 22 June 1964, Pearce 1275 (OKL).

SOUTH DAKOTA: Bon Homme Co.: 7 mi N Tabor, 23 June 1965, McGregor 19421 (KANU). Brookings Co.: Brookings, 23 June 1893, Thornber 3148 (SDC-2, SDU). Charles Mix Co.: S end Ft. Randall Reservoir, 18 July 1965, Harms 2492 (KANU). Clay Co.: Vermillion River, 6 June 1913, Over 5031 (SDU). Codington Co.: Near Lake Kampeska, 15 June 1957, Dugle 118 (SDU). Corson Co.: 5 mi W Mahto, 26 June 1967, Stephens 12347 & Brooks (KANU). Custer Co.: 2 mi N of S entrance to Black Hills National Forest along Hwy 385, 23 June 1979, Freeman 186 (KSC). Day Co.: Waubay Wildlife Refuge, 6 June 1972, Roberts 8 (SDC). Deuel Co.: Gary, July 1892, Horkins s.n. (SDC). Fall River Co.: 1.8 mi S Hot Springs, 7 June 1980, Freeman 533 (KSC). Grant Co.: 14.5 mi W Milbank, 27 June 1971, Stephens 48926 (KANU). Gregory Co.: 9 mi N & 9 mi E Gregory, 3 September 1978, Smith 40 (SDU). Hughes Co.: East Pierre, 1892, Adams 22 (SDC). Jackson Co.: Near headquarters of Badlands National Monument, 17 June 1967, Stockert 86-67 (SDU). Jones Co.: 10 mi S Murdo, 5 July 1973, Stephens 66628 (KANU). Lawrence Co.: Jct Hwy 14A & I-90, 24 June 1979, Freeman 200 (KSC). Lincoln Co.: 0.5 mi S Newton Hills State Park exit, 23 June 1957, Messerli 21 (SDU). Lyman Co.: 3 mi W Chamberlain, 7 June 1929, Palmer 37001 (MO). Meade Co.: Sturgis at Bear Butte, 14 June 1924, McIntosh 260 (RM, SDU). Mellette Co.: 2.5 mi E Norris, 6 June 1970, Stephens 39145 & Brooks (KANU). Minnehaha Co.: Corson, 12 June 1925, Solheim 112 (RM). Pennington Co.: 2 mi W jct Hwy 385 & 16 along Hwy 385, 23 June 1979, Freeman 188 (KSC). Potter Co.: Cheyenne Agency, Forest City, 3 September 1892, Griffiths & Schlosser 283 (SDC). Roberts Co.: August 1897, Towne 5259 (SDC). Shannon Co.: 17 mi NW Sharps Corner, 8 June 1970, Stephens 39358 & Brooks (KANU). Stanley Co.: Ft. Pierre, 26 June 1855, Hayden s.n. (MO). Todd Co.: 6 mi W Mission, 3 June 1966, Stanley 194 (KSP, SDU). Tripp Co.: Rahn Lake, 26 June 1979, Freeman 229 (KSC). Turner Co.: 10.5 mi S & 4 mi W Marion, 25 June 1960, Harms 416 (KANU). Union Co.: Sec. 1, T92N, R50W, 29 May 1969, Van Bruggen 5550 (SDU). Washabaugh Co.: White River bridge near Martin, 11 June 1957, Lindstrom 85 (SDU). Yankton Co.: Lesterville Access Area along Lewis and Clark Lake, 30 May 1977, Van Bruggen & Johnson s.n. (SDU).

TEXAS: Callahan Co.: Near Baird, April 1882, Reverchon 1342 (MO, NY). Gillespie Co.: Sandy creek, Jermy 280 (MO).

WYOMING: Crook Co.: 3.7 mi N Keyhole State Park, 8 June 1980, Freeman 543 (KSC); Sand Creek near Beulah, 20 June 1950, Porter 5342 (MO, NY, OKL). Sheridan Co.: Little Goose Grade, 15 July 1896, Nelson 2333 (NY, RM). Weston Co.: 1 mi W South Dakota State Line, 7 June 1980, Freeman 535 (KSC).

Figure 66. Great Plains Distribution of Penstemon grandiflorus



13. Penstemon haydeni S. Watson

Pentstemon haydeni S. Wats., Bot. Gaz. (Crawfordsville) 16: 311. 1891. Type: "on the Dismal River in Thomas County, Nebraska, about 100 miles west of the 100th meridian.", Webber 4959 collected July 12, 1889. (Isotypes: MO!, NEB-2!, NY!).

Stout perennial herb. Stems decumbent to ascending, (1.5)2-4.5 dm tall, glabrous, 1 to many from a subterranean caudex surmounting a deep taproot. Leaves entire, glabrous and somewhat glaucous, firm; basal and lower cauline leaves linear to linear-lanceolate, (2.5)5.5-11(13) cm long, 0.3-1 cm wide, acuminate to acute, sessile and clasping, upper cauline leaves linear to occasionally lanceolate, 6-11(12) cm long, 0.7-3 cm wide, acuminate with a long narrow tapering tip, sessile and clasping, the vegetative shoots with long linear leaves. Thyrse 6-16 cm long, with (4)6-10(12) verticillasters, very compact, cylindrical and not secund, leafy-bracted, individual cymes 4-6 flowered, flowers fragrant, peduncles glabrous, absent or if present then less than 2 mm long, pedicels glabrous, 2-8 mm long; bracts longer than broad and very distinct from cauline leaves, the lower bracts ovate, 5.8-12 cm long, 2-4.5 cm wide, tapering to a long narrow acuminate or caudate tip, bases cordate and broadly overlapping, concealing the peduncles and most pedicels. Calyx glabrous, sepals subequal, linear to linear-lanceolate, 8-13 mm long, 1-3 mm wide, acuminate, entire, herbaceous throughout or with scarious margins near the base; corolla 23-25 mm long, distinctly bilabiate, milky blue to milky lavender, glabrous internally and externally, the throat 9-11 mm broad, well inflated and ventricose posteriorly, moderately ampliate, lined internally with magenta nectar guides anteriorly in mature unopened or freshly opened flowers, lobes of the upper lip arched-projecting, lobes of the lower lip projecting to spreading; staminode 13-16 mm long from its point of attachment, included, distally

flattened, minutely bifurcate and slightly recurved, densely pubescent near the tip with golden-yellow hairs to 1 mm long; fertile stamens included, anther-sacs 1.8-2 mm long, purple, lined with white along the sutures, widely divergent, dehiscing the full length and across the connective, prominently papillose along the sutures; style 18-19 mm long, glabrous. Capsule 13-16 mm long. Seeds 2.5–4 mm long, discoid, finely reticulate, light brown to brown. $n = 8$.

Endemic to the sandhills of northwestern Nebraska in Cherry, Hooker, and Thomas Counties. A population has also been reported from the vicinity of Cresent Lake in Garden County (A.T. Harrison, pers. comm.), but no vouchers have yet been seen. Flowering from late May to early July.

Morphologically, Penstemon haydeni is one of the most striking members of the Coerulei, due to its compact cylindrical inflorescence with prominent long-acuminate bracts and its habit of forming large multi-stemmed clumps. The stems of P. haydeni root adventitiously, thus maintaining the plant in shifting sands of dune blowouts. The species is apparently unique in the Coerulei in that its flowers possess a distinctive fragrance.

The flowers of Penstemon haydeni bear a remarkable resemblance to those of P. grandiflorus. Both species have corollas that are distinctly bilabiate, inflated and ventricose posteriorly, moderately ampliate, lined internally on the anterior surface with magenta guidelines and colored milky blue to lavender or pale lavender externally, and staminodes bearded near the tip.

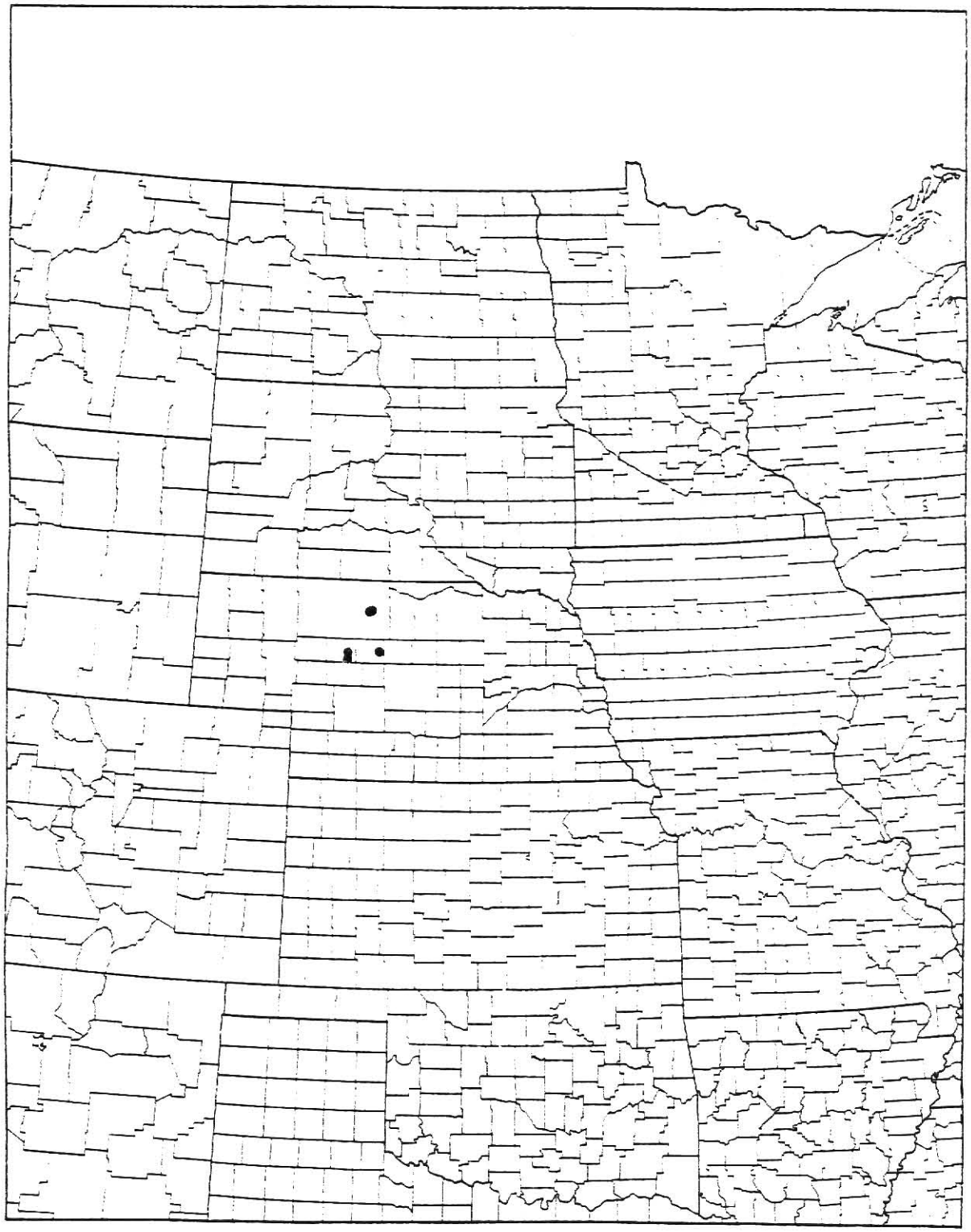
The leaves and bracts of P. haydeni show little resemblance to P. grandiflorus, except that in both species the leaves and bracts are firm, glabrous, and glaucous. Instead, the linear shape of the leaves and the long-acuminate bracts of P. haydeni are suggestive of P. angustifolius. Thus,

the chimeric appearance of P. haydeni and its sympatric occurance with P. grandiflorus and P. angustifolius leads one to suspect that the species may have evolved through hybridization of the two latter species. A strong circumstantial case for such an evolution of P. haydeni can be generated if one considers the geologic events of the Pleistocene Epoch in relation to putative distributions of P. grandiflorus and P. angustifolius during that time.

During the Pleistocene, Penstemon grandiflorus probably had a more southern distribution, ranging from Kansas to Texas and represented today by scattered relict populations in Oklahoma and Texas (Pennell, 1935). Penstemon angustifolius was also undoubtedly affected during this time and was probably distributed to the west against the Rocky Mountains and to the southwest of the Great Plains. These two species were most likely allopatric during this period of displacement. It was also during the Pleistocene when periglacial winds gave rise to the Nebraska sandhills.

With the recession of the Wisconsin Glacier, arenaceous glacial outwash and eolian sands deposited periglacially provided habitats suitable for both species in the central and northern Great Plains. Also present were numerous new and unexploited habitats which served as "testing grounds" for newly evolved and older species alike. As Penstemon grandiflorus and P. angustifolius progressively extended their ranges northward, the two species probably became partially sympatric in the central Great Plains. It was in this area where glacial recession had left radically new habitats available for colonization. Hybridization of the two species could have resulted in hybrid plants capable of invading the unexploited dune blowout habitat, and it is quite possible that Penstemon haydeni evolved in this manner in the Nebraska sandhills.

Figure 67. Great Plains Distribution of Penstemon haydeni



REPRESENTATIVE SPECIMENS:

UNITED STATES:

NEBRASKA: Cherry Co.: NE end Dewey Lake in Valentine National Wildlife Refuge, 6 June 1980, Freeman 525 (KSC); Kennedy, 15 June 1898, Bates s.n. (RM); Dewey Lake, 3 June 1897, Bates s.n. (RM). Vicinity of Hackberry Lake, August 1912, Dworak s.n. (NEB-4); Valentine Lakes Refuge, 1 June 1937, Tolstead 45 (NEB); Valentine Lakes Refuge at N end Dewey Lake, 15 June 1937, Tolstead s.n. (NEB); Near Valentine, 7 June 1897, Bates s.n. (NY). Hooker Co.: 3.7 mi N McPherson County Line along Hwy 97, 5 June 1980, Freeman 522 (KSC); Dismal River S of Mullen, 14 June 1931, Winter s.n. (SDC, SDU); 3.6 mi N McPherson County Line along Hwy 97, 6 June 1979, Harrison 982 (NEB); 6 mi N McPherson County Line along Hwy 97, 8 June 1979, Barnes & Heinisch s.n. (NEB). Thomas Co.: Near Plummer Ford, Dismal River, 6 July 1893, Rydberg 1506 (NEB-2, NY-2, SDC); Halsey, Winter s.n. (SDU). Unknown Stations: Sandhills at Loup Fork, Hayden s.n. (MO-2); Dismal River, 6 July 1893, Saunders 1006 (SDC).

14. Penstemon jamesii Bentham in DC.

Pentstemon jamesii Benth. in DC., Prod. Syst. Regn. Veg. 10: 325. 1846. Penstemon jamesii subsp. typicus Keck, Bull. Torrey Bot. Club 65: 239. 1938. Type: "in montibus Scopulosis (James in itinere Longii !)", probably from Union County, New Mexico, fide Keck (1938). (Holotype: NY!; Phototype: NY!).

Pentstemon similis A. Nels., Bull. Torrey Bot. Club 25: 548. 1898. Type: Nelson redescribed this southwestern species under this name as he mistakenly thought P. jamesii was the species from the Red Desert of Wyoming which is in fact P. cleiburnei Jones. He cites Fendler 575 and 579 as representative of P. similis. No type specimen was designated. Lectotype is chosen using the first specimen cited by Nelson as representative of the species. Lectotype: A. Fendler 575, collected on "Dry gravelly hills, Santa Fe, May-July 1847", in Santa Fe County, New Mexico. (Lectotype: MO!, F, GH, NY, PH, US, CI).

Herbaceous perennial. Stems erect or ascending, 1-4.5(5.2) dm tall, glabrate to retrorsely puberulent below and glandular-pubescent above, 1-7(10) stems arising from a simple or branched woody caudex surmounting a taproot. Leaves entire to undulate or serrate, glabrous to puberulent; basal leaves linear to (ob)lanceolate, 2-8(10.5) cm long overall, (0.2)0.5-1(1.3) cm wide, acute to obtuse, subsessile to petiolate, the petioles occasionally winged; cauline leaves linear to lanceolate, 2-10(11) cm long, 0.5-1.5 cm

wide, acute or rarely obtuse, sessile and scarcely clasping. Thyrse 5-20 (24) cm long, with 2-8 verticillasters, compact to elongate and interrupted, secund, leafy-bracted, individual cymes 2-5 flowered, peduncles and pedicels glandular-pubescent, peduncles appressed or erect, to 1.5 cm long, pedicels 1-6 mm long; bracts lanceolate, glandular-pubescent, the lower ones to 9 cm long and 1.5 cm wide. Calyx glandular-pubescent, sepals lanceolate to lance-ovate, 8-12 mm long, 2-3 mm wide, entire, acuminate to acute, herbaceous throughout or with narrow scarious margins towards the base; corolla 24-32(35) mm long, strongly bilabiate, pinkish or pale lavender to violet-blue, viscid glandular-pubescent externally, throat 9-15 mm broad, abruptly much-inflated and ventricose-ampliate, usually sparsely glandular-puberulent internally, lined internally on the anterior and posterior surfaces with magenta or violet-blue guidelines, the guidelines passing onto both lips of the limb, palate moderately to densely pilose with whitish hairs and rounded, lobes of the upper lip arched-projecting, lobes of the lower lip spreading to reflexed; staminode 14-17 mm long from its point of attachment, conspicuously exserted, flattened somewhat distally and slightly recurved, the terminal 10-14 mm bearded, hairs at the tip golden-yellow and tortuous, to 3.5 mm long, medial hairs shorter and retrorse; fertile stamens included, anther-sacs 1-1.2 mm long, tan, glabrous, widely divaricate, dehiscent throughout, becoming explanate; style 17-18 mm long, glabrous. Capsule 14-17 mm long. Seeds 2-3 mm long, angular, finely reticulate, black. $\underline{n} = 8$.

Sandy-loam to sand or gravel in high plains or gently sloping hills. Morton County, Kansas and southeastern Colorado south to western Texas and eastern New Mexico east of the Rio Grande River.

D.D. Keck (1938), in his study of Section Cristati (Rydb.) Pennell

(Section Aurator Keck) recognized Penstemon jamesii as having three subspecies; subsp. jamesii, subsp. ophianthus, and subsp. breviculus. Subsequent field work prompted Nisbet & Jackson (1960) to raise subsp. breviculus to specific rank and Holmgren (1978b) to return subsp. ophianthus to the level of species where it was described by Pennell in 1920.

Penstemon jamesii is a variable species throughout its range with respect to length and width of the corolla, pubescence of stems and leaves, length of stems, degree of serration of the leaves, and compactness of the thyrse.

REPRESENTATIVE SPECIMENS:

UNITED STATES:

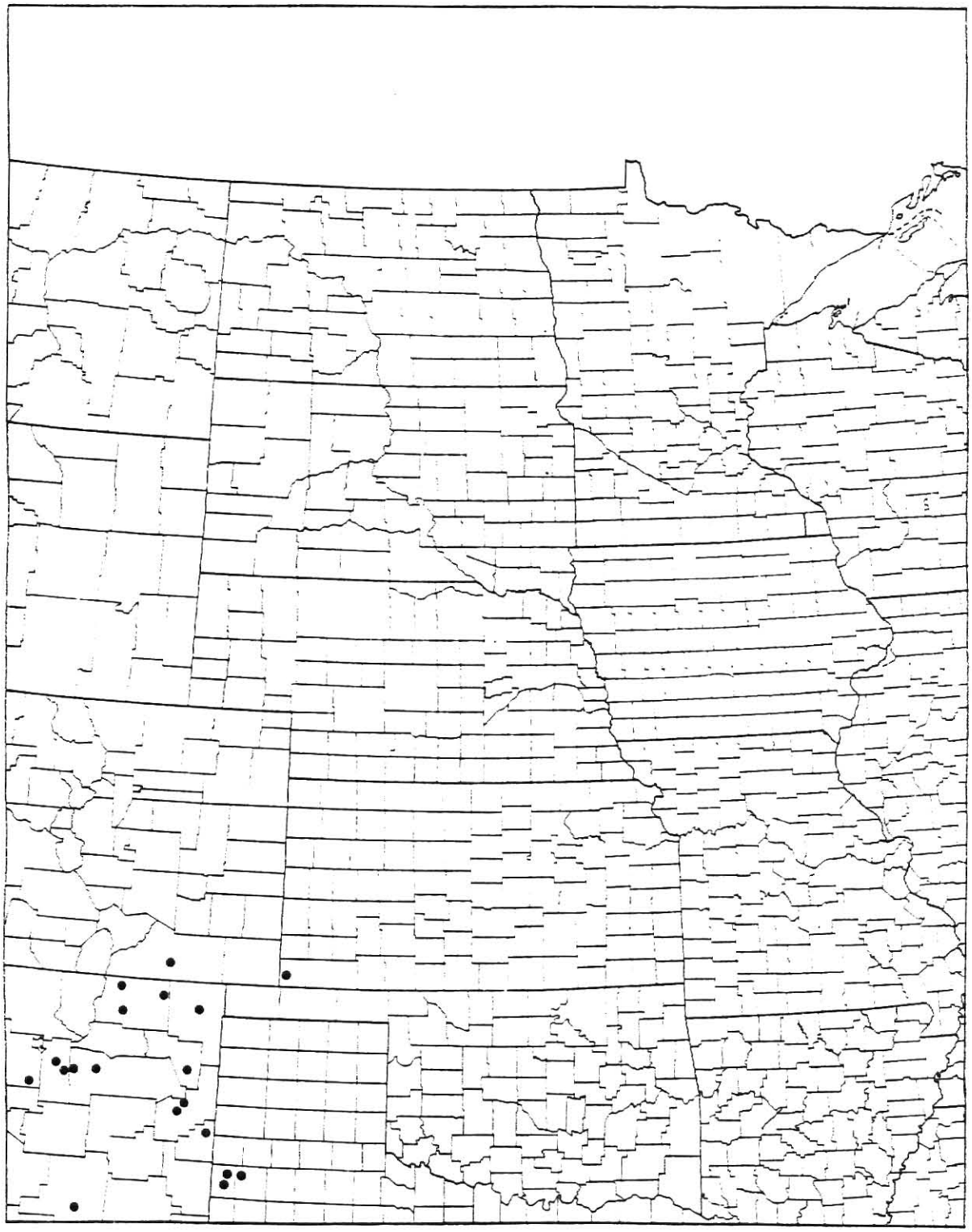
COLORADO: Las Animas Co.: Sec. 31, T33S, R54W, 7 June 1977, Barrington s.n. (OKLA).

KANSAS: Morton Co.: 9 mi N and 2 mi W of Elkhart, 27 May 1970, Bare 2276 (KANU).

NEW MEXICO: Colfax Co.: Johnson Mesa near Folsom, 17 June 1941, Nelson & Nelson 4701 (RM). Curry Co.: 14.7 mi S of Broadview, 21 May 1980, Freeman 423 (KSC). Eddy Co.: White's Camp, Carlsbad Caverns, 24 May 1931, Nelson 11408 (RM). Harding Co.: 34.3 mi NW of Harding Co. Line along Hwy 39, 21 May 1980, Freeman 430 (KSC). Lincoln Co.: Lincoln, 8-19 May 1902, Earle 653 (NY). Sandoval Co.: Las Palomas, Sandia Mountains, 30 August 1914, Ellis 480 (NY). San Miguel Co.: Near Pecos, 25 June 1949, Pennell & Pennell 26786 (NY, RM). Santa Fe Co.: Santa Fe, 28 May 1897, Heller & Heller 3605 (KANU, KSC, MO, NEB, NY). Quay Co.: 9.8 mi S of Tucumcari, 21 May 1980, Freeman 427 (KSC); 2.5 mi NE of Tucumcari, 21 May 1980, Freeman 429 (KSC).

TEXAS: Bailey Co.: Muleshoe Wildlife Refuge 20 mi S of Muleshoe, 1 July 1964, Rowell 10355 (OKL, OKLA, TTC). Brewster Co.: 10 mi E of Alpine, 21 April 1929, Ingram 2751 (NY). Culberson Co.: Van Horn's Wells, 12 June 1858, Thurber 570 (NY). Jeff Davis Co.: Davis Mountains, June 1936, Hinckley 626 (NY). Presidio Co.: Hwy 90 1 mi N of Paisano Campground, 8 May 1949, Hinckley 4674 (NY).

Figure 68. Great Plains Distribution of Penstemon jamesii



15. Penstemon laxiflorus Pennell

Penstemon laxiflorus Pennell, Acad. Nat. Sci. Phila. Monogr. 1: 229. 1935. Penstemon australis Small subsp. laxiflorus (Pennell) Bennett, Phytologia 9: 58. 1963. Type: "sandy, rocky woods, McAlester, Pittsburg County, Oklahoma, collected in flower and young fruit May 27, 1920, F.W. Pennell 10586" (Holotype: PH; Isotypes: MO!, NY!, F).

Penstemon panciflorus (pauciflorus) Buckley, Proc. Acad. Nat. Sci. Philadelphia 13: 461. 1862. Type: "Past (post) oak woods south of Fort Belknap. May." (Holotype: PH, not seen).

Herbaceous perennial. Stems erect or assurgent, 2.5-6.5(7) dm tall, spreading or retrorsely puberulent below and glandular-pubescent near the inflorescence, 1-5 stems arising from a simple or branched herbaceous caudex surmounting a taproot. Leaves subentire or more commonly serrate to dentate, nearly glabrous to puberulent, slightly lighter beneath; basal leaves (ob)ovate to spatulate, 2.5-9 cm long overall, 0.8-2.5 cm wide, acute to obtuse, subsessile or petiolate, the petiole sometimes winged; cauline leaves lanceolate to oblanceolate, (2)3-9(11) cm long, (0.2)0.5-2.2 cm wide, acute to obtuse, sessile and frequently clasping. Thyrse 5-26(32) cm long, with 3-7 verticillasters, interrupted, individual cymes 2-6 flowered, peduncles ascending or spreading, glandular-pubescent, to 6.5 cm long, pedicels lax, glandular-pubescent, 1-7 mm long; bracts much reduced and resembling the upper cauline leaves, the lower ones to 5.5 cm long and 1.8 cm wide. Calyx glandular-pubescent, sepals lance-ovate to ovate, 2.5-5.5 mm long, 2-3 mm wide, acuminate to acute, entire, slightly to distinctly scarious margined or seldom herbaceous throughout, often tinged deep-purple; corolla 20-28(30) mm long, bilabiate, white or more commonly suffused with pink or mauve, glandular-pubescent externally, throat 4-8 mm broad, slightly to moderately inflated and gradually ampliate, slightly flattened, lined internally with reddish-purple nectar guides, the guidelines passing well

onto the lobes of the lower lip and slightly onto those of the upper lip, prominently 2-ridged within anteriorly, palate up-arched and partially restricting the orifice, bearded with whitish or pale yellow eglandular hairs, lobes of the upper lip spreading, those of the lower lip projecting well beyond the upper; staminode 15-20 mm long from its point of attachment, prominently exserted, flattened and occasionally slightly recurved at the tip, the distal 8-10 mm densely bearded with stiff yellow-orange hairs to 1.5 mm long; fertile stamens included, anther-sacs 1-1.3 mm long, purple, lined with white along the sutures, the entire external surface minutely papillose, prominently papillose along the sutures, divaricate, dehiscent nearly to the apices and across the connective, not becoming explanate; style 14-20 mm long, glabrous. Capsule 8-10 mm long. Seeds 0.7-1 mm long, slightly angular to rounded, finely reticulate, brown to dark brown. $n = 8$.

Sandy or sandy-loam acid soil from Georgia and the Florida panhandle west to the 99th meridian; northern Arkansas and central Oklahoma south to the Gulf Coast. Commonly encountered on the Coastal Plain from central Alabama to central Texas. Flowering from early April to early June.

Bennett (1963b) reduced P. laxiflorus to a subspecies of P. australis. While such a change may be warranted, the specific status of P. laxiflorus is herein maintained, as an examination of the relationship of these two taxa was not undertaken in this study, nor were any data in favor of such a taxonomic realignment presented by Bennett.

REPRESENTATIVE SPECIMENS:

UNITED STATES:

ALABAMA: Mobile Co.: 1 mi N Satsuma, 14 April 1963, Iltis, Kawano, &

Crosswhite 21413 (OKL). Pike Co.: Near Lake Greeson, 4 May 1955, Demaree 36670 (KANU). Polk Co.: Cossatot River near Cove, 3 May 1955, Demaree 36602 (KANU). Sevier Co.: Gillham, 3 May 1955, Demaree 36577 (KANU). Union Co.: 1 mi N Calion, April 1965, Amason P6585 (OKL-2).

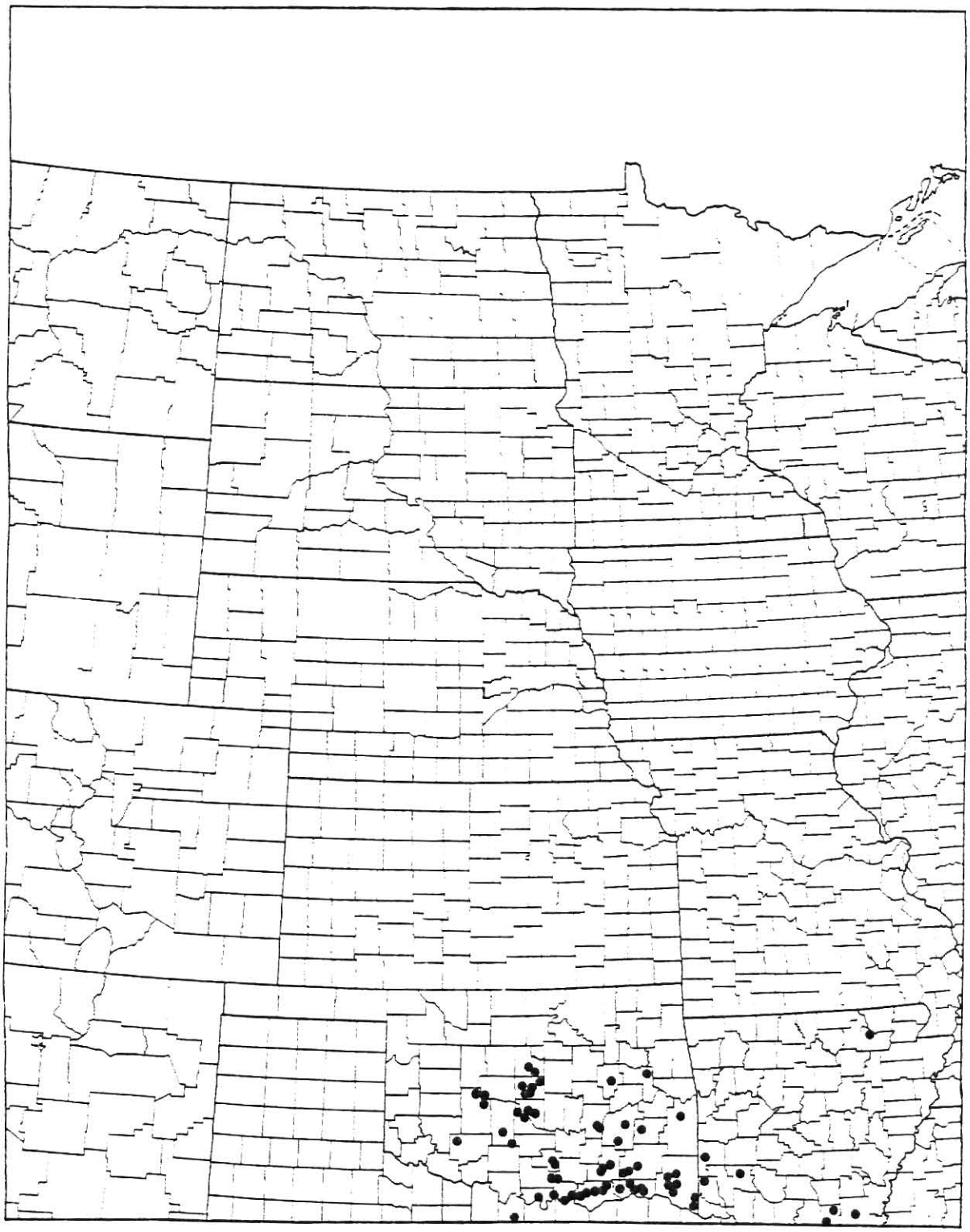
ARKANSAS: Bradley Co.: Warren, 1 May 1943, Demaree 24362 (KANU, OKL). Drew Co.: Ladelle, 2 May 1941, Demaree 21998 (OKL). Lawrence Co.: Imboden, 9 May 1951, Demaree 30434 (OKL).

LOUISIANA: Grant Parish: 4 mi SE Montgomery, 2 April 1967, Shinners 31698 (OKL).

OKLAHOMA: Atoka Co.: 12 mi S Atoka, 5 May 1945, Hopkins, Nelson & Nelson 1098 (MO, OKL, RM). Bryan Co.: 3 mi W Durant, 9 May 1963, Taylor & Taylor 1593 (OKL). Caddo Co.: Near Hinton, 15 June 1913, Stevens 943 (MO, NY, OKL, OKLA). Canadian Co.: 9 mi S Hinton, 10 May 1968, Stephens 20217 (KANU). Carter Co.: N city limits Dickson along Hwy 177, 19 May 1980, Freeman 408 (KSC). Choctaw Co.: 2 mi NW Hugo, 19 April 1946, Nelson, Nelson, & Goodman 5534X (MO, OKL, RM). Cleveland Co.: 120th Ave SE in Norman, 18 May 1980, Freeman 399 (KSC); Little Axe Area of Thunderbird Lake E of Norman, 18 May 1980, Freeman 400 (KSC); 3.8 mi E Hwy 77 along Pauline's Patch Road, 11 May 1968, Massey & Perino 2015 (KANU, OKL, OKLA). Comanche Co.: SW of Grama Flat Lake in Wichita Mts. Wildlife Refuge, 18 May 1942, McMurry 1165 (OKL). Grady Co.: 18 mi S Chickasha, 16 May 1942, Waterfall 3647 (MO, OKL, OKLA). Hughes Co.: 4 mi SE Calvin, 5 May 1961, Waterfall 16008 (OKLA). Johnston Co.: 0.4 mi E Carter Co. Line along Hwy 177, 19 May 1980, Freeman 409 (KSC). Latimer Co.: W of Wilburton, 3 May 1935, Pullin s.n. (KSC). LeFlore Co.: 2-3 mi NW Poteau, 25 April 1950, Anderson 121 (OKL). Logan Co.: Experiment Station Farm, 12 May 1934, Goodman 2124 (MO, NY, OKL, RM). Love Co.: W edge Jimtown along Hwy 32, 20 May 1980, Freeman 414 (KSC). McClain Co.: 7.5 mi SW Norman, 15 May 1937, McClellan 98 (OKL-2). McCurtain Co.: Near Idabel, 18 May 1916, Houghton 3629 (MO, NY, OKL). Marshall Co.: 3 mi N Woodville, 19 May 1980, Freeman 410 (KSC). Murray Co.: 1 mi E & 3 mi S Davis, 24 May 1945, Waterfall 6033 (OKLA). Muskogee Co.: Vicinity of Muskogee, 15 May 1883, Oyster s.n. (NEB). Oklahoma Co.: 3 mi E & 3 mi S Edmond, 17 May 1941, Waterfall 2701 (OKL, OKLA). Okmulgee Co.: Okmulgee, 4 May 1927, Elrod s.n. (MO). Pittsburg Co.: 4 mi N McAlester, 30 May 1957, Rogers s.n. (OKLA). Pushmatah Co.: 3 mi NE Antlers, 14 May 1966, McWilliam P6668 (OKL, OKLA).

TEXAS: Austin Co.: 2 mi NW Wallis, 22 April 1959, Correll & Rollins 21044 (MO). Bastrop Co.: 7 mi W Paige, 26 April 1947, Bailey & Barkley 17T112 (IND, OKL, RM-2). Brazos Co.: 2 mi SW College Station, 20 April 1946, Cory 51619 (NY). Burleson Co.: 8 mi W Wilcox, 11 April 1965, Massey & Massey 844 (OKL). Burnet Co.: Fairland, 17 May 1920, Pennell 10478 (NY). Chambers Co.: 7-10 April 1936, Tharp 257 (NY). Dallas Co.: Near Buchmans Dam, 2 May 1941, Lundell & Lundell 10422 (MO, NY). Denton Co.: 1 mi NE Denton, 18 April 1938, McCart 963 (NY). Fall Co.: 3.75 mi N Bremond, 19 April 1946, Cory 51552 (NY, RM). Guadalupe Co.: Kingsburg, 23 April 1917, Palmer 11643 (MO). Hamilton Co.: Along Leon River 9 mi NE Hamilton, 29 May 1947, Cory 53805 (NY). Hardin Co.: Fletcher, 25 April 1916, Palmer 9549 (MO). Harris Co.: Houston, 18 April 1872, Hall 407 (MO, NY-2). Hays Co.: San Marcos, 1898, Stanfield s.n. (NY). Hood Co.: Old Grandbury Road,

Figure 69. Great Plains Distribution of Penstemon laxiflorus



4 May 1955, Hoisington 264 (OKL). Hopkins Co.: W edge Sulphur Springs, 1 May 1957, Correll 16103 (MO). Jackson Co.: 3 mi NE Ganado, 22 April 1959, Correll & Rollins 21028 (NY). Kaufman Co.: 15 mi E Kaufman, 20 April 1940, Lundell & Lundell 8505 (NY-2). Liberty Co.: Dolen, 20 April 1914, Young 17 (MO). Lynn Co.: Between Tahoka & Lubbock, 29 April 1952, Small & Wherry 12156 (NY). McLennan Co.: 2 mi SE Robinson, 4 May 1949, Cory 55654 (NEB). Milam Co.: Milano, 2 May 1917, Palmer 11775 (MO). Montague Co.: 5 mi NW Forestburg, 12 May 1939, McCart 1729 (NY). Montgomery Co.: Willis, March-April, annon. s.n. (MO). Morris Co.: NE edge Lone Star, 23 May 1958, Correll & Lundell 18804 (NY). Navarro Co.: 5.7 mi E Dawson, 3 May 1949, Cory 55622 (NDA). Newton Co.: Along Hwy 87, 24 May 1959, Correll, Johnston, & Edwin 22273 (NY). Polk Co.: Livingston, 12 April 1914, Palmer 5212 (MO). Smith Co.: 1 mi N & 1 mi E Troup, 9 April 1949, Cory 55575 (NDA). Tarrant Co.: 1.75 mi W Hurst, 16 April 1948, Cory 54357 (IND, KANU, NEB); 3 mi S Polytechnic, 3 May 1914, Ruth 462 (KSC, NDA, NY, RM). Travis Co.: Austin, 15-16 May 1920, Pennell 10443 (NY). Victoria Co.: Guadalupe River above Victoria, 15 October 1857, Schott s.n. (NY). Wise Co.: 3 mi S Bridgeport, 13 April 1946, Whitehouse 15260 (NY).

16. Penstemon nitidus Douglas ex Bentham in DC.

Pentstemon acuminatus β minor Hook., Flora Bor. Amer. 2: 97. 1838. Pentstemon nitidus Dougl. ex Benth. in DC., Prod. Syst. Nat. Regn. Veg. 10: 323. 1846. Penstemon nitidus (subsp.) typicus Penn., Notul. Nat. Acad. Nat. Sci. Philadelphia 95: 6. 1942. Type: "in collibus siccis ad flumina Saskatchawan, Assinaboin et Red River", type labeled by Douglas, "Pentstemon nitidum Common on the Red dear and Eagle Hills of the Sascatchawan river, as also on the Assineboine and Red River." (Holotype: K; Phototypes: NY!, PH).

Herbaceous perennial. Stems erect or assurgent, (0.5)1-3.5(4) dm tall, glabrous and glaucous, 1-7 stems arising from a thick crown or short-branched woody caudex surmounting a taproot. Leaves entire, thick, firm, glabrous and often heavily glaucous; basal leaves linear-lanceolate to oblanceolate or spatulate, 1.5-10 cm long overall, 0.2-2.7 cm wide, acute to ovate or frequently mucronate, often tufted and anthocyanic, petiolate, the petioles occasionally winged; cauline leaves lanceolate to lance-ovate below, lance-ovate to ovate above, (1.1)1.8-8.5 cm long, (0.3)0.5-2.8(3.2) cm wide, acuminate to acute or frequently mucronate, clasping to cordate-clasping. Thyrse (2)5-17 cm long, with (2)4-10 verticillasters, compact to elongate, scarcely to distinctly interrupted, narrow, cylindrical and not secund,

individual cymes 2-5 flowered, peduncles absent or if present then usually less than 5 mm long, pedicels glabrous, 1-10 mm long, usually tinged purple or lavender; bracts resembling the upper cauline leaves below, much-reduced above, the lower ones to 7 cm long and 2.8 cm wide, acuminate to acute, bases clasping to cordate-clasping. Calyx glabrous and somewhat glaucous, sepals lanceolate to lance-ovate, 3-8 mm long, 1-3 mm wide, acuminate, margins narrowly scarious towards the base, entire to slightly erose, green or tinged lavender to purple; corolla (10)13-15(18) mm long, tubular-salverform, bilabiate, deep blue or rarely pink, glabrous externally, throat 4-6 mm broad, moderately ampliate, lined internally on the anterior and posterior surfaces with violet or purple guidelines, the guidelines passing barely onto the lobes of the limb, lobes of the upper lip spreading, lobes of the lower lip projecting, palate glabrous or sparingly bearded with white eglandular hairs; staminode 8-11 mm long from its point of attachment, reaching the orifice or slightly exserted, flattened distally and recurved, densely bearded at the tip with golden-yellow hairs to 1.5 mm long, more sparingly bearded away from the tip for 1/3 to 1/2 its length; fertile stamens included or the longer pair reaching the orifice or slightly exserted, antherssacs 0.7-1.2 mm long, purple, lined with white along the sutures, externally minutely papillose, particularly along the sutures, divergent, dehiscing nearly to the apices and across the connective, not becoming explanate; style 8-10 mm long, glabrous. Capsule 9-13 mm long. Seeds 2.5-3.5 mm long, angular, finely reticulate, brown to dark brown. $\underline{n} = 8$.

Rocky to gravelly soil in prairies, hillsides, and at low elevations in the Northern Rocky Mountains. Southern Manitoba south of the Assiniboine River west to southeastern British Columbia; south through western North Dakota and Montana to northern Wyoming.

In western North Dakota, extreme eastern Montana, and northeastern Wyoming, P. nitidus is sympatric with P. angustifolius var. angustifolius, also of section Coerulei. Cronquist, writing in Hitchcock et al. (1959), states, "P. angustifolius is consistently narrow-leaved, and has somewhat larger corollas and anthers than P. nitidus, but the distinction is not always very sharp, especially when P. nitidus var. polyphyllus is taken into account." He later continues, "The ranges of P. nitidus and P. angustifolius come together in e. Montana and w. N.D., and it is possible that monographic study will necessitate the treatment of these several taxa (except P. acuminatus) as geographic races of a single species, under the binomial P. angustifolius Pursh."

However, an examination of much herbarium material and limited field study in the area of sympatry indicate the two taxa, while similar, are distinct and best maintained as separate species. Penstemon angustifolius var. angustifolius is characterized by its linear to linear-lanceolate cauline leaves, normally acuminate to acute, lanceolate bracts, corolla 14-18 mm long, anther-sacs 0.9-1.4 mm long, and the common occurrence of a scabrid-puberulence on the stem, leaves, bracts, and sepals of plants. By contrast, P. nitidus normally has cauline leaves lanceolate to ovate and frequently mucronate, bracts lance-ovate to ovate, corolla (10)13-15(18) mm long, anther-sacs 0.7-1.2 mm long, and totally glabrous and frequently heavily glaucous stems, leaves, bracts, and sepals.

In Granite, Missoula, Powell, and Silver Bow Counties of Montana and Lemhi County, Idaho, a variety of P. nitidus differing slightly from nomenclaturally typical plants has been recognized as P. nitidus var. polyphyllus (Penn.) Cronq. This variety has slightly longer and narrower sepals, bracts, and leaves than var. nitidus and the corolla is usually pilose internally

on the antherior surface. However, the distinction between these two varieties is often less than glaring and field studies are needed to evaluate the relationship of the two varietal taxa.

REPRESENTATIVE SPECIMENS:

UNITED STATES:

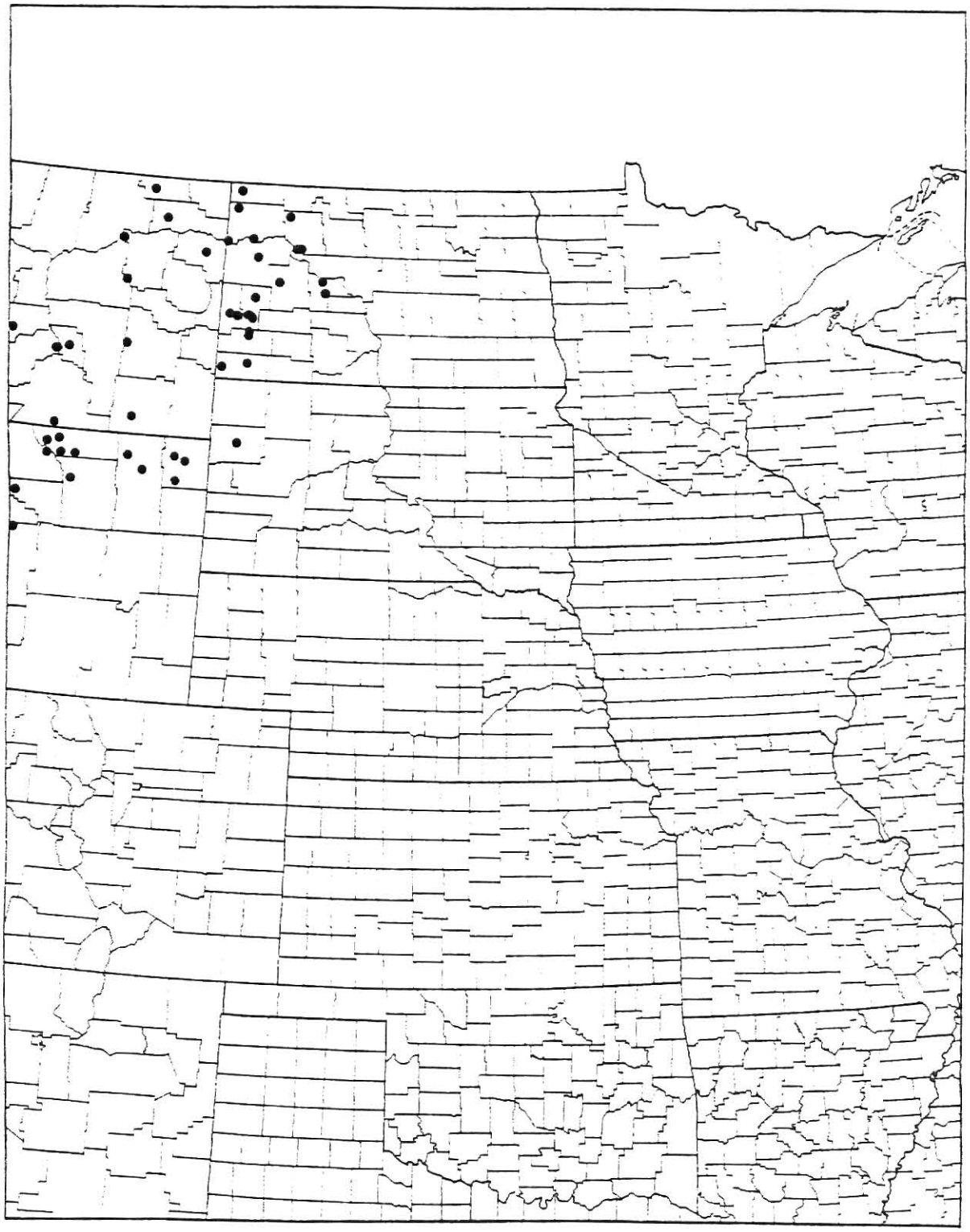
MONTANA: Beaverhead Co.: July 1888, Tweedy 71 (NY). Big Horn Co.: 5 mi S Wyola, 4 September 1937, Pennell 21369 (NY). Cascade Co.: Belt, 11 May 1937, Keller 2 (NY). Custer Co.: Hathaway, 10 May 1936, Woolfolk s.n. (NY). Daniels Co.: 13 mi W Four Buttes, 9 June 1980, Freeman 545 (KSC). Fergus Co.: Half Moon Canyon 5 mi from mouth in Big Snowy Mts., 5 July 1945, Hitchcock & Muhlick 11959 (MO, NY). Gallatin Co.: 1 mi SE Bozeman, 5 May 1947, Booth 1505 (KANU, NDA); Bozeman, 27 May 1899, Blankinship s.n. (CS, OKL, OKLA, RM). Garfield Co.: 32 mi E Jordan, 21 June 1974, Stephens 78490 (KANU). Lewis and Clark Co.: Gate of the Mountains along Missouri River, 9 May 1946, Williams s.n. (RM). McCone Co.: 1 mi E Ft. Peck Dam spillway, 20 June 1974, Stephens 78332 (KANU). Musselshell Co.: 36 mi W Roundup, 10 May 1952, Wright 10 (KANU). Park Co.: 9 mi NW Wilsall, 27 July 1921, Suksdorf 1047 (MO, NY). Powder River Co.: 1 mi N Brodelus, 21 May 1965, McMullis 313 (OKLA). Richland Co.: 25 July 1938, Coey 26 (NEB). Roosevelt Co.: Ft. Peck Indian Res., 20 May 1936, Weber N7-1294 (NDA). Sweet Grass Co.: Sweet Grass hills, May 1918, Kemp s.n. (NY). Teton Co.: Big Muddy from Great Falls to 30 mi N, 15 May 1900, Wilcox 11 (NY). Treasure Co.: 7 mi E of Big Horn, 15 June 1937, Pennell 20462 (NY). Yellowstone Co.: Custer, 12 May 1890, Blankinship 21 (MO).

NORTH DAKOTA: Billings Co.: Medora, 29 May 1904, Waldron 2320 (NDA, RM). Bowman Co.: 16 mi S & 1 mi W Marmarth, 27 May 1970, Zaczkowski 2068 (NDA). Divide Co.: Fortuna, 25 May 1961, Stevens 2381 (NDA). Dunn Co.: Killdeer Mts., 8 June 1938, Stevens s.n. (NDA). Golden Valley Co.: 5 mi W & 4 mi S Medora, 4 June 1969, Zaczkowski 218 (NDA). McKenzie Co.: Gorham, 22 May 1938, Moran 331 (NDA, OKL, RM). Mercer Co.: 10 mi N & 2 mi E Zap, 29 June 1967, Stephens 12662 & Brooks (KANU). Mountrail Co.: 7 mi S & 3 mi W Powers Lake, 7 June 1971, Hegstad 7743 (NDA). Slope Co.: 7.5 mi N & 6.5 mi W Amidon, 10 June 1978, Larson 6240 (NDA). Williams Co.: 15 mi SE Williston along Missouri River, 20 June 1945, Stevens s.n. (NDA).

SOUTH DAKOTA: Butte Co.: Shepherd's Monument along Hwy 85 NE of Belle Fourche, 24 June 1979, Freeman 202 (KSC).

WYOMING: Big Horn Co.: Shell Creek in Big Horn Mts., 16 June 1937, Pennell 20477 (NY). Campbell Co.: 15.8 mi N Gillette, 10 June 1980, Freeman 548 (KSC). Crook Co.: 15 mi NW Hulett along Little Missouri River, 9 June 1935, Ownbey 656 (MO, NY, RM-2). Fremont Co.: SE of Thermopolis and E of Wind River Canyon on N flank of Owl Creek Range, 15 July 1960, Fisser 277a (RM). Johnson Co.: Along Hwy 16 at South Fork Inn in Big Horn Mts., 12 August 1938, Pennell & Schaeffer 24404 (NY). Sheridan Co.: Little Tongue

Figure 70. Great Plains Distribution of Penstemon nitidus var. nitidus



River Canyon, 25 June 1936, Williams & Williams 3113 (MO, NY, RM).
Washakie Co.: W of Worland, 5 May 1962, Nichols 305 (RM).

17. Penstemon oklahomensis Pennell

Penstemon oklahomensis Penn., Acad. Nat. Sci. Phila. Monogr. 1: 237. 1935. Type: "dry soil, open woodland or prairie, Sapulpa, Creek County, Oklahoma, collected in flower, May, 1924, by Charles B. Williams." (Holotype: PH; Isotype: NY!).

Herbaceous perennial. Stems mostly erect, (1.5) 3.5-5.5 dm tall, spreading or retrorsely puberulent below, glandular-pubescent midway up the stem, 1-2 (4) stems arising from a short, typically slender herbaceous caudex surmounting a taproot. Leaves subentire to obscurely or sharply serrate or denticulate, puberulent, paler beneath; basal leaves (ob)lanceolate to obovate or spatulate, 2.5-8(11) cm long overall, 0.5-2.4(3.2) cm wide, acute to obtuse, subpetiolate to petiolate; cauline leaves linear to lanceolate, (2.5)6-12 cm long, 0.4-2 cm wide, acute to acuminate, somewhat clasping. Thyrse (5)8-18(25) cm long, with (2)3-6 verticillasters, narrow, interrupted, individual cymes 2-4(6) flowered, peduncles appressed or erect, glandular-pubescent, to 4 cm long, pedicels glandular-pubescent, 0.2-0.9 cm long; bracts much reduced, linear to linear-lanceolate and resembling the cauline leaves, the lower ones to 6 cm long and 0.6 cm wide. Calyx glandular-pubescent, sepals lanceolate to ovate, 5-7 mm long, 2-3 mm wide, acute to acuminate, entire, margins scarious particularly near the base; corolla 24-32 mm long, bilabiate, white to yellowish-white and unlined within, glandular-pubescent externally, tube slender, throat 6-8 mm broad, scarcely inflated and barely ampliate, slightly flattened, prominently 2-pleated internally on the anterior surface, palate strongly up-arched and closing the orifice, bearded with dense yellow hairs passing slightly onto the lobes of the lower lip, lobes of the upper lip spreading, lobes of the lower lip projecting and extended well beyond the

upper lip; staminode 18-20 mm long from its point of attachment, slightly exserted, flattened and densely bearded the distal 14-16 mm with stiff yellow-orange hairs to 1.5 mm long; fertile stamens included, anther-sacs 1-1.5 mm long, tan and usually tinged purple, the entire external surface minutely papillose, scarcely to prominently papillose along the sutures, divaricate, dehiscent throughout and across the connective, not becoming explanate; style 20-22 mm long, glabrous. Capsule 8-13 mm long. Seeds 0.7-1 mm long, rounded to slightly angular, finely reticulate, brown to dark brown. n = 8.

Sandy-loam to loam soil in rolling prairies or open woodlands. Restricted almost wholly to the Osage Plains of Oklahoma from Osage County southeast to Pushmataha and Bryan Counties; west to Comanche County. Flowering from late April to mid-June.

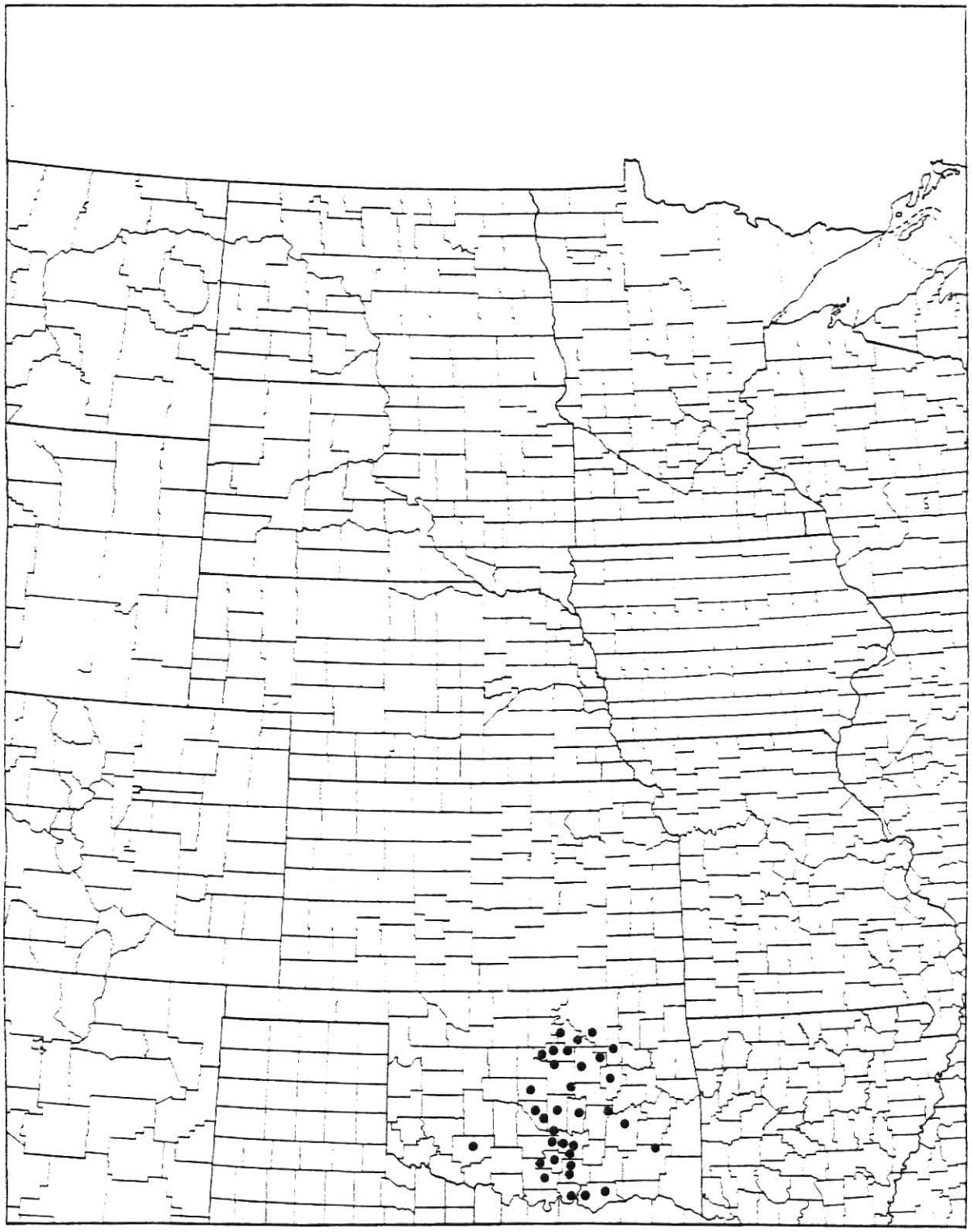
Penstemon oklahomensis is a beautiful species with its long, slender, and declined flowers. It is the only member of Section Penstemon in the Great Plains having its orifice totally obstructed by a strongly up-arched palate.

REPRESENTATIVE SPECIMENS:

UNITED STATES:

OKLAHOMA: Bryan Co.: 0.25 mi NE & 1 mi E Caddo, 6 July 1977, Taylor & Wright 24873 (OKL). Carter Co.: 3.5 mi N of Admore, 28 April 1962, Goodman 7270 (OKL). Cleveland Co.: 3.9 mi W of Little Axe Area of Lake Thunderbird, 5 May 1980, Freeman 402 (KSC). Comanche Co.: Ft. Sill, 6 May 1916, Clemens 11774 (MO, RM). Creek Co.: Sapulpa, 28 April 1895, Bush 881 (MO, NY). Garvin Co.: 1 mi S of Stratford, 19 May 1980, Freeman 404 (KSC). Hughes Co.: 2 mi SW of Dustin, 7 May 1961, Waterfall 16025 (OKLA). Johnston Co.: 3 mi E of Mill Creek, 28 April 1956, Goodman 6251 (KANU, OKL). Lincoln Co.: 1 mi E and 2 mi S of Perkins, 17 May 1954, Waterfall 11872 (OKL, OKLA). McClain Co.: 2.4 mi S of intersection Hwy 177 & 3W, 19 May 1980, Freeman 403 (KSC). Marshall Co.: 3 mi E and 0.25 mi S of Kingston, 19 May 1980, Freeman 411 (KSC). Murray Co.: 2 mi W of Sulphur, 3 May 1969, Goodman 7913 (OKL). Oklahoma Co.: 2.75 mi S of Harrah, 10 May 1941, Waterfall

Figure 71. Great Plains Distribution of Penstemon oklahomensis



2668 (OKL, OKLA). Okmulgee Co.: Okmulgee Indian Territory, 25 April 1891, Carleton 85 (KSC, NEB). Osage Co.: 4.7 mi E of Hominy, 18 May 1980, Freeman 393 (KSC). Pawnee Co.: 2 mi W of Cleveland, 18 May 1980, Freeman 396 (KSC). Payne Co.: 0.35 mi N of jct Hwy 18 & 51, 18 May 1980, Freeman 397 (KSC); 4 mi N and 0.5 mi E of Stillwater, 1 May 1968, McDonald 51 (KANU). Pittsburg Co.: 10 mi N of Limestone Gap, 16 May 1877, Butler 106 (MO, NY). Pontotoc Co.: 1 mi S of Ada, 24 April 1948, Robbins 2945 (NY, OKL). Pottawatomie Co.: 10 mi S of Tecumseh, 22 April 1932, Barkley 70 (MO, OKL). Pushmataha Co.: 2 mi NW of Albion, 7 May 1937, McLean 69 (OKL, OKLA). Seminole Co.: 10 mi E of Seminole, 4 May 1934, Harlow s.n. (OKL). Tulsa Co.: Chandeler Park, Tulsa, 1 May 1964, Chesnut 63 (OKLA).

18. Penstemon pallidus Small

Pentstemon pallidus Small, Fl. Southeastern U.S. 1060, 1337. 1903. Type: "Bedford, New York, N.L. Britton, June, 1900." (Holotype: NY!).

Penstemon arkansanus (var.) pubescens Penn., Proc. Acad. Nat. Sci. Philadelphia 73: 494. 1922. Type: "sandstone woodland, Penters Bluff, Izard County, Arkansas, collected in late flower and fruit, June 1, 1920, F.W. Pennell 10679." (Holotype: NY!; Isotypes: GH, MO, US).

Herbaceous perennial. Stems erect or ascending, 2.5-5.5(6.5) dm tall, retrorsely puberulent with eglandular hairs and with glandular-villose pubescence below and glandular-pubescent near the inflorescence; 1-6 stems arising from a typically short and slender herbaceous caudex atop a taproot. Leaves subentire or more commonly undulate to obscurely or sharply serrate or dentate, pubescent above and below, appearing somewhat velvety, usually distinctly lighter beneath; basal leaves (ob)ovate to spatulate, 2-12(18) cm long overall, 0.5-3.5(4) cm wide, acute to obtuse, subsessile or petiolate, the petioles sometimes winged; cauline leaves lanceolate to lance-ovate or ovate, 2.2-10 cm long, 0.4-2.4 cm wide, narrowly to broadly acute, sessile and often distinctly clasping. Thyrse 5-26(30) cm long, with 3-8 verticillasters, interrupted and triangular in outline when pressed, individual cymes 2-8(16) flowered, peduncles and pedicels glandular-pubescent, peduncles ascending or spreading, to 5 cm long, pedicels 1-3 mm long; bracts much reduced, linear-lanceolate to lanceolate and resembling the upper cauline

leaves, the lower ones to 7.2 cm long and 2.2 cm wide. Calyx glandular-pubescent, sepals ovate, 2.5-5 mm long, 1.5-3 mm wide, acuminate to acute, entire or occasionally obscurely erose, margins slightly to distinctly scarious, seldom herbaceous throughout, often tinged reddish-purple; corolla 16-22 mm long, bilabiate, white or tinged mauve, glandular-pubescent externally, tube slender, throat 4-7 mm broad, slightly to moderately inflated and gradually ampliate, flattened somewhat, lined internally on the anterior surface with reddish-purple guidelines, the guidelines occasionally passing onto the lobes of the lower lip, prominently 2-ridged within on the anterior surface, palate somewhat up-arched and bearded with whitish to yellow eglandular hairs, lobes of upper lip spreading, those of the lower lip projecting or spreading slightly, extended beyond the upper lip; staminode 11-12 mm long from its point of attachment, distinctly exserted, flattened and slightly recurved distally, pubescent on the terminal 8-9 mm, moderately to densely bearded at the tip with stiff yellow to golden-yellow hairs to 1.5 mm long, more sparingly bearded away from the tip; fertile stamens included, anther-sacs (0.8)1-1.2 mm long, pale to deep purple, lined with white along the sutures, the entire external surface minutely papillose, slightly to prominently papillose along the sutures, widely divaricate, dehiscent nearly to the apices and across the connective, not becoming explanate; style 12-14 mm long, glabrous. Capsule 5-7 mm long. Seeds 0.5-0.7 mm long, rounded to slightly angular, finely reticulate, brown to dark brown. $n = 8$.

Loamy to sandy-loam soil in prairies and rocky deciduous forests. Maine west to northeastern Minnesota; south to Georgia and eastern Kansas. Flowering from mid-April in northern Arkansas to early July in Minnesota and Maine.

Pennell (1935) suggested P. pallidus has extended its range in a manner similar to P. digitalis and P. tubaeflorus, although it is impossible to

delimit precisely the native range of the species. It is thought that the species originally occupied the Mississippi and Ohio River Valleys from northern Arkansas north into Iowa and Illinois and east up the Ohio River into New England.

Bennett (1963b) reduced Penstemon arkansanus Pennell to a subspecies of P. pallidus. The former species occurs in southwestern Missouri, Arkansas, and eastern Oklahoma, just outside the Great Plains and it is restricted almost wholly to the Ozark Plateau. McWilliam (1967), on the other hand, has argued that P. arkansanus should be maintained as a distinct species. Regardless of the nomenclature, the two taxa bear many similarities and are undoubtedly closely related.

REPRESENTATIVE SPECIMENS:

UNITED STATES:

ARKANSAS: Baxter Co.: Ellis, 14 May 1950, Demaree 28950 (KANU, OKL). Boone Co.: Along Hwy 62, 22 May 1939, Bebb 4051 (OKL). Carroll Co.: W of Eureka Springs, 19 May 1939, Bebb 3994 (OKL). Fulton Co.: Salem, 10 May 1947, Demaree 25990 (KANU, OKL). Green Co.: Lafe, 6 May 1951, Moore 510246 (OKL). Independence Co.: Pleasant Plains, 8 May 1965, McWilliam P6591 (OKL). Lawrence Co.: Imboden, 9 May 1951, Demaree 30434 (KANU). Marion Co.: 0.5 mi N of Caney, 4 May 1968, Stephens 20056 (KANU). Searcy Co.: 21 May 1939, Bebb 4011 (OKL). Sharp Co.: Hardy, 18 May 1947, Demaree 26078 (KANU, OKL). Stone Co.: Arkansas State Forest Hdqtrs, Mountain View, 8 May 1965, McWilliam P6589 (KANU, OKL). White Co.: White-Independence Co. Line on Hwy 167, 8 May 1965, McWilliam P6592 (OKL).

ILLINOIS: Champaign Co.: Champaign, 1876-79, Taft s.n. (KSC). Peoria Co.: Horseshoe Bottom overlook, 15 May 1957, Chase 14426 (KSC). Piatt Co.: Allerton Park near Monticello, 20 May 1951, Jones 19020 (NEB). Whiteside Co.: Fulton, 25 May 18--, Burgess s.n. (KSC). Winnebago Co.: Rockford Co.: Rockford, 1879, Bebb s.n. (OKL).

IOWA: Appanoose Co.: 4 July 1897, Fitzpatrick & Fitzpatrick s.n. (RM). Davis Co.: 3 mi W & 2 mi N of Floris, 13 May 1939, Hayden 9533 (NY). Decatur Co.: 23 June 1900, Anderson s.n. (RM). Johnson Co.: Iowa City, Hitchcock s.n. (KSC). Lee Co.: Keokuk, 1 June 1897, Shimek s.n. (NY). Lucas Co.: Near Fry Hill Cemetary, 19 June 1957, Van Bruggen 2184 (SDU). Mahaska Co.: 1.5 mi N of Eddyville along Des Moines River, 29 July 1938, Augustine 464 (OKL). Muscatine Co.: S of Muscatine, 1935, Estle & Brown s.n. (NY).

Van Buren Co.: Near Farmington, 19 May 1929, Palmer 35839 (NY). Wapello Co.: Above Cliffland along Des Moines River, 27 October 1939, Hayden 9535 (NY).

KANSAS: Douglas Co.: Baldwin City Cemetary 1 mi S of Baldwin City, 17 May 1980, Freeman 389 (KSC); Baldwin City Cemetary 1 mi S Baldwin City, 25 May 1981, Freeman & Freeman 968 (KSC). Jefferson Co.: 3 mi NW of Williamstown, 30 May 1948, McGregor 1520 (KANU). Wilson Co.: 3.5 mi S of Altoon, 18 May 1980, Freeman 390 (KSC); 3.5 mi S of Altoon, 10 May 1972, Stephens 52640 (KANU, NDA, NY).

KENTUCKY: Clay Co.: Tyner, 2 June 1943, McFarland 41 (OKL). Cumberland Co.: 1.5 mi W of Burkesville, 18 May 1968, Brooks 5653 (KANU).

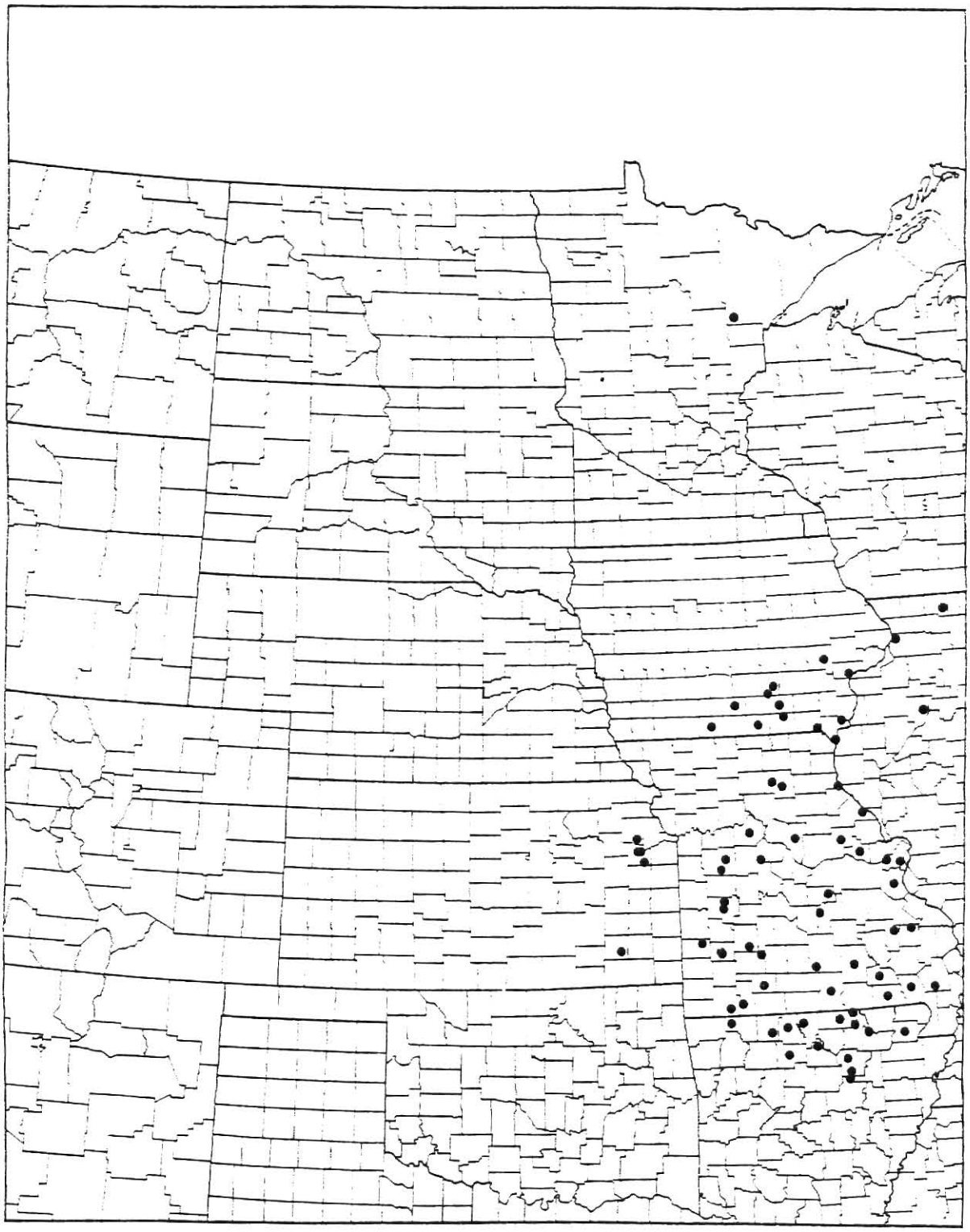
MINNESOTA: St. Louis Co.: Jct of Prairie Lake Rd & Hwy 2 at Gowan, 6 July 1950, Lakela 10650 (NEB, NDA).

MISSOURI: Barry Co.: Eagle Rock 2 June 1897, Bush 131 (KSC). Barton Co.: 6 mi N of Milford, 19 May 1957, Palmer 65098 (KANU). Boone Co.: N of Columbia, 24 May 1935, Rickett 763 (FHKSC). Butler Co.: Poplar Bluff, 1 May 1949, Demaree 27668 (OKL). Carter Co.: Big Spring State Park, 7 May 1972, Becker 69 (KANU). Christian Co.: Christian Center, 10 June 1923, Pennell 11643 (RM). Cooper Co.: Otterville, 19 May 1936, Bush 15524 (KSC). Dade Co.: 5 mi E of Greenfield, 11 May 1949, Palmer 49035 (KSC). Greene Co.: Galloway, 10 June 1923, Pennell 11635 (NY). Howell Co.: Hutton Valley, 9 June 1923, Pennell 11601 (NDA, NY). Iron Co.: Ironton, 6 May 1921, Payson 2410 (RM). Jefferson Co.: Seckman, 17 May 1973, Christ s.n. (NY). Johnson Co.: 1 mi NW of Warrensburg, 30 May 1980, Freeman & Wetter 453 (KSC); 1.2 mi N of jct Hwy PP & JJ, 30 May 1980, Freeman & Wetter 455 (KSC). Macon Co.: W of Callao, 20 May 1947, Ripley & Barneby 8280 (NY). Madison Co.: Mine La Motte, 22 May 1926, Palmer 30272 (NY). Maries Co.: Lane's Prairie, 8 May 1934, Bush 13489a (KSC). Marion Co.: Hannibal, 9 June 1917, Davis 7469 (KSC). Montgomery Co.: Near Mineola, 17 May 1938, Rollins 2044 (NY). Phelps Co.: Jerome, 21 May 1914, Kellogg 59 (NY). Pike Co.: Clarksville, 20 May 1912, Davis 245 (NY). Polk Co.: Near Brighton in Hickory Creek Cemetary, 28 May 1968, Sutherland 1591 (KANU, *KNSC, NEB). Ripley Co.: Pleasant Grove, 21 July 1897, Mackenzie 376 (KSC, NY). St. Clair Co.: 0.6 mi N of County Rd B along Hwy 13, 30 May 1980, Freeman & Wetter 457 (KSC). St. Louis Co.: Allenton, 12 June 1923, Pennell 11682 (NEB, OKL). Saline Co.: Blue Lick, 16 May 1934, Bush 13516 (KSC, NY). Shannon Co.: Montier, 15 May 1894, Bush 442 (NY). Stoddard Co.: Bernie, 2 August 1895, Bush 346 (NY-2). Stone Co.: 5 mi S of Cape Fair, 30 April 1949, Steyermark 67490 (NY). Texas Co.: Cobool, June 1890, Barnhart 457 (NY). Warren Co.: Truesdale, 25 May 1917, Davis 7328 (RM).

NEW HAMPSHIRE: Strafford Co.: Dover, 9 June 1938, Mills 980 (OKL).

NEW YORK: Tompkins Co.: Near Slaterville Swamp, Smith 929 (SDC).

Figure 72. Great Plains Distribution of Penstemon pallidus



19. Penstemon procerus Douglas ex Graham

Pentstemon procerum Dougl. ex Grah., Edinburg New Philos. J. 7: 348. 1829. Pentastemon confertus Dougl. β violaceus Trautv., Bull. Acad. Imp. Sci. Saint-Petersbourg 5: 344. 1839. Pentstemon confertus Dougl. β caeruleo-purpureus A. Gray, Proc. Amer. Acad. Arts 6: 69. 1862. Pentstemon confertus Dougl. (var.) procerus (Dougl. ex Grah.) Cov., Contr. U.S. Natl. Herb. 4: 169. 1893. Penstemon procerus subsp. typicus Keck, Amer. Midl. Naturalist 33: 144. 1945. Type: "raised at the Botanic Garden, Edinburgh, from seeds gathered by Mr. Drummond. It was also found by Mr. Douglas on the north-west coast of America", probably from along the Saskatchewan River in Alberta, Canada, fide Keck (1945). (Holotype: K, not seen).

Pentstemon micranthum Nutt., J. Acad. Nat. Sci. Philadelphia 7: 45. 1834. Lepteiris parviflora Raf., New Fl. N. Amer. 2: 73. 1836. Pentstemon procerus Dougl. ex Grah. var. micrantus (Nutt.) Jones, Bull. Montana State Univ. Biol. Ser. 15: 45. 1910. Type: "In the valleys of the Rocky Mountains, near the sources of the Columbia.", collected by N.B. Wyeth, July 11 1833, possibly in southwestern Teton County, Wyoming, fide Dayton (1926). (Holotype: PH; Isotypes: BM, NY!; Phototypes: GH, NY!).

Penstemon procerus (subsp.) pulverus Penn., Contr. U.S. Natl. Herb. 20: 366. 1920. Type: "collected on moist meadow knolls, north of Swan Lake, Yellowstone National Park, Wyoming, in flower, July 7, 1915, by F.W. Pennell (no. 6036)." (Holotype: NY; Isotypes: F, GH, K, MO!, PENN, RM, US).

Slender herbaceous perennial. Stems erect or assurgent, (0.5)1-4.5(7) dm tall, glabrate to minutely puberulent, solitary to many and tufted from a somewhat suffrutescent aerial caudex. Leaves entire, glabrous to puberulent; basal leaves often poorly developed or wanting, when present oblanceolate to eliptic or ovate, 2-6(10) cm long overall, 3-15(18) mm wide, acute to obtuse; cauline leaves lanceolate to oblanceolate, 2-5(8) cm long, 5-10(21) mm wide, acute, mostly sessile and clasping. Thyrse (1.5)2-15(23) cm long, with (1)2-5(11) dense verticillasters, capitate to elongate and cylindrical, the lower verticillasters distinctly interrupted, individual cymes many flowered, peduncles appressed or erect, glabrous to puberulent, to 3.8 cm long, pedicels glabrous to puberulent and normally not longer than 2 mm; bracts linear-lanceolate to lanceolate and resembling the upper cauline

leaves. Calyx glabrous to puberulent and occasionally densely so, sepals ovate to obovate, 1.5-6 mm long, 1-2 mm wide, truncate or acute to long-attenuate, nearly entire to erose, margins scarious; corolla 6-11 mm long, slightly bilabiate, deep blue to violet-blue and lighter anteriorly and within, glabrous externally, tube slender, throat 2-3 mm wide, scarcely ampliate, unlined or obscurely to distinctly lined internally with violet-blue guidelines, obscurely 2-ridged anteriorly within, palate sparingly to densely bearded with whitish-yellow or yellow eglandular hairs, lobes of the upper lip arched-projecting to spreading, lobes of the lower lip spreading; staminode 4.5-6.5 mm long from its point of attachment, included and slightly expanded distally, glabrous or more commonly bearded on the distal 0.5-1 mm with golden-yellow hairs to 0.7 mm long; longer pair of fertile stamens reaching the orifice or slightly exserted, anther-sacs (0.3)0.4-0.8 mm long, brown to dark brown, glabrous, divergent, dehiscing throughout and across the connective, becoming explanate or nearly so; style 5-7 mm long, glabrous. Capsule 3-5 mm long and frequently anthocyanic prior to dehiscence. Seeds 0.6-1 mm long, rounded to slightly angular, finely reticulate, dark brown. $\underline{n}$ = 8, 16.

Loamy to rocky loam soil in meadows in the extreme northwestern Great Plains and in high meadows, brushy slopes, and open forests in the Rocky Mountains and mountains of the Colorado Plateau, Columbia Plateau, Great Basin, and Sierra Cascade. Southern Alaska south to southern Colorado; extreme northwestern North Dakota (Burke County) west to the Pacific.

Penstemon procerus is a variable species with as many as six subspecies recognized by some authors. The species barely enters the Great Plains in the far northwest in North Dakota and Montana. Our plants are referable to subsp. procerus, which is distributed from southern Alaska to southern

Colorado and from northwestern North Dakota west to the eastern half of Washington. It is most abundant in the Rocky Mountains. Penstemon procerus subsp. procerus is distinguished from other subspecies by its poorly developed basal rosette, sepals that are usually 3-6 mm long and long-attenuate, corolla 6-11 mm long, and anther-sacs 0.4-0.8 mm long.

REPRESENTATIVE SPECIMENS:

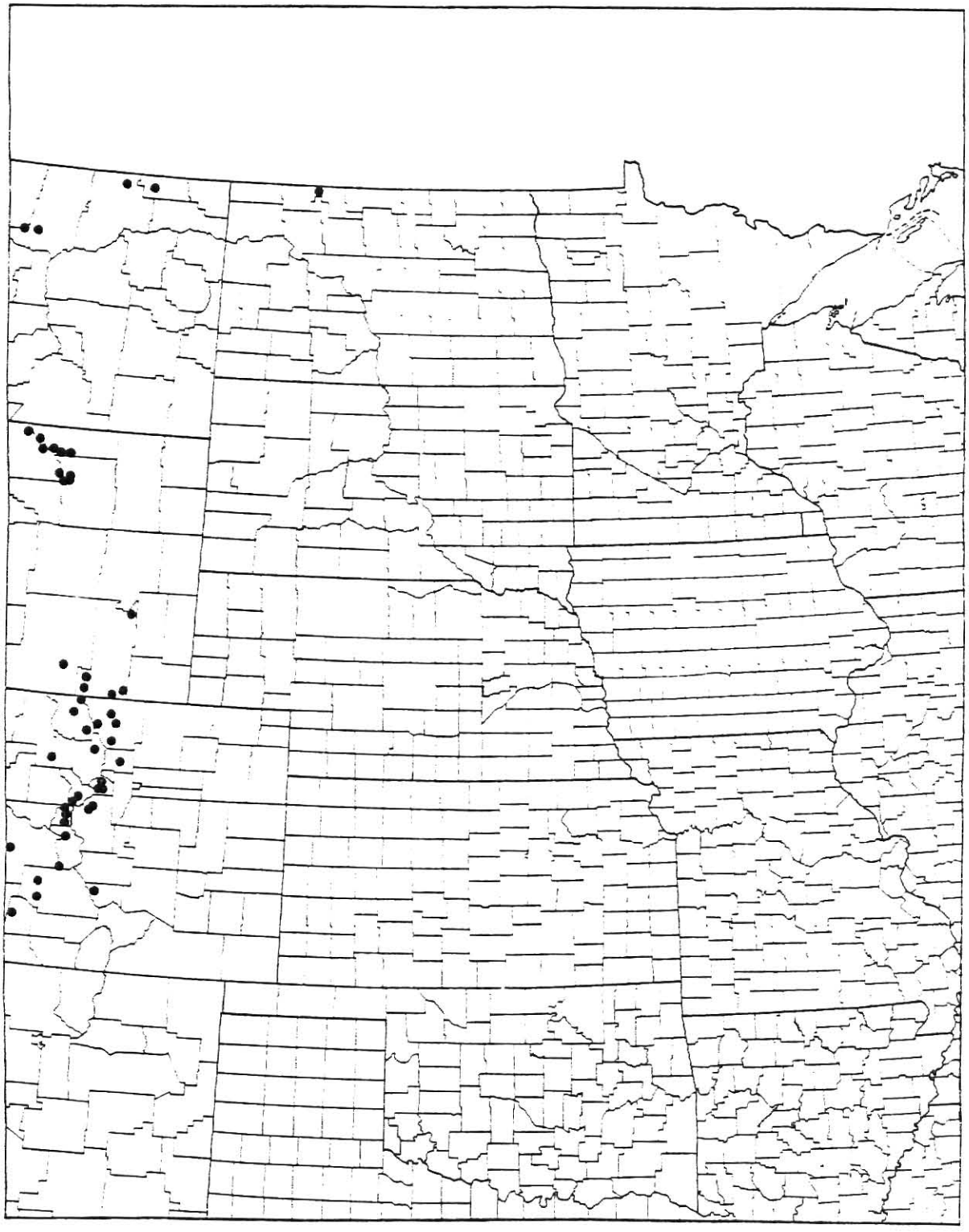
UNITED STATES:

COLORADO: Boulder Co.: Hessie, 3 July 1948, Weber 4230 (KANU). Chaffee Co.: Mt. Harvard, 1896, Clements 43 (NEB, NY). Clear Creek Co.: Vicinity of Gray's and Torrey's Peak, 13 July 1930, Keck 859 (MO, NY). Custer Co.: Westcliffe, 1896, Clements 415 (NEB). Garfield Co.: Trapper's Lake, 30 July 1930, Hermann 5498 (NY). Grand Co.: Grand Lake, 11 July 1957, Liggett 2294a (CS). Gunnison Co.: Cement Creek Valley in West Elk Mts., 12 July 1948, Langenheim 575-48 (NY). Jackson Co.: Walden, 8 July 1903, Godding 1502 (NDA, MO, NY). Lake Co.: Tennessee Pass, 24 June 1893, Saunders s.n. NEB-4, NY, SDC). Larimer Co.: 19 July 1895, Baker 8192 (NY, RM-2, NEB, MO); along Hwy 14 between Poudre Park & jct Red Feather Lakes road, 11 August 1973, Atwood & Higgins 5801 (NY, SDU). Mineral Co.: 0.75 mi above Lost Trail Campground above Rio Grande Reservoir, 20 July 1969, Nicely 46 (OKL). Moffat Co.: Blue Mt., 24 July 1947, Boyd 125 (CS). Montrose Co.: Near Mud Lake, 17 July 1939, Lancaster, Doran, & Bunderson s.n. (CS). Park Co.: Between Como & Boreas, 2 August 1895, Cowen s.n. (CS, MO). Routt Co.: E of Tonopas along Hwy 84, 26 July 1970, Clark 602 (NY). Saguache Co.: Saguache Park along Upper Saguache Creek, 8 July 1936, Rollins 1331 (MO, NY). Summit Co.: 4.5 mi N Silverthorne along Hwy 9, 27 July 1973, McCreary 585 (CS).

MONTANA: Beaverhead Co.: 14 mi NW Wisdom, 21 July 1945, Hitchcock & Muhlick 12610 (MO, RM). Carbon Co.: 25 mi SW Red Lodge in Beartooth Mts., 24 July 1955, Cronquist 7970 (KANU, RM). Deer Lodge Co.: Storm Lake in Anaconda Mts., 21 July 1946, Hitchcock & Muhlick 14846 (MO, RM). Flathead Co.: Columbia Falls, 4 June 1894, Williams s.n. (NDA, RM). Gallatin Co.: Fairy Lake at Bozeman, 31 July 1938, Cotner 257-49 (KANU, NDA, RM). Granite Co.: Near Phillipsburg, 19 July 1946, Hitchcock & Muhlick 14716 (MO, RM). Meagher Co.: 2 mi S Rimrock Ridge in western Little Belt Mts., 11 July 1945, Hitchcock & Muhlick 12210 (MO, RM). Missoula Co.: Lolo Pass, 1 September 1962, Crosswhite & Crosswhite 62-314X (CS, MO, NDA, RM). Park Co.: 1 mi E Cooke City, 18 July 1969, Seiler 687 (NDA). Phillips Co.: Midale, 30 June 1903, Umbach 214 (OKL, RM). Powell Co.: 8 mi NE Helmville, 1 July 1948, Hitchcock 17850 (RM). Ravalli Co.: 1 mi S Palisade Peak Ranger Station, 10 August 1946, Hitchcock & Muhlick 15372 (MO, RM). Stillwater Co.: N slope Mt. Haystack at head of Boulder Creek, 8 August 1945, Hitchcock & Muhlick 13446 (MO, RM).

NORTH DAKOTA: Burke Co.: N end DesLacs Game Reserve, 28 June 1971, Hegstad 8142 (NDA).

Figure 73. Great Plains Distribution of Penstemon procerus var. procerus



WYOMING: Albany Co.: Medicine Bow Mts., 30 June 1930, Solheim 223 (NDA, RM). Big Horn Co.: 10-15 mi E Kane, 23 June 1936, Williams & Williams 3069 (MO, NY, RM). Carbon Co.: Copperton, 5 August 1901, Tweedy 4303 (NY). Fremont Co.: Union Pass, 11 August 1894, Nelson 833 (MO, NY, RM-2). Johnson Co.: E slope Big Horn Mts. at headwaters of Clear Creek & Crazy Woman River, 20 July-15 August 1900, Tweedy 3415 (NY, RM). Lincoln Co.: 4 mi W Kemmerer, 15-16 June 1931, Pennell 15131 (NY, RM). Park Co.: 5 mi W Beartooth Lake, 12 July 1950, Porter 5460 (NY, OKL, RM). Sheridan Co.: 1 mi N Arrowhead Lodge along Hwy 14, 3 September 1962, Crosswhite & Crosswhite 62-397X (CS, NDA, RM-2). Sublette Co.: Saltlick Mt. NE of Kendall, 7 August 1922, Payson 2950 (MO, NY, RM); Merna, 23 July 1922, Payson & Payson 2793 (MO, NY, RM). Sweetwater Co.: Bush Ranch, 10 June 1900, Nelson 7107 (MO, NEB, NY). Teton Co.: Hoback Canyon, 23 June 1932, Williams & Pierson 701 (MO, NY, RM-2). Uinta Co.: Along Bear River at Evanston, 30 May 1932, Hanna 888 (MO). Yellowstone National Park: Wraith Falls, 7 July 1899, Nelson & Nelson 5707 (KANU, KSC, MO, NEB, NY-2, RM-2).

20. Penstemon secundiflorus Bentham in DC.

Pentstemon secundiflorus Benth. in DC., Prod. Syst. Nat. Regn. Veg. 10: 325. 1846. Type: "in montibus Scopulosis (Fremont!).", collected during Fremont's second expedition, probably in eastern Colorado, fide Pennell (1920). (Holotype: NY!).

Penstemon secundiflorus (subsp.) lavendulus Penn., Contr. U.S. Natl. Herb. 20: 358. 1920. Type: "collected on bluff on Baculite Mesa, altitude 1,530 Meters, six miles northeast of Pueblo, Pueblo County, Colorado, in flower, June 7, 1915, by F.W. Pennell (no. 5739)." (Holotype: NY; Isotypes: GH, MO, RM, US, not seen).

Penstemon versicolor Penn., Contr. U.S. Natl. Herb. 20: 358. 1920. Type: "collected on high prairie (mesa) east of Pueblo, Pueblo County, Colorado, in flower, June 5, 1915, by F.W. Pennell (no. 5732)." (Holotype: NY!; Isotypes: RM!, US).

Herbaceous perennial. Stems erect or assurgent, (1.5)2-4.5(5) dm tall, glabrous and somewhat glaucous, 1-5(8) stems arising from a thick crown or short-branched woody caudex surmounting a taproot. Leaves entire, firm, glabrous and slightly glaucous; basal leaves oblanceolate to spatulate, 2-8(10.2) cm long overall, 0.2-2.5 cm wide, acute to obtuse or occasionally mucronate, often tufted, especially in vegetative shoots, petiolate, the petioles occasionally winged; cauline leaves lanceolate to lance-ovate or ovate, (1.6)2-7.8 cm long, 0.3-2.4 cm wide, clasping to cordate-clasping,

gradually reduced upward, the upper half of the stem with leaves normally equaling or longer than the internodes. Thyrse 6-24(31) cm long, with (2) 3-10(12) verticillasters, elongate, loose to moderately compact, secund, individual cymes few to many flowered, peduncles glabrous, 2-15(21) mm long, erect or slightly spreading, pedicels glabrous, 1-4 mm long; bracts resembling the upper cauline leaves below, much-reduced above, the lower ones to 7 cm long and 2 cm wide, acuminate, bases clasping to cordate-clasping. Calyx glabrous and somewhat glaucous, sepals lance-ovate to ovate, 4-6(7) mm long, 2.5-4 mm wide, short-acuminate to acute, margins broadly scarious and usually erose, green or tinged lavender or purple; corolla 15-25 mm long, tubular-salverform, scarcely bilabiate, pink to lavender or pale to deep blue, glabrous externally, throat 4-7 mm broad, slightly ampliate, scarcely ventricose anteriorly, lined internally on the anterior and posterior surfaces with prominent reddish or reddish-purple nectar guides, the guidelines passing slightly onto the lobes of the upper and lower lips, lobes of the upper and lower lips projecting or more commonly spreading, the limb usually appearing relatively flat, palate sparsely bearded with white eglandular hairs; staminode 10-13 mm long from its point of attachment, included or reaching the orifice, rarely exserted, very broadly flattened distally, the tip abruptly recurved and bifurcate, densely bearded with pale yellow to golden-yellow hairs for 1/3 to 1/2 its length, the hairs to 2 mm long; fertile stamens included or the longer pair reaching the orifice, anther-sacs 1-1.4 mm long, purple, lined with white or tan along the sutures, externally minutely papillose, divergent, dehiscing nearly to the apices and across the connective, not becoming explanate; style 9-15 mm long, glabrous. Capsule 9-12 mm long. Seeds 2.5-3.5 mm long, angular, finely reticulate, brown to dark brown. $\underline{n} = 8$.

Rocky to gravelly slopes in prairies, foothills, mesas, and at low elevations in the Southern Rocky Mountains. Southeastern Wyoming south through central Colorado east of the continental divide to northeastern and northcentral New Mexico. In Colorado, east to Lincoln County and west to Lake County.

The corolla color of Penstemon secundiflorus is variable, a phenomenon shared by most other members of Section Coerulei. Additionally, leaf shape and corolla length may vary considerably from plant to plant in and between populations.

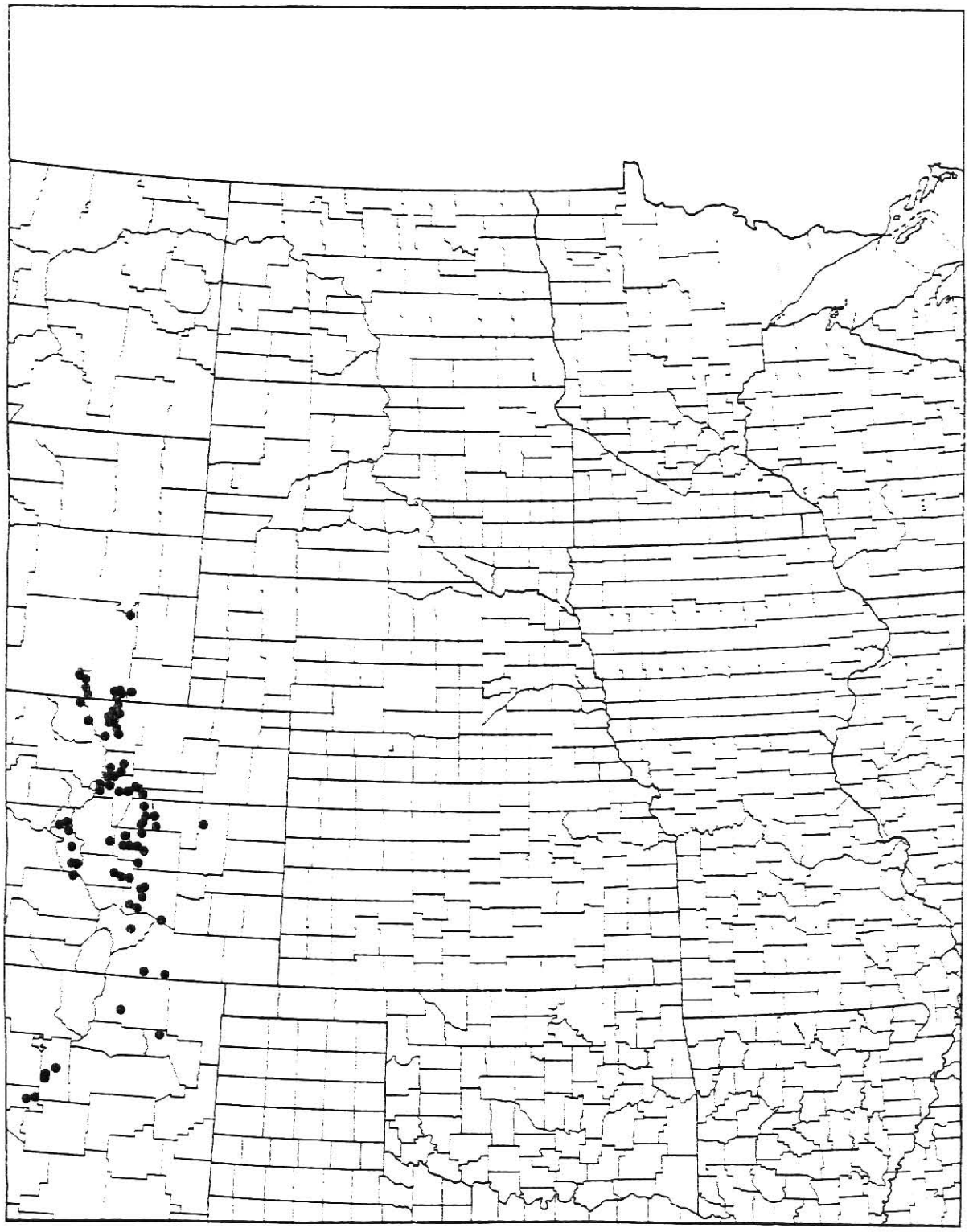
REPRESENTATIVE SPECIMENS:

UNITED STATES:

COLORADO: Arapaho Co.: 10 mi SE Denver, 3 June 1951, Slagg 15 (KSC). Boulder Co.: Sunshine Canyon NE of Boulder, 23 May 1941, Robbins 413 (NY). Chaffee Co.: Salida, 19 June 1898, Baker, Earle, & Tracy 15 (NEB, NY, RM). Clear Creek Co.: Near Empire, 13 July 1892, Patterson 254 (NY, OKL). Denver Co.: W of Valverde, 15 June 1915, Pennell 5839 (NY). Douglas Co.: 4 mi S Franktown in Castlewood State Recreation Area, 4 June 1980, Freeman 496 (KSC). Elbert Co.: 2.3 mi W Elizabeth, 4 June 1980, Freeman 498 (KSC). El Paso Co.: 0.1 mi NE of El Paso Co. Line along Hwy 115, 4 June 1980, Freeman 492 (KSC); Colorado Springs, July 1893, Saunders s.n. (NEB-3, NY); Crystal Park, 25 June 1901, Clements & Clements 83 (KANU, NEB-2, NY, RM-2). Fremont Co.: 1.4 mi W jct Hwy 120 & 50 along Hwy 120, 4 June 1980, Freeman 490 (KSC); Along Arkansas River near Portland, 21 May 1949, Weber 4679 (KANU, OKL, RM). Gilpin Co.: Rollinsville, 22 June 1914, Overholts s.n. (NY). Huerfano Co.: Walsenburg, 2 June 1931, Nelson 11524 (RM). Jackson Co.: Camp Creek, 6 July 1903, Goodding 1457 (NDA, NY, RM). Jefferson Co.: 0.25 mi NW of North Table Mesa, 29 May 1970, Arp 865 (NEB). Lake Co.: 13.5 mi S Leadville, 10 July 1930, Keck 837 (NY). Larimer Co.: 4.3 mi S Wyoming State Line along Hwy 287, 11 June 1980, Freeman 582 (KSC); 5.8 mi W Poudre Park along Hwy 14, 12 June 1980, Freeman 585 (KSC); Horsetooth Gulch, 7 June 1899, Crandall 1824 (CS, NEB, NY, RM). Las Animas Co.: 3 mi E San Francisco Creek & 8 mi NW Trinchera, 13 July 1937, Rollins 1862 (MO, NY). Lincoln Co.: 2 mi W & 15 mi N Limon, 28 June 1935, Ownbey 772 (RM). Park Co.: Lake George, 4 June 1941, Crane 16 (OKLA-2). Pueblo Co.: 3.1 mi S jct I-25 & Hwy 165 along I-25, 4 June 1980, Freeman 488 (KSC); W of Pueblo, 4 August 1915, Pennell 6315 (MO, NY, RM-2). Saguache Co.: Alder, 17 June 1935, Ramaley & Johnson 14613A (NY). Teller Co.: 10 mi N Woodland Park, 28 June 1969, Spalding 11 (CS).

NEW MEXICO: Bernalillo Co.: Cedro Canyon, 12-15 mi SE Albuquerque, 15 June 1941, Nisbet 848 (NY). Colfax Co.: Urraca Mesa on Philmont Scout Ranch near

Figure 74. Great Plains Distribution of Penstemon secundiflorus



Cimarron, 13 June 1968, Hartman 1916 (RM). Harding Co.: 10 mi N Mills, 22 May 1939, Nisbet 27 (NY). Santa Fe Co.: Santa Fe, 13 May 1897, Heller & Heiler 3520 (KSC, NEB, NY).

WYOMING: Albany Co.: Pole Mt. region, 28 June 1943, Porter 3236 (MO, NY, OKLA, RM); Sand Creek, 1 June 1900, Nelson 7028 (MO, NEB, NDA, NY, RM); 4.9 mi N of Colorado State border along Hwy 287, 11 June 1980, Freeman 578 (KSC). Laramie Co.: W of Cheyenne & 7.4 mi E Albany Co. Line along I-80, 11 June 1980, Freeman 574 (KSC).

21. Penstemon tubaeflorus Nuttall

Pentstemon tubaeflorum Nutt., Trans. Amer. Philos. Soc. 2(5): 181. 1837. Type: "In wettish prairies, from Fort Smith to Red river." (Holotype: BM; Isotype: NY!, PH).

Robust herbaceous perennial. Stems mostly erect, 2.5-8.5(10) dm tall, glabrous, stems solitary or 2(4) from a short stout herbaceous caudex surmounting a short taproot. Leaves entire to undulate or obscurely serrate, glabrous; basal leaves obovate to spatulate, 2.5-11 cm long overall, 0.6-3.8 cm wide, obtuse to rounded, tapering to a petiolar base; cauline leaves lanceolate to lance-ovate, 1.5-10(13.5) cm long, 0.4-2(3.8) cm wide, acute to obtuse, sessile to distinctly clasping, lower cauline leaves large and separated by short internodes, upper cauline leaves much reduced and separated by longer internodes, the upper half of the stem appearing somewhat naked except for the inflorescence. Thyrse 8-30(40) cm long, with 4-8(12) distinct verticillasters, individual cymes 3-9 flowered or occasionally many-flowered and extremely congested in robust plants, peduncles appressed or ascending, to 6 cm long, mostly glabrous except those immediately below the pedicels and then only sparingly glandular-pubescent; bracts greatly reduced, the lower ones to 5 cm long and 1 cm wide. Calyx glandular-pubescent, sepals lance-ovate to ovate, 2.5-5 mm long, 1.5-2.5 mm wide, acuminate to acute, entire, herbaceous or with narrowly scarious margins; corolla 15-22 mm long, barely bilabiate, funnelform and slightly decurved, glistening white with

viscid glandular hairs externally and internally, throat 4-6 mm broad, barely inflated and moderately ampliate, unlined and unpleated internally, lobes of the upper lip spreading, lobes of the lower lip projecting slightly or spreading; staminode 9-11 mm long from its point of attachment, included or reaching the orifice, flattened only slightly distally and distinctly recurved, the terminal 3-4 mm sparsely bearded with yellow or sordid-yellow hairs to 0.8 mm long; fertile stamens included or the longer pair reaching the orifice, anther-sacs 0.8-1 mm long, dark brown or black, glabrous, widely divaricate, dehiscent throughout and across the connective, becoming explanate; style 10-12 mm long, glabrous. Capsule 7-10 mm long. Seeds 1-1.3 mm long, rounded to slightly angular, finely reticulate, tan to dark brown. n = 16.

Rich loam or sandy-loam soil in a variety of habitats ranging from open prairie to deciduous woodlands. New England west to northeastern Nebraska. South to northern Mississippi, northwestern Louisiana and sporadically in eastern Texas. Flowering from May to early July.

Plants in the Midwest and Great Plains probably occupy the native range of P. tubaeflorus, whereas those found in New England and surrounding areas are undoubtedly adventive, fide Pennell (1935). These naturalized plants in New England tend to be taller and more slender than plants in the species' original range. Fernald (1949) designated the taller and slender adventive plants of New England as var. achoreus Fernald. Plants in the Great Plains and Midwest are thus referable to var. tubaeflorus.

Penstemon tubaeflorus spreads relatively easily as its success in New England readily testifies. In the Great Plains, the species shows some westward extension of its presumed original range as it is now found at numerous localities in westcentral and northcentral Kansas and eastern Nebraska where it was unknown as recently as the 1930's. Most of these new

localities are disturbed habitats such as roadsides, old fields, and pastures where it occasionally forms extensive stands.

Boivin (1967) suggested the orthography of the epithet tubaeflorus should be corrected to tubiflorus. As a consequence, the "corrected" epithet was again sporadically utilized, having been used by some earlier authors. However, in a rebuttal to Boivin's correction, Crosswhite (1969) showed the correct form was in fact tubaeflorus based on Nuttall's etymological intentions when he published the epithet.

REPRESENTATIVE SPECIMENS:

UNITED STATES:

ARKANSAS: Baxter Co.: Buffalo City, 22 May 1921, Buchholz s.n. (FHKSC). Johnson Co.: Between Oark and Catalpa, 18 August 1966, McWilliam P6690(OKL). Lonoke Co.: Carlisle, 30 May 1938, Demaree 17604 (OKL). Madison Co.: 2 mi S Brashears Corners, 19 June 1952, Moore 520762 (OKL). Poinsett Co.: Weiner, 23 June 1949, Demaree 27900 (OKL). Polk Co.: Near Old Cove, 1966, McWilliam P6676 (OKL). Pulaski Co.: N of Little Rock Air Force Base, 9 May 1965, McWilliam P6596 (OKL). Scott Co.: 1 mi from jct Nella Rd and Hwy 71 & 270 along Nella Rd, 21 May 1966, McWilliam P6673 (OKL). Washington Co.: 1 mi N of campus in Fayetteville, June 1960, Hines & McCormick 30 (KANU).

INDIANA: Daviess Co.: 4 mi N Washington, 5 June 1934, Deam 54999 (IND). Knox Co.: 4 mi S Vincennes, 8 July 1915, Deam 17074 (IND).

KANSAS: Allen Co.: N city limits of Iola, 7 June 1979, Freeman 121 (KSC). Anderson Co.: 1 mi S jct Hwy 169 & 57, 7 June 1979, Freeman 119 (KSC). Atchison Co.: 3.5 mi S & 0.5 mi W Lancaster, 21 June 1973, Brooks 4650 & Seiler (KANU). Bourbon Co.: 2 mi E Bronson, 25 June 1969, Stephens 32482 & Brooks (KANU, NY). Chase Co.: 10.8 mi S Council Grove, 6 June 1979, Freeman 113 (KSC); 15.9 mi S Council Grove, 6 June 1979, Freeman 115 (KSC). Chautauqua Co.: 3 mi E Cedarvale, 7 June 1960, Hulbert 3874 (FHKSC, KSC). Cherokee Co.: 4 mi S Galena, 24 May 1967, Stephens 11071 (KANU, NY, OKLA). Clark Co.: Englewood, 1959, annon. s.n. (KSC). Cloud Co.: 10 mi W & 1 mi N Miltonvale, 13 June 1980, Freeman 603 (KSC). Coffey Co.: 1.5 mi E Gridley, 7 June 1979, Freeman 118 (KSC). Cowley Co.: 20 mi E Arkansas City, 3 June 1967, Koch 3728 (KSC, NEB, OKLA). Crawford Co.: 5.5 mi N & 2 mi W Arma, 19 June 1970, Johnson & Bare 2614 (KANU, NDA). Douglas Co.: Baldwin City Cemetary 1 mi S Baldwin City, 25 May 1981, Freeman & Freeman 969 (KSC). Elk Co.: 1.5 mi W Grenola, 8 June 1979, Freeman 130 (KSC). Ellsworth Co.: 0.5 mi E Terra Cotta, 16 June 1975, McGregor 27032 (KANU-2). Franklin Co.: 2 mi N Homewood, 5 June 1965, Henderson 65-297 (KANU, MO). Geary Co.: Along I-70, 3.5 mi W jct I-70 & Hwy 177, 13 June 1981, Freeman & Sherwood 1003 (KSC).

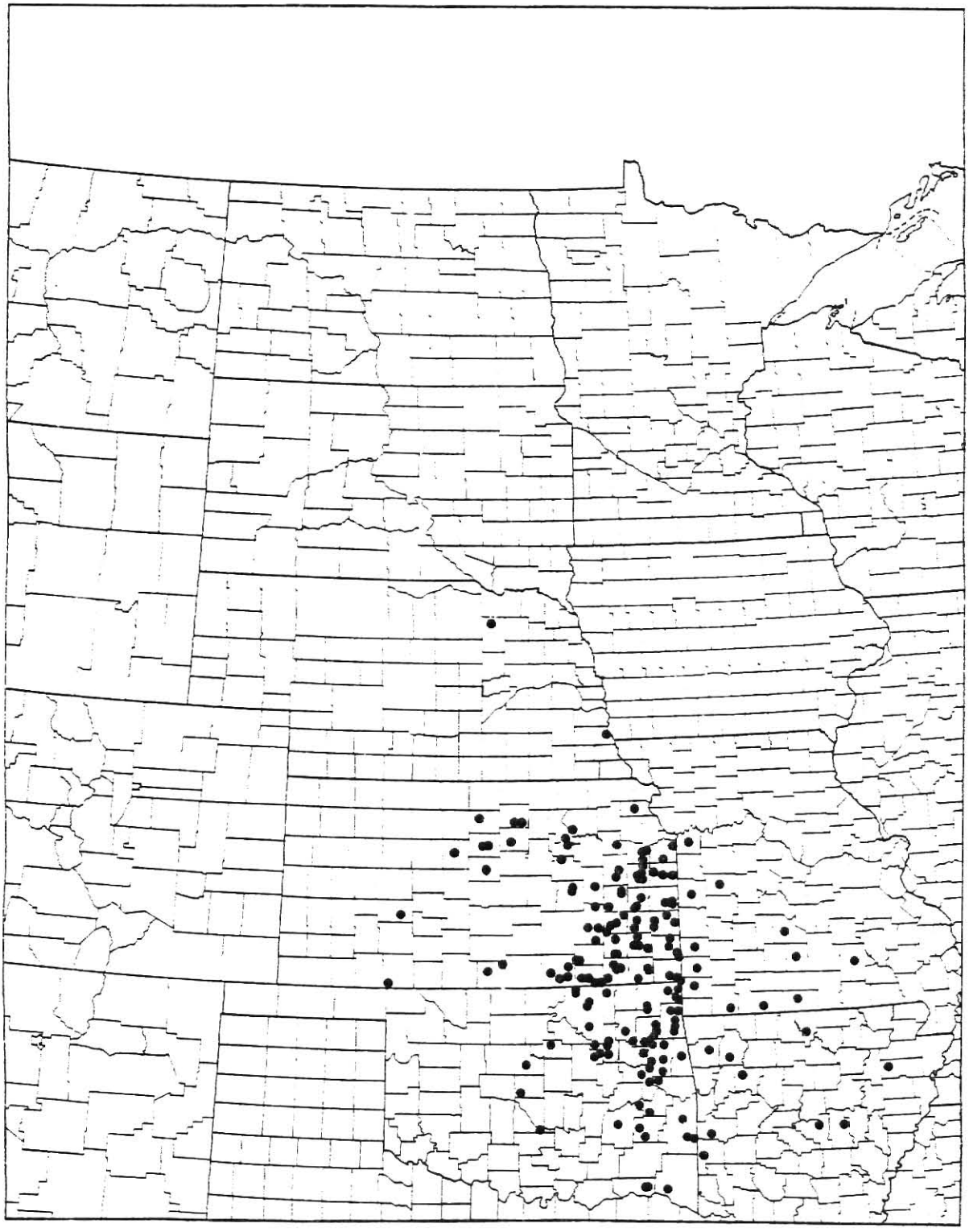
Greenwood Co.: 1.5 mi N Madison, 7 June 1979, Freeman 116 (KSC). Harper Co.: 3.5 mi E Attica, 8 June 1979, Freeman 133 (KSC). Hodgeman Co.: 1 mi S & 4.5 mi E Jetmore, 14 June 1972, Stephens 55109 (KANU-2, NDA, NY). Johnson Co.: Prairie Center, June 1890, Pellet s.n. (KSC-2, MO). Labette Co.: 3 mi NW Oswego, 9 June 1955, Lathrop & McGregor 3733 (KANU). Lincoln Co.: 2 mi W Lincoln, 10 June 1979, Freeman 151 (KSC); 3.4 mi W & 1 mi N Vesper, 31 May 1981, Freeman 992 (KSC). Linn Co.: Pleasanton, 19 June 1929, Rydberg & Imler 88 (KANU, NY). Lyon Co.: 4 mi E Emporia, 9 June 1953, McGregor 4317 (KANU). Miami Co.: Between Olathe & Pleasanton, 18 June 1929, Rydberg & Imler 21 (KANU-2, NY). Mitchell Co.: Glen Elder Reservoir, 17 June 1965, McGregor 27080 (KANU-2). Montgomery Co.: Between Caney & Havana, 1 July 1929, Rydberg & Imler 429 (KANU), KSC). Morris Co.: Kelso, 1939, Good 6 (KSC). Neosho Co.: 6 mi E Chanute, 7 June 1979, Freeman 122 (KSC). Osage Co.: 8 mi S Lyndon, 9 June 1960, Hulbert 4001 (KSC). Ottawa Co.: 3.5 mi S Minneapolis, 10 June 1979, Freeman 153 (KSC). Pottawatomie Co.: Spillway State Park along Hwy 13, 11 June 1979, Freeman 155 (KSC); Spillway State Park along Hwy 13, 6 October 1979, Freeman 322 (KSC). Riley Co.: South Pasture on Konza Prairie Research Natural Area, 13 June 1979, Freeman & Wilson 156 (KSC). Russell Co.: 4 mi N Russell, 16 June 1975, McGregor 27044 (KANU-2). Shawnee Co.: 3.1 mi W & 1.8 mi S Shawnee Heights, 20 June 1970, Magrath 5494 (KANU). Wilson Co.: 4.7 mi E Fall River, 7 June 1979. Freeman 126 (KSC). Woodson Co.: Woodson County State Lake & Park, 8 June 1976, Brooks 12105 (KANU, MO, NY).

MISSOURI: Barry Co.: Eagle Rock, 2 June 1897, Bush 137 (KSC). Barton Co.: Near Newport, 20 June 1950, Palmer 50242 (KSC). Bates Co.: 1 mi N Butler, 30 May 1980, Freeman & Wetter 463 (KSC). Henry Co.: 5 mi N Clinton, 5 June 1953, Tolstead 12827 (NEB). Jackson Co.: Sheffield, 12 June 1894, Bush 342 (NY, OKL). Jasper Co.: Neck City, 1 July 1920, Palmer 18168 (NY). Laclede Co.: Lebanon, 11 June 1923, Pennell 11646 (NY, RM). Newton Co.: 7 mi W & 2 mi S Diamond, 1 June 1969, Wilkins 155 (TTC-2). Ozark Co.: Along Hwy 5, 3 June 1937, Gates 20199 (KSC). Shannon Co.: 4 mi N Eminence, June 1941, Steyermark 28831 (NY). Taney Co.: Swan, 9 June 1899, Bush 105 (NY). Wright Co.: 2 mi SE Cedar Gap along Bryant Creek, 29 July 1937, Steyermark 23736 (NY).

NEBRASKA: Antelope Co.: 3 mi N Royal at Grove Lake Special Use Area, 8 July 1972, Wells 96 (SDU). Otoe Co.: Nebraska City, 30 June 1938, Weaver s.n. (NEB-3).

OKLAHOMA: Adair Co.: 23 mi NE Tahlequah, 12 June 1954, Wallis 1630 (OKLA). Cherokee Co.: 3 mi E & 1 mi N Ft. Gibson, 2 June 1958, Wallis 7073 (KANU, OKL). Choctaw Co.: 4.5 mi W Ft. Towson, 29 May 1961, Waterfall 16039 (OKLA). Craig Co.: 10 mi W Vinita, 5 June 1947, Waterfall 6863 (OKL, OKLA). Creek Co.: Sapulpa, 16 May 1895, Bush 1199 (KSC, MO, NY). Delaware Co.: 8 mi E Grove, 16 June 1956, Wallis 3272 (OKLA). Haskell Co.: 5 mi S Kinta, 9 June 1940, Hopkins & Bebb 5124 (OKL). Latimer Co.: 7 mi W Wilburton, 21 May 1944, Hopkins, Nelson, & Nelson 502 (OKL, RM). LeFlore Co.: Ouichita National Forest, 17 May 1936, Demaree 12757 (MO, OKL). Logan Co.: Near Guthrie, 8 July 1916, Keyser 6017 (NY, OKL). McCurtain Co.: Near Shawneetown, 28 May 1916, Houghton 3889 (MO, NY, OKL). McLain Co.: 1.5 mi E Rosedale, 2 June 1968, Massey, Massey, & Hoisington 2054 (OKL). Mayes Co.: 1 mi E Spavinaw, 14 June 1957, Wallis 4087 (OKLA). Muskogee Co.: 3 mi E Ft. Gibson, 2 May

Figure 75. Great Plains Distribution of *Penstemon tubaeflorus* var. *tubaeflorus*



1958, Wallis 7042 (KANU, OKL). Oklahoma Co.: Oklahoma City, 1945, Hyde s.n. (OKL). Osage Co.: 4.7 mi E Hominy, 18 May 1980, Freeman 393 (KSC). Ottawa Co.: 0.5 mi NE Quapaw, 12 May 1958, Wallis 7261 (KANU, OKL). Payne Co.: 5 mi N & 3 mi E Stillwater, 22 May 1970, Stanford 3671 (OKLA). Pittsburg Co.: W of McAlester, 27 May 1920, Pennell 10595 (MO, NY, OKLA). Rogers Co.: 3.5 mi W Claremore, 3 June 1955, Willson s.n. (OKL). Sequoyah Co.: 6 mi NE Gore, 31 May 1958, Wallis 7015 (KANU, OKL, OKLA). Tulsa Co.: 2 mi SE Tulsa, 9 May 1940, Hawk 8 (KSC). Wagoner Co.: Wagoner, 28 May 1920, Pennell 10610 (MO, NY). Washington Co.: 2 mi W, 2 mi N, & 1 mi W Copan, 28 May 1974, Stephens 76941 (KANU).

22. Penstemon virens Pennell in Rydb.

Pentstemon virens Pennell in Rydb., Fl. Rocky Mts. 773, 1966. 1917. Type: "Stony hillsides, foothills north of Morrison, Colo., 1915, Pennell 5821" (Holotype: NY; Isotypes: COLO, GH, RM, US, not seen).

Caespitose herbaceous perennial. Stems erect or assurgent, 1-4 dm tall, slender, spreading to retrorsely puberulent in lines below and glandular-pubescent near the inflorescence, arising from a branching suffrutescent caudex. Leaves entire to serrulate or denticulate, glabrous and bright green; basal leaves lanceolate to oblanceolate or spatulate, 2-10.2 cm long overall, 0.4-1.5 cm wide, petiolate, tufted; cauline leaves lanceolate to lance-ovate, 1.8-5(7) cm long, 0.3-1.4 cm wide, acuminate to acute, sessile or the upper clasping. Thyrse 5-18 cm long, with 3-6(8) distinct or indistinct verticillasters, individual cymes 2-5 flowered, peduncles puberulent to glandular-pubescent, erect, green or tinged deep-purple, to 2 cm long, pedicels glandular-pubescent, 0.5-2.5 mm long, often deep-purple; bracts somewhat prominent below and much reduced above, the lower ones to 4 cm long and 1 cm wide. Calyx glandular-pubescent, sepals lance-ovate to ovate, 2-4.5 mm long, 1.5-2.5 mm wide, acuminate to acute, with margins narrowly scarious near the base, usually tinged reddish-purple especially near the tip; corolla 10-16(18) mm long, bilabiate, pale to dark blue tinged violet, typically somewhat lighter anteriorly and near the tube, pale internally, glandular-pubescent

externally, throat 3-5 mm broad, slightly inflated and moderately ampliate, flattened slightly, lined internally with reddish-purple or bluish-purple guidelines, the guidelines reaching the orifice on the anterior surface, weakly 2-ridged within anteriorly, palate moderately bearded with whitish eglandular hairs, lobes of the upper lip spreading to somewhat recurved, lobes of the lower lip spreading and exceeding the upper lip; staminode 8-10 mm long from its point of attachment, included or reaching the orifice, barely if at all flattened distally, the tip feebly recurved, the distal 4-5 mm pubescent, densely bearded at the tip with stiff golden-yellow hairs to 1.3 mm long, much more sparingly bearded away from the tip; fertile stamens included, anther-sacs 0.6-0.8 mm long, deep-purple, the entire external surface minutely papillose, divaricate, dehiscent nearly to the apices and not across the connective, not becoming explanate; style 8-11 mm long, glabrous. Capsule 5-7 mm long. Seeds 1-1.3 mm long, rounded to slightly angular, finely reticulate, dark brown. n = 8.

Gravelly or rocky, frequently granitic, soil on wooded or brushy slopes in the foothills and eastern slope of the Southern Rocky Mts. Northcentral Wyoming in the Big Horn Mountains south to Las Animas County, Colorado. Flowering from late May to early August.

P. virens is frequently encountered in the foothills of the Southern Rockies in central Colorado. There, it frequently forms extensive mats and is often found in habitats with P. secundiflorus.

REPRESENTATIVE SPECIMENS:

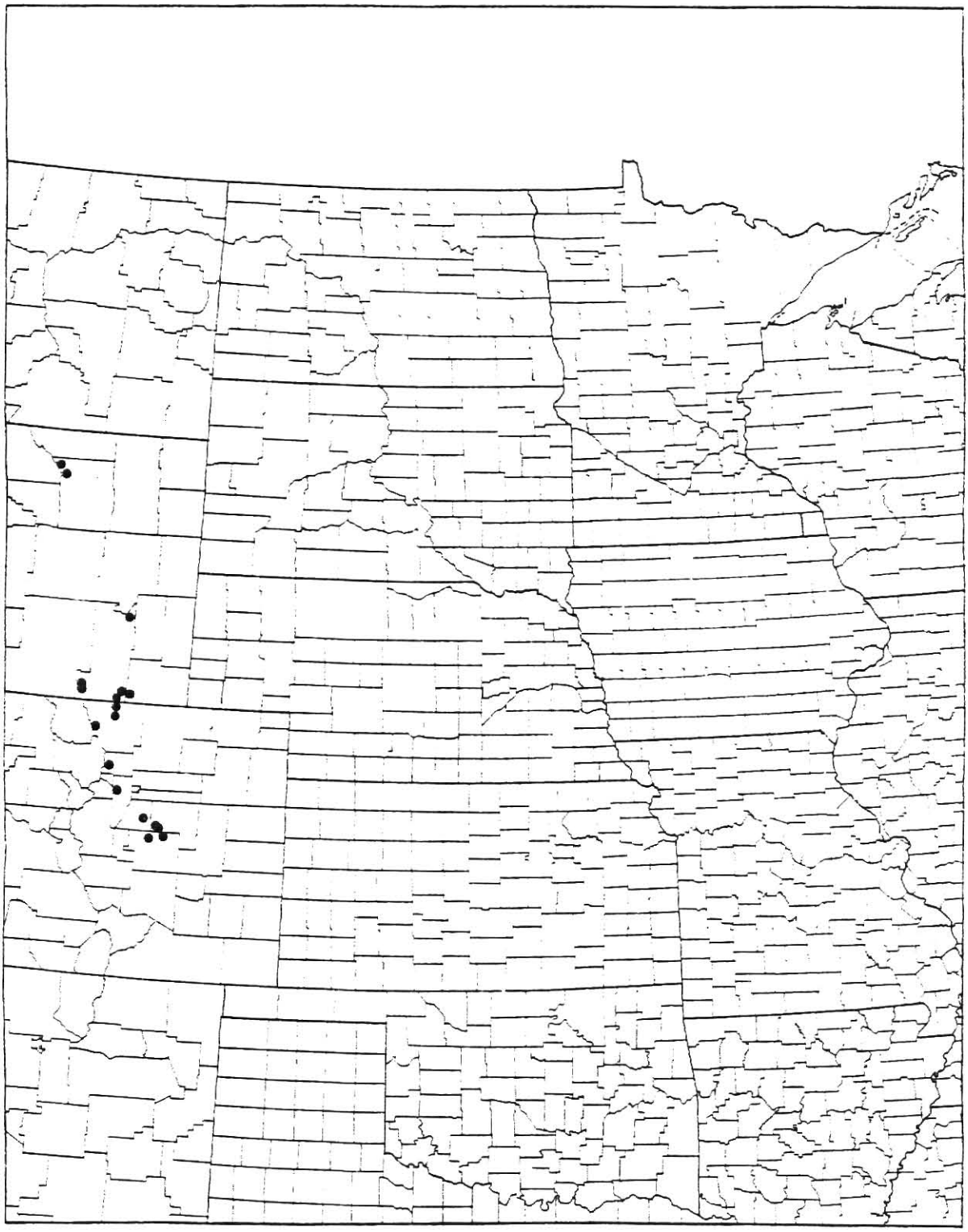
UNITED STATES:

COLORADO: Boulder Co.: 8 mi N Nederland, 6 August 1960, Crosswhite 1296 (NDA). Douglas Co.: 4 mi S Franktown in Castlewood State Recreation Area, 4 June 1980, Freeman 497 (KSC). Elbert Co.: 2.3 mi W Elizabeth, 4 June 1980,

Freeman 499 (KSC). El Paso Co.: 3 mi W Black Forest, 4 June 1980, Freeman 495 (KSC). Jefferson Co.: Chief Hosa Campground 20 mi W Denver, 26 July 1980, Freeman 737 (KSC). Larimer Co.: 4.3 mi S Wyoming State border at Virginia Dale, 11 June 1980, Freeman 583 (KSC); 5.8 mi W Poudre Park, 13 June 1980, Freeman 586 (KSC).

WYOMING: Albany Co.: 4.9 mi N Colorado State border along Hwy 287, 11 June 1980, Freeman 579 (KSC). Johnson Co.: 1 mi S & 8 mi W Buffalo, 27 June 1970, Stephens 40812 & Brooks (KANU). Laramie Co.: 7.4 mi E Albany Co. Line along I-80, 11 June 1980, Freeman 575 (KSC).

Figure 76. Great Plains Distribution of Penstemon virens



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A BIOSYSTEMATIC STUDY OF THE GENUS PENSTEMON (SCROPHULARIACEAE) IN THE GREAT PLAINS

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B.S., Wartburg College, 1978

AN ABSTRACT OF A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Division of Biology

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1981

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ABSTRACT

Twenty-two species of Penstemon are known to occur in the Great Plains of North America. In this physiographic region, the genus displays an array of sectional and subsectional diversity as representatives of peripheral floras are found along with Plains endemics. This investigation presents and integrates data obtained from cytology, palynology, chromatography, and gross morphology, to yield a taxonomic treatment of the Great Plains members of the genus. First reported chromosome counts for P. albidus, P. angustifolius var. angustifolius, P. auriberbis, P. buckleyi, P. cobaea var. purpureus, P. fendleri, P. haydeni, and P. oklahomensis indicate these taxa to be $n = 8$ or $2n = 16$. Counts for other taxa are consistent with those previously reported. Phenolic compound profiles obtained through 2-dimensional chromatography provide support for sectional boundaries previously inferred from morphological studies, and they provide some insight into species relationships in the taxa examined. Palynological studies seem to indicate the genus is stenopalynous. Pollen of those taxa examined is oblate spheroidal to prolate spheroidal in equatorial view and spherical to angular in polar view. Grains are tricolpate with variable endoapertures and exine sculpturing typically varies from microperforate to perforate. A key to the taxa is provided and each taxon is treated with a description, nomenclatural alignment, and discussion of ecology and distribution within the study area.