Revision of the genus Petalostemon (Leguminosae)

Don Kimberly Wemple
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Iowa State University of Science and Technology
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REVISION OF THE GENUS PETALOSTEMON
(LEGUMINOSAE)

by

Don Kimberly Wemple

A Dissertation Submitted to the
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Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

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Dean of Graduate College

Iowa State University
Of Science and Technology
Ames, Iowa

1965
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INTRODUCTION

Petalostemon as herein delimited comprises 29 species of North American papilionoid legumes of the tribe Psoraleae (Rydberg 1928a, 1928b; Isely 1958, 1962; Lersten and Wemple to be published). The genus is distinguished from other members of the tribe by the possession of both of two basic characters: 1.) there are only five stamens; 2.) the four petals other than the standard are inserted at the apex of the staminal tube and alternate with the filaments, while the standard is inserted at the floral base.

The original objective of this investigation was the delimitation of the taxa within Petalostemon. However, it was soon evident that a reconsideration of the generic limits of Petalostemon was desirable if not essential. A considerable proportion of the research efforts herein reported were, therefore, directed towards the latter end; particularly the interrelationships of Petalostemon and Dalea. Both phases of these investigations are presented in this paper.

1The most recent worldwide treatment of the Leguminosae (Hutchinson 1964) divides the Psoraleae into two tribes, Daleae and Psoralieae. Petalostemon and its close relative Dalea are placed in the former tribe. Evidence contrary to Hutchinson's division is presented by Lersten and Wemple (to be published).
METHODS AND MATERIALS

Field collections and observations

Field studies of *Petalostemon* were conducted during the growing seasons 1961-1964 inclusive. All species of the genus were observed in situ except those few indigenous to the Great Basin and the Pacific Northwest. In addition to insight into the distribution, breeding mechanisms and ecological relationships of the species, living material was collected and placed in the greenhouse for additional study.

Greenhouse cultivation

Plants were grown from both rootstocks and seeds. The rootstocks were collected in the field; after removal of the tops they were transported to the greenhouse in polyethylene bags. The potting medium was Iowa prairie soil with approximately 25% coarse river sand added to facilitate drainage.

Following threshing and scarification, seeds were germinated on moistened blotter paper in Petri dishes placed in a 20° constant temperature chamber in the Iowa State University Seed Laboratory. When seedlings were 1--2 cm long they were transferred to five inch pots, approximately five seedlings per pot. No further transfers were necessary. Voucher specimens of all plants cultured were deposited in ISC.
Hybridization studies

A program of controlled cross pollinations in the greenhouse was initiated in an attempt to elucidate genetic relationships within the genus. Since most species of Petalostemon are obligately emtomophilous, there is no self fertilization in an insect free greenhouse; therefore, the common practices of "bagging" and emasculation are unnecessary. Pollination was carried out by using a stamen as a pollen applicator -- merely touching it to the stigmas of the female parent. Complete pollination of a spike usually took about two weeks because the flowers open sequentially.

In the field, fruits are presumably shaken from the rachis by wind and rain action. Lacking this dispersal force in the greenhouse, the fruits remain attached to the rachis and can conveniently be collected when the seeds of a whole spike mature. The resulting seeds were germinated in the same manner as those collected in the field.

Cytological studies and pollen analysis

Cytological material was obtained in part from germinated seeds. Root tips were cut off when they attained a length of 1--2 cm and immediately placed in a one-fourth strength nutrient solution (Hoagland and Arnon 1950) with 0.02 percent actidione, a mitotic inhibitor. After 7--8 hours treatment they were fixed in 3:1 alcohol-acetic acid for twenty four hours. The root tips were then hydrolyzed for 8--9 minutes in
1 Normal HCl at 60° and placed in Feulgen stain for 45--70 minutes. Following "squashing," the slides were made permanent by the liquid CO₂ freezing technique (Bowen 1956).

Meiotic counts were obtained from buds collected in the field as well as the greenhouse. Fixation was by 3:1 alcohol-acetic acid and the preferred stain was propiocarmine. All cytological illustrations were made using the Zeiss Drawing Attachment. Voucher specimens of all plants from which successful counts were obtained were deposited in ISC.

Pollen was collected from living plants, both in the field and the greenhouse, as well as from herbarium specimens. Semi-permanent slides were prepared using lactophenol-cotton blue (Sass 1958; Stone 1963) as a combination stain and mounting medium. Fresh pollen can be studied within a few hours; samples from herbarium specimens require 24 hours to allow the stain to penetrate and inflate the dehydrated grains. Length, width and stainability were recorded. The latter characteristic is an approximation of viability of fresh pollen. From each sample ten lengths and widths were measured using an ocular micrometer at 430x magnification. Each species was sampled at least twice. An average length and width was calculated for each pollen sample as well as an average for all samples from a given species. Range, arithmetic mean and standard deviation were calculated. A record was kept of the percentage of blue-staining grains in each sample.
**Herbarium study**

Over 4,000 herbarium specimens were studied during the course of this investigation. I should like to express my appreciation to the curators of the following institutions who made them available. Those herbaria denoted by an asterisk supplied type material only. Abbreviations used for all herbaria cited in this paper are those of Lanjouw and Stafleu (1964).

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<td>*P</td>
<td>Muséum National d'Histoire Naturelle Laboratoire de Phanérogame (France)</td>
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Synonyms for each species are listed in the taxonomic treatment. The procedure of Isely (1962) is used to indicate the basis for inclusion of each name as follows:

1. Type specimen or photograph of same examined.
2. Original description examined.
3. Name utilization follows that of another author who has examined an original specimen or type.
4. Name utilization follows that currently accepted; typification not verified.

Multiple designations, e.g. (1)(2), indicate congruity between the sources of information indicated. The appropriate number(s) follows the citation of each name.

The distributional maps are based on specimens studied by the author. The specimens are cited in the appendix. Only representative specimens (one from each county) of the wider ranging or more common species are cited. Those of the less frequently collected or local species are all cited.
Clearing techniques

The vascular anatomy of the flowers of *Petalostemon* and related genera was studied by means of clearings (Brady, Wemple and Lersten 1964). Herbarium specimens were the major source of material, supplemented by fresh flowers killed and fixed in FAA or GRAF III (Sass 1958). They were cleared in 5% NaOH and chloral hydrate, stained with safranin and mounted in Piccolyte. Clearing without staining, using Hoyer's Solution (Anderson 1954) was found to be a valuable and timesaving technique. Permanent slides were made directly from dissected specimens, softened in a wetting agent (Pohl 1954), and without resorting to tedious dehydration, mounted in Hoyer's Solution.

Certain aspects of anatomy not clearly observable by clearing techniques were studied by means of microtome sections. These were prepared and stained by conventional methods (Sass 1958).
The first specimen of Petalostemon returned to the Old World was collected by Walter. A description was included in his *Flora Caroliniana* (1788) as "Anonymos Kuhnia affinis. pinnat." It is the plant we now know as Petalostemon caroliniense. The following year (1789), Lamarck provided Walter's specimen with a conventional binomial, *Kuhnistera caroliniensis*. Both Walter and Lamarck considered the plant a composite.

In the same year as Lamarck's publication, A. de Jussieu, in *Genera Plantarum* (1789) seems to have included the Walter species within Dalea -- a resurrection of the name used by Linnaeus in the first edition of *Genera Plantarum* (1737) but subsequently dropped. Although not mentioning the Walter specimen by name, Jussieu (p. 355) follows the description of Dalea with:

Speciem habeo siccam, habitu flosculosam Eupatorii instar sed Daleae ferè congenerem cui calix communis polyphyllus inbricatus multiflorus, calix proprius inferus 5-partitus plamosus, petala 5 subaequalia unguiculata, caetera similia.

Ten years later (1799a), "Tableau du regne Vegetal, selon la methode de Jussieu" by E. P. Ventenat appeared. He corroborated the fact that Jussieu was indeed speaking of Walter's plant (p. 395).
La plante dont Jussieu donne une courte description après avoir exposé les caractères du Dalea, est, selon Michaux, L'Anonymos de Walter.

Ventenat then clearly set forth the differences between this specimen and other species of Dalea concluding by maintaining the Lamarck genus Kuhnlstera as separate from Dalea. He included under the latter genus both 5 and 10 staminate species, thus amending Jussieu's original concept of the genus. Although Ventenat cited no species per se, his description of a representative Dalea is clearly that of D. purpurea, a species that he eventually named in 1800.

Ventenat's previously stated views were expanded in Dissertation sur le Genre Dalea (1799b), recognizing as distinct genera, Dalea and Kuhnlstera, but again presenting no species names. The following year (1800) his description of Dalea purpurea appeared. This species, now Petalostemon purpureum (Vent.) Rydb., was described as one of a number of "rare and unusual" plants growing in the gardens of J. M. Cels in Paris. The seeds of this species were apparently collected in Illinois by Michaux several years before and passed into the hands of J. M. Cels.

The year 1803 saw the publication of Michaux' Flora Boreali-Americana. In it, Kuhnlstera was considered akin to the pentastaminate members of Dalea and both were included in the new genus Petalostemum. Michaux, or L. C. Richard who wrote the diagnoses for the Flora (Barneby 1965), chose to
ignore Lamarck's specific epithet (caroliniensis) for Walter's specimen, although Lamarck's generic name, Kuhnrietera, was cited in synonymy. The species was called Petalostemum corymbosum. Other species named were P. candidum, P. carneum and P. violaceum. The latter falls within the circumscription of Dalea purpurea, but Ventenat was not cited.

Prior to the publication of the Flora Boreali-Americana, Willdenow's third volume of Species Plantarum was issued (1802, according to Schubert 1942). Willdenow recognized both five and ten staminate species in the genus Dalea, enumerating three with five stamens, D. candida (citing P. oandldum Michx.), D. violacea (citing P. violaceum Michx.) and D. kuhnrietera (citing Lamarck as well as Walter).

Poiret (1804) included all the aforementioned species with the ten-staminate Daleas in the genus Psoralea, a treatment similar to the later works of Linnaeus. Subsequently, in Dictionnaire des Sciences Naturelles (1818) he again rejected the idea of separate generic ranking for the pentastamine species (p. 459).

Le genre Petalostemum de Michaux ne peut être séparé des dalea, quoique ses fleurs ne renferment souvent que cinq étamines, seul caractère qui le distingue. He recognized D. purpurea, D. carnea, D. candida and D. corymbosa.

In summary, as of 1818, the species of the taxon herein
called Petalostemon, had been placed under four different generic names, Kuhnistera, Petalostemon, Dalea and Psoralea. No subsequent authors have included the species as a part of Psoralea; that genus was later more precisely defined to exclude those species possessing only one flower per subtending bract, pinnate leaves composed of more than three leaflets and petals inserted anywhere other than at the floral base. With the exception of Shinners (1949), no authors have included the species of Petalostemon within Dalea (although Barneby (1965) strongly argues for their merger). Rather, Dalea has been limited to species possessing (7) 9–10 stamens, a more or less papilionoid corolla and petals inserted either at the floral base or part way up on the androecial tube — a definition more in line with that of Michaux than that of Jussieu. Barneby (1965), in fact, recommended conservation of Dalea, sensu L. C. Richard in Michx. over other definitions of the genus. Petalostemon was adopted for all the penta-staminate species by most authors, e.g. Pursh (1814), Candolle (1825), Don (1832), Torrey and Gray (1838) and Endlicher (1840) among classical treatments. Others maintained both Petalostemon and Kuhnistera as separate genera, e.g. Bartling (1830) and Lindley (1853) -- a practice continued into the twentieth century by Small (1903, 1933), Rydberg (1919–1920) and most recently, Hutchinson (1964).

Kuntze (1891) revived Kuhnistera in place of Petalostemon based on its prior publication, and made new combinations for
the nineteen species known at that time. As one of the adherents to the American code which adopted Kuhnistera, A. A. Heller published "Notes on Kuhnistera" (1896), a definitive work at that time. It included twenty two species with critical synonymy and nomenclatural notes. The next complete treatment of the genus was by Rydberg (1919-1920), who, as above indicated, separated Petalostemon from Kuhnistera including forty two species in the former and two in the latter. This was the last complete summary of the genus to this date although Isely (1958) in a generic summary of the tribe Psoraleae reconsidered the problems in the delimitation of the genus. Since the conservation of Petalostemon over Kuhnistera (Briquet 1912), all authors have employed Petalostemon, at least for the species other than P. caroliniense and P. adenopodum. Kuhnistera has been maintained as a separate genus by Rydberg (1919-1920), Small (1903, 1933) and Hutchinson (1964) as previously stated. Isely (1958) as well as authors of two recent Carolina floras, Wilbur (1963) and Radford, Ahles and Bell (1964), unite all species under Petalostemon.

There has been controversy over alternative spellings of the noun Petalostemon as well as interpretation of gender (masculine or neuter). Michaux originally used the spelling Petalostemum in conjunction with neuter specific epithets. Most authors since the original publication have used Petalostemon, some considering it masculine, others neuter.
Rydberg (1919-1920) comments in a footnote, "Originally published as *Petalostemum*, but incorrect as *ｼﾇﾑﾞ* is masculine and has a long 0 in the final syllable." Shinners (1949, p. 81) employed Michaux's original spelling and adds a footnote:

In the list of *nomina conservanda* making up Appendix III of the *International Rules of Botanical Nomenclature* (cf. Brittonia 6: 67, 1947), this is altered to the etymologically proper form of *Petalostemon* -- in flagrant violation of Article 59 of the same Rules, expressly forbidding such corrections!

I have herein adopted both the spelling and gender indicated by the *Nomina Generica Conservanda* in the citation of the generic type, *Petalostemon candidum*. 
DELIMITATION AND VALIDITY OF PETALOSTEMON

As pointed out by Issely (1958), the validity of the genus Petalostemon rests on an understanding of the floral morphology of both Petalostemon and Dalea. Since no acceptable morphological interpretation has yet been made, taxonomic viewpoints have been less than unanimous. Michaux (1803) almost certainly interpreted the petals as staminodes, hence the implication of his name, "petal-stamen." On the basis of an anatomical study, Moore (1936) offered evidence supporting the hypothesis that all five of the Petalostemon "petals" are staminodes. His conclusions were based on the vascular pattern of the floral receptacle, as reconstructed from serial microtome sections of Petalostemon candidum. He also cleared flowers of this species by boiling them in concentrated lactic acid. Issely (1958, 1962) accepted Moore's interpretation with some reservations as did Turner (1959). Gleason (1952) and Porter (1957), on the other hand, accepted only the four apical appendages as staminodes and interpreted the standard as the only remnant of the true corolla. Neither Gleason nor Porter referred to Moore's work. These various floral interpretations have obscured the true relationship of Petalostemon to the large genus Dalea, to which it is certainly closely allied.

Petalostemon can usually be distinguished from Dalea by two basic characters: 1.) there are only five stamens; 2.)
the four petals other than the standard are inserted at the apex of the staminal tube alternating with the filaments (Fig. 1).

Most species of *Dalea* have nine or ten stamens and nearly all have a distinctly papilionoid corolla. In some species all five petals are inserted on the hypanthium below the staminal tube. More commonly the wing and keel petals are attached at some point on the staminal tube (Fig. 2). In some species, however, the four anterior petals are inserted almost at the apex of the staminal tube, approximating, but not quite attaining, the *Petalostemon* condition. This is found in Rydberg's segregate genus *Thornbera* (Rydberg 1919-1920), a part of *Dalea* in the broad sense. In gross appearance certain species of *Dalea* and *Petalostemon* are easily confused. An additional taxonomic separation of the two genera has been based on petal claw length (Rydberg 1919-1920; Wiggins 1940), however, Shinners (1949) demonstrated that this character was not consistent in all species and partially on this basis included the Texas species of *Petalostemon* in *Dalea*.

The question of whether the petals are true petals or staminodes is a critical one in understanding the relationship between *Dalea* and *Petalostemon* and a reappraisal of certain aspects of floral morphology of *Petalostemon* was undertaken with special regard to the questions of petal origin, petal insertion and stamen number.
Fig. 1. *Petalostemon pulcherrimum*. Above, entire flower with subtending bract. Below, flower with calyx removed. O, ovary; S, staminal tube; A, "apron".

Fig. 2. *Dalesa aurea*. Above, entire flower. Below, flower with calyx removed, keel petals spread and one wing petal disarticulated from its socket on the staminal tube. The standard is elevated and the carpel raised to show their relationship.
The nature of the corolla

Clearings, whole mounts and serial sections of the apex of the staminal tube of Petalostemon show clearly that each apical petal has its own articulation socket (Fig. 3, 4). A socket is found at the base of the standard also (Fig. 5, 6). The claw of each petal tapers down to a blunt point and inserts into the flanged socket of the tube. The claw is tenuously attached by the vascular bundle and one or two layers of small cells. The entire structure is apparently an adaptation for petal abscission. Similar structures are not uncommon among other angiosperms (Pfeiffer 1928; Sharsmith 1961).

The filaments arise smoothly from the staminal tube with no indication of even a constriction, much less a specialized socket (Fig. 3). If one is to assume that the petals are in reality staminodes, it is then necessary to presume modifications resulting not only in filament flattening but also in socket formation at the base of the sterile stamens.

The apical petals of Petalostemon are frequently described as bilaterally symmetrical. They are not. This is particularly evident in P. pulcherrimum (Fig. 13). The laminae of the lateral petals are quite asymmetric and the claws are offset to one side. The venation pattern also varies. While one of the side veins extends into the major part of the lamina in the lateral petals, it is the center vein that supplies most of the lamina in the medial petals. Although the
Fig. 3. Tangential section of the apex of the staminal tube of *Petalostemon occidentale*. A petal claw in its socket is central, flanked by filaments which are continuous with the tube.

Fig. 4. Clearing of the apex of the staminal tube of *P. candidum*. The petal claw has been removed but the socket is clearly seen flanked by two filaments.

Fig. 5. Clearing of the dorsal portion of carpel and apron with attached standard claw of *P. pulcherrimum*. Arrow indicates socket and union of claw and apron.

Fig. 6. Transverse section through the base of the flower of *P. occidentale*. The carpel is surrounded by the staminal tube below and the apron above. The attachment of the standard claw is indicated by the arrow.

Fig. 7. Clearing of the floral base of *P. occidentale* showing the pedicel traces radiating out as calyx bundles (C), and the gynoecial bundles (G), coalescing into the discontinuity plate.

Fig. 8, 9. Clearings of the floral base of *P. tenuifolium*. Fig. 8 with the discontinuity plate in focus and Fig. 9 with the plate below the field of focus but with the androecial bundles sharply in focus. A, androecial bundles; S, standard bundle.

Fig. 10. Radial section of the staminal tube of *Dalea aurea* showing a petal claw in a socket on the side of the tube.

Fig. 11. Clearing of the staminal tube apex of *Petalostemon emarginatum*. The upper arrow indicates the apex of the tube, the lower, the position of the socket.

Fig. 12. Clearing of the staminal tube of *Dalea gigantea*. The arrow indicates the position of a socket.
petals are not papilionoid-shaped wings and keels, there is a dimorphism between lateral and medial petals that is consistent within a species.

At the base of the flower, in the area of the receptacle, is the "discontinuity plate" (Brady, Wemple & Lersten 1964). As in the species of Dalea examined, the plate is the result of a merging of the gynoecial traces at the base of the carpel and the horizontal proliferation of the associated tracheoidal cells (Fig. 7, 8). The xylem of the carpel is not connected to the xylem of the pedicel. Another xylem discontinuity is found between the petal and stamen bundles and the rest of the floral vasculature. The bundles from the apical petals and stamens pass down the tube but the xylem ends abruptly just short of, but lateral to, the discontinuity plate. The xylem of the standard bundle has a similar ending (Fig. 8, 9).

These discontinuities are consistent and predictable in all species of Petalostemon and Dalea examined and differ among species only in size and shape of the discontinuity plate. In all cases the plate is mature prior to anthesis and shows little or no further development between anthesis and mature fruit. Discontinuities and discontinuity plates appear to be definitive floral characteristics of all members of the tribe Psoraleae (Lersten & Wemple to be published).

Three theories concerning the nature of the corolla in Petalostemon may be considered:
1. a. Five stamens are modified to staminodes.
   b. The standard is also a staminode.
   c. There is a complete loss of all petals as well as their traces in the receptacle.

2. a. Four stamens are modified to staminodes.
   b. The standard is the only remnant of the corolla.
   c. There is a complete loss of wing and keel petals as well as their traces in the receptacle.

3. a. The four petals attached to the apex of the androecial tube are true petals.
   b. The standard is an unmodified papilionoid standard.
   c. There is a complete loss of one whorl of stamens and their traces.

The first alternative is unlikely because the standard has the shape and insertion typical of that in most papilionoid flowers and in addition encloses the other petals and stamens in the bud, another characteristic of a "good" standard. A further argument against this theory is that to suggest that the standard is a staminode would indicate a derivation from a diadelphous condition. Dalea, admittedly has a true corolla and is monadelphous with either nine or ten stamens. If the hypothesis of staminodial origin is to be considered in Petalostemon, it is more plausible for the apical structures than for the standard.

The second theory, that only the apical petals are staminodes, also seems unlikely because of the possession by the petals (but not the filaments) of articulation sockets.
Similar sockets are found in those species of *Dalea* in which the wing and keel petals are inserted on the staminal tube (Fig. 10, 12). There is also a socket at the base of the standard in *Petalostemon* indicating homology with the apical petals. In some species of *Petalostemon* there is dimorphism between the lateral and medial apical petals; this is additional evidence for the rejection of the second hypothesis.

Moore's (1936) interpretation of the flower of *Petalostemon* seems to lack validity; for example, his statement (p. 287), "The sterile members of the androecium alternate with the calyx lobes and thus seem to be the outer members of the stamen whorl," is perplexing. From his preceding discussion it would seem that petal traces and the traces of the inner whorl of stamens would alternate with calyx lobe traces. The outer whorl of stamen traces would be on the same radii as the calyx lobe traces. In response to a second point, "The stamen traces are cast off in two alternating sets," it is apparent from whole mount clearings and serial sections that Moore could not possibly have seen these traces departing from the stele because the xylem is completely discontinuous in this area. In serial sections through the *Petalostemon* discontinuity area, interpretation of vascular structure is almost impossible. Without knowledge gained from whole flower clearing one would most certainly have been inclined to disregard these sections as artifacts. It is possible that Moore did just that and then, relying on his observations in other
papilionoid genera, extrapolated to the vascular anatomy of Petalostemon, fitting them into his preconceived idea of loss of petals and staminodial development in Petalostemon.

Barneby (pers. comm. 1964) has pointed out that if the petal claws in Dalea and Petalostemon are really fused to the androecial tube then articulation sockets have developed in the claws themselves — an "unprecedented development in the legumes." An alternative explanation is that the part of the tube below the petal sockets is in reality an asymmetrically developed hypanthial ring. When the petals are all inserted at the base of the calyx, as they are in many species of Dalea, they seem clearly to arise from an hypanthium. When wing and keel petals are inserted a short way up the tube it is not difficult to imagine that one side of the ring (the side opposite the standard) is extended upward. When the extreme stage is reached, as in Petalostemon, in which the petals are inserted a great distance from the floral base, the hypothesis of hypanthial extension possibly seems fantastic but every stage between the two extremes is evident. Further support for the hypothesis of hypanthial extension is that in all species of Petalostemon examined, the standard does not insert at the very base of the flower but arises from a socket on the "apron" (Fig. 1, A). The tissue of the apron is continuous with that of the staminal tube, and it could possibly represent the dorsal development of the asymmetrical hypanthial ring and the androecial tube the ventral.
A condition of petal insertion similar to that found in Petalostemon has been reported in Hesperolinon (Linaceae). Sharsmith (1961), in her monograph of the genus, also invoked the hypothesis of hypanthial extension.

Variations in petal placement and stamen number

Dalea has traditionally been separated from Petalostemon because it usually has nine or ten stamens; the petals are not inserted at the apex of the tube; and the keel petals are usually connate at their tips. Tendencies toward the Petalostemon morphological pattern, however, have been found in three separate sections of Dalea.

Among members of Rydberg's segregate genus, Thombera, the petals are inserted very high on the androecial tube (Fig. 14). However, of the Thombera species examined, none have the petals precisely at the apex and interdigitated with the filaments as in Petalostemon, and all have nine or ten stamens.

In another line of Dalea (sect. Polygonoides of Rydberg's genus Parosela) the petals are inserted at the middle of the tube or lower, but the stamen number varies. Close examination of D. polygonoides discloses flowers with as few as five stamens, but the numbers seven and eight are most common. In all flowers of this species, the staminal tubes have nine vascular bundles below the level of the sockets regardless of stamen number, but in flowers having seven or eight stamens,
Fig. 13. Apical petals of *Petalostemon pulcherrimum* arranged in the same position as they are on the staminal tube.

Fig. 14. Apex of the staminal tube of *Dalea cliffortiana*. Socket level is indicated by the arrow.

Fig. 15. Tube apex of a 7-staminate *Dalea polygonoides*. Arrows indicate vascular bundles on the same radius continuing above two of the sockets.

Fig. 16. Tube apex of a 5-staminate *Dalea polygonoides*. None of the sockets have bundles on the same radius continuing above them.

Fig. 17. Tube apex of a 6-staminate *Petalostemon obovatum*. The auxillary stamen filament is behind the socket on the right.

Fig. 18, 19. Tube apices of *Petalostemon tripetalus*. Petal sockets are seen at the bases of the micrographs. Arrows indicate "rudimentary" filaments.
"double bundles" are present. Each double bundle consists of a petal and a filament trace on the same radius. Flowers with seven stamens have two double bundles and flowers with eight stamens have three double bundles. The outer trace of each double bundle supplies a petal and the inner continues above the level of the petal socket with the other bundles to the filaments (Fig. 15). In flowers with five stamens, all of the bundles are single — there are nine bundles below the sockets and only five above (Fig. 16). The similarity here to the condition found in Petalostemon is obvious. In Petalostemon nine bundles traverse the entire length of the androecial tube, four supplying the petals through sockets at the apex and the remaining five supplying the filaments.

A third Dalea line showing Petalostemon-like characteristics is indicated by Barneby's account of a Dalea of subg. Trichopodium (Barneby pers. comm. 1964). This species has:

vegetative and calycine characters unquestionably of that group and therefore not at all suggestive of any known Petalostemon, but it is pentandrous and has four inner petals all separate and inserted close up to the point where the stamens come free from each other. This very distinct undescribed species is technically a Petalostemon, but obviously a Dalea (and is sympatric, on the coast of Sonora, with decandrous Daleae similar in appearance).

Variation in stamen number and petal placement typical of
Dalea are also found in Petalostemon. One collection of *Petalostemon obovatum* (Wemple & Jackson, 724), endemic to southern Texas, has about 40% of its flowers with six stamens. The petals are inserted at the apex of the tube but one of the nine bundles of the tube is double and a filament arises from the outer surface of the tube behind a socket, one bundle passing into the petal, the other entering the filament (Fig. 17).

Two annual species, originally described as *Petalostemon* but herein excluded from this genus, were studied. *P. tripetalus* has but two or three subapical petals and normally five stamens. Between the "normal" five filaments are invariably found rudiments of filaments. Sometimes the latter consist of only "bumps" of tissue without vascular supply, but in other instances filaments develop to almost the same length as the alternating ones and have a visible xylem supply (Fig. 18, 19). The vascular bundles of the lower tube number eight in flowers with three anterior petals and seven in the flowers with two petals. Xylem vessels that pass into the "rudimentary" filaments arise de novo about two-thirds the distance up the tube. This was the only observation made of such a phenomenon. *P. emarginatum* has petals inserted below the apex of the tube (Fig. 11). *P. tenuifolium*, *P. compactum*, *P. flavescens* and *P. ornatum* also have the petals inserted slightly below the apex but not as far below as *P. emarginatum*. Although the first four species are clearly *Petalostemon* in
gross morphological aspects, *P. emarginatum*, an annual, is almost indistinguishable from many of the annual Daleas.

**Conclusions**

There is apparently no clearly defined disjunction between *Petalostemon* and *Dalea*, and evidence from vegetative anatomy and floral morphology indicate a common ancestry. A chromosome number of $n = 7$ is shared by both genera, also indicative of a close relationship. Notwithstanding the similarities between the two genera, *Petalostemon* represents a highly specialized branch within the heterogeneous daleoid complex. This specialization has resulted in both the loss of one whorl of stamens and the migration of four petals to the apex of the staminal tube. The species of *Dalea* possessing petalostemoid characteristics appear to arise from diverse sections of the genus and perhaps represent specialized and independent, albeit somewhat convergent evolutionary trends. A complete reassessment of the placement of *Petalostemon* must await revision of the remainder of the daleoid complex but it is feasible at present to redefine the generic delimitations of *Petalostemon* excluding all taxa possessing more than five stamens as well as those with petal insertions substantially below the apex of the staminal tube.

The reticulate, often convergent pathways taken by the evolutionary processes in many groups often makes generic lines somewhat indistinct. This is certainly true in many
groups of legumes and emphatically true in other plant families (e.g. Cruciferae, Gramineae). Therefore, at least more than one viewpoint of what constitutes generic delimitation in a particular taxon is admissible. The alternative to the present disposition of Petalostemon, as advocated by Shinners (1949) and Barneby (1965) would be to reduce it to some sub-generic ranking within Dalea; but again, the same problems would be encountered only at a different taxonomic level. The acceptance of Petalostemon, as herein defined, seems to result in a reasonably natural genus of perennials, easily definable from the melange that is Dalea.
DELIMITATION OF SUBGENERIC TAXA

Two lines are evident within my delimitation of the genus Petalostemon. The first is represented by the species originally collected by Walter and herein called P. caroliniense. Michaux (1803), or L. C. Richard who wrote Michaux’s diagnoses, was the first to unify Kuhnistera with what were considered the pentastaminate members of Dalea in the new genus Petalostemon, a position with which I concur. Rydberg, in the most recent revision of the Psoraleae (1919-1920), considered the differences shown by Kuhnistera to be sufficient to merit generic status. The basic characteristics used to substantiate separation of the Kuhnistera are: 1.) spikes disposed in a corymbose manner; 2.) sterile involucral bracts subtending individual spikes; and 3.) plumose, filiform calyx lobes. I consider the three taxa composing Kuhnistera to belong within Petalostemon because all of the primary identifying characters of the latter genus are found, in addition to these specialized characteristics which seem merely exaggerations of those found in other species of Petalostemon. For example, Petalostemon multiflorum possesses an inflorescence with a somewhat corymbose structure. Sterile bracts subtending flower spikes are present in all of the southeastern species of Petalostemon as well as many other species throughout the range of the genus. None, however, exhibit the degree of bract expansion found in P. caroliniense. An approach to the
plumose-filiform lobes of *P. caroliniense* is found in *P. ornatum* of the Pacific Northwest. In short, the features characteristic of subgenus *Kuhnistera* are merely quantitatively but not qualitatively different from those of other species of the genus. With the above considerations in mind, I have adopted DeCandolle's (1825) viewpoint: one genus, *Petalostemon*, with two subgeneric categories.

Within subgenus *Petalostemon* certain groupings can be made based on morphological similarities. I have recognized these groups by using Rydberg's (1919-1920) technique of unofficial sectional names. It is clear from my work that at least some of these sections are more than mere phenotypic associations. The Purpurei, for example, are almost completely interfertile, whereas, hybridization between one of its members and another species outside the section is rare. The same is true of the Candidi. Although compatibility studies did not cover all species and sections it seems clear that morphologically based relationships have a sound genetic basis within this genus.
COMPATIBILITY STUDIES

During the fall of 1962, a program of controlled cross pollinations was begun in an attempt to elucidate the genetic relationships between the species of Petalostemon. Parent plants representing 11 of the 31 species were grown either from seed or field-collected rootstocks and maintained under greenhouse conditions during the course of the experiment. Cross pollinations were made, the seeds harvested, counted, planted and progeny grown. In a few cases, second generation hybrids were produced. In addition to the insights into the genetic relationships of the species, this part of the research provided an almost constant supply of cytological material, flowers and pollen for further investigations.

Petalostemon proved to be an ideal subject for this type of biosystematic research because the plants rarely set seeds if kept in an insect free environment. The mechanisms preventing self-pollination are not primarily genetic; rather, they are morphological. Almost all species are protandrous, the anthers are exserted and the pollen exposed prior to stigmatic receptiveness. Additionally, the filaments diverge from the longitudinal axis of the flower so that the anthers are spatially quite remote from the stigma when it does become receptive. Another factor involved is that the style is long and the stigma extends well beyond the anthers. One species that lacks both divergent filaments as well as an elongate
style is *P. obovatum*. This species is entirely self pollinating in the greenhouse, setting seeds readily without outside intervention.

The degree of interfertility between species was measured by the percentage of seeds set in a given cross. Usually all the pods of a particular spike were examined. This number ranged from a minimum of 20 to a maximum of 261. The average number of pods examined for each cross was 32. The results of all attempted cross pollinations are shown in Table 1. A seed set of less than 10% is interpreted as indicating complete intersterility. This small percentage appears to represent infrequent self pollinations, often resulting from stylar bending that allows a stigma of one flower to touch the anther of a contiguous one. In Table 1, the species are arranged according to sectional groupings based on morphological similarities. It will be seen that within a given section, fertility between the species is high, while between sections it is quite low, if existent at all. As a result of progeny analysis, only one intersectional hybrid was verified, that from a cross between *P. candidum* and *P. tenuifolium*, with the former the pistillate parent. *P. candidum* is white flowered while *P. tenuifolium* is purple. The hybrid was intermediate in color as well as all other characteristics. A possible second intersectional cross indicated in Fig. 20 by the question mark is based on rather indirect evidence. The cross was between *P. villosum* and *P. occidentale*, the former the
Table 1. Results of attempted cross-pollinations in the genus *Petalostemon*. All numbers are expressed in percentage of seed set. The asterisk (*) signifies a self-pollination or progeny phenotypically like the female parent.

<table>
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<tr>
<th>Female parents</th>
<th>(A)</th>
<th>(B)</th>
<th>(C)</th>
<th>(D)</th>
<th>(E)</th>
<th>(F)</th>
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pistillate parent. The progeny, phenotypically, was like *P. villosum* but most of the flowers were abnormal. Many lacked corolla segments and/or stamens, others showed various kinds of androecial fusions. These abnormalities could have been the result of self pollination resulting in increased homozygosity of deleterious recessive genes, however; no other *P. villosum* crosses showed such abnormalities, including several self crosses.

Within sections, all crosses showed phenotypic intermediciy between both parents with but few exceptions. One of the exceptions was the unique retrorse calyx pubescence characteristic of *P. tenue* (*P. stanfieldii*). Of the progeny examined when this species was the staminate parent, none had retrorse calyx pubescence even though intermediacy was seen in all other characteristics. It is possible that this character is controlled by a single recessive gene.

One of the anticipated results of these crosses was the synthesis of one or several of the preexisting species of *Petalostemon*. A cross between *P. gattingeri* and *P. purpureum* resulted in such a synthesis. The progeny of this cross was phenotypically identical with *P. arenicola*. Although the present range of the two parents is allopatric, it is possible that sympatry existed in the past and that hybrid populations proved adapted to a particular "ecological niche" and persisted. However, phenotypic resemblance is equivocal and need not imply the derivation of an entire species from two extant
species. A specimen is in ISC.

Another result of this study was the discovery that male sterility within populations is a relatively common phenomenon in Petalostemon. This is not an artifact of greenhouse culture. It first came to my notice in the greenhouse when certain plants of *P. purpureum*, *P. candidum* and *P. multiflorum* consistently produced flowers with shrunken anthers containing no pollen yet appeared fully female fertile and set seeds when pollinated with pollen from other plants. Later, close observation in the field showed that indeed, the field populations contained both male sterile and male fertile plants. On a prairie remnant adjacent to the Ames High School, Story Co., Iowa, both *P. purpureum* and *P. candidum* grow sympatrically. Ten of 12 *P. purpureum* and 27 of 35 *P. candidum* plants collected here were male sterile.

The obvious advantage of male sterile plants in pollination experiments is that the possibility of accidental self-pollination is eliminated. All three male sterile species in cultivation have thus yielded unequivocal data in this study. One aspect of this male sterility phenomenon is that the progeny of these plants resulting from hybridization with another species in the same section are always male sterile even though they are intermediate in all other phenotypic aspects. This characteristic is possibly the result of one
or a group of dominant genes.

Some evidence has accumulated from the studies involving these male sterile plants indicating that "foreign" pollen can induce parthenogenetic seed formation. Crosses involving male sterile *P. candidum* plants and some of the purple species, e.g. *P. purpureum*, *P. tenuifolium*, *P. pulcherrimum* and *P. arenicola*, produced relatively high seed set yet the progeny were phenotypically like the pistillate parent. It is probable that embryo development is parthenogenetic and the foreign pollen merely acts as a trigger for this type of reproduction. Although all the specimens of *P. occidentale* used were fully male fertile, perhaps parthenogenetic seed formation was responsible for the high seed set with pollen from *P. tenuifolium* and *P. villosum* (Table 1). In this case, too, all the progeny were phenotypically *P. occidentale*.

In summary, there are genetic barriers between the sections of the genus. Thus two species belonging to different sections can exist sympatrically with little, if any genetic interchange. Within sections, however, interfertility is common, but geographical or ecological separation of species is almost always found. If two species belonging to the same section come in contact, hybrids result. Such a situation undoubtedly occurs in southeastern Oklahoma resulting in hybridizations between *P. purpureum*, *P. pulcherrimum* and *P. decumbens*. From my greenhouse study, the hybrids seem fully fertile and vigorous but this in no way measures their ability
to compete in their natural environments. Their success is probably variable, but if given the appropriate favorable environment, they will persist.

Compatibility within the four sections tested (Purpurei, Phleoides, Candidi and Villosi) is summarized in Fig. 20. Compatibility within selected members of section Purpurei is summarized in Fig. 21.
Fig. 20. Diagram showing attempted crosses between members of the sections of Petalostemon. The arrows indicate the direction of pollen transfer. Attempted crosses where less than 5% seed set resulted are indicated by a broken line. The solid lines indicate verified hybrids were produced.
Fig. 21. Diagram showing attempted crosses between members of section Purpurei in Petalostemon. The arrows indicate the direction of pollen transfer. Attempted crosses wherein less than 5% seed set resulted are indicated with a broken line. The thin, solid line represents 5-10% seed set. The wide, solid line represents a seed set greater than 10%.
Cytological studies using root tips and microsporocyte preparations were made on eleven species, eight interspecific hybrids and one F₂ interspecific hybrid. Eight of the species counts have not previously been reported. A summary of my counts and those of other workers is presented in Table 2 and selected illustrations of the meiotic and mitotic figures are shown in Figs. 22, 23. Voucher specimens for each of the counts were deposited in ISC except when otherwise noted.

All counts previously made as well as my own show *Petalostemon* to possess a diploid number of 14. There were no consistent meiotic abnormalities either in the species or the hybrids that I examined. Occasional examples of binucleate pollen mother cells, such as those reported by Sen and Krishnan in *Clitoria ternata* (1961), were observed.

An attempt was made to study meiosis in specimens of *Petalostemon* that were male sterile, but I was unable to observe any meiotic figures in anther preparations from these plants. It is possible that the disturbance resulting in male sterility takes place prior to meiosis, perhaps in pollen mother cell formation.
Table 2. Chromosome numbers reported in the genus Petalostemon. All counts are $2n = 14$. The asterisk (*) indicates previously unreported counts.

<table>
<thead>
<tr>
<th>Species</th>
<th>Reference and/or collection data</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. glandulosum</td>
<td>Turner (1956).</td>
</tr>
<tr>
<td>(synonymous with P. phleoides in this treatment)</td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>Reference and/or collection data</td>
</tr>
<tr>
<td>---------------------</td>
<td>-----------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>*P. microphyllum</td>
<td>Wemple: from seeds collected in Callahan Co., Texas by N.C. Henderson, Wemple greenhouse No. 65B.</td>
</tr>
<tr>
<td>P. stanfieldii</td>
<td>Turner (1956). (synonymous with P. tenue in this treatment)</td>
</tr>
<tr>
<td>*P. tenuifolium</td>
<td>Wemple: from seeds collected in Ochiltree Co., Texas, Wallis 4806.</td>
</tr>
<tr>
<td>P. villosum</td>
<td>Ledingham (1957).</td>
</tr>
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</table>
Fig. 23. Meiotic figures in interspecific hybrids of *Petalostemom*. A. *P. tenuifolium* × *P. arenicola*;  
1. pachytene, 2. anaphase II. B. *P. arenicola* × *P. tenuifolium*. C. *P. arenicola* × *P. pulcherrimum*, two cells. D. *P. arenicola* × *P. purpureum*.  
E. *P. gattinieri* × *P. tenuifolium*, two cells.  
F. *P. pulcherrimum* × *P. purpureum*, two cells.  
G. (*P. tenuifolium* × *P. arenicola*) × self
POLLEN ANALYSIS

Pollen investigations, particularly those involving size and shape relationships, have heretofore been undertaken mainly by paleobotanists. The topic can hardly be introduced without mention of the works of G. Erdtman (1952, 1954), but the primary focus of these books, even though they are taxonomic in implication, is the study of fossil pollen. Two recent papers have pointed out the importance of pollen analysis as an additional tool for the systematist dealing with modern plants (Horton 1963; Stone 1963).

Horton and Stone utilized freshly collected pollen for their studies. I used fresh pollen also, but found it is equally feasible, in the case of Petalostemon, to use pollen from herbarium sheets. Drying apparently has little effect on the exine and if the investigator is interested primarily in external dimensions of the grains, 24 hours in lactophenol and cotton blue, is sufficient to inflate the grains to their normal size.

The pollen of Petalostemon varies in shape from sub-prolate to prolate (Erdtman 1954). The larger pollen grains of the section Purpurei tend to be more elongate than those of the other sections which possess smaller, more spheroidal grains. The trioolpate grains appear only slightly sculptured under 430x magnification. They bear no irregularities or protuberances.
To the naked eye the pollen is yellow or orange; the color is due to an orange liquid which adheres to the grains. This substance is immiscible in lactophenol but has not been further characterized. It is especially prevalent in members of section Purpurei — the species that possess yellow-orange or orange pollen. Representatives of the other sections have yellow pollen.

Pollen viability, as tested with cotton blue, is high in almost all species. In all except *P. tenuifolium* and *P. villosum* the number of aborted or non-staining pollen grains was always less than 1%. *P. tenuifolium* was unique in that the grains showed wide variations in size and shape. This is indicated by the relatively wide range of both length and width measurements as well as a large standard deviation for both (Table 3, Fig. 24). In addition to size and shape variation, there was invariably 5–15% non-staining pollen in each sample. *P. villosum*, while having uniform pollen size, usually showed about 10% non-staining pollen.

Measurements and their analysis are presented in Table 3 and Fig. 24. The species are grouped according to sections and within the sections, on variations in pollen size and shape. It is evident that the measured pollen characteristics coincide with the external morphological characteristics upon which the sections are based.

Several tentative generalizations can be drawn from this data: 1.) Members of section Purpurei seem related in the
Table 3. Pollen analysis of species of Petalostemon. Asterisk (*) indicates that all measurements were from dried pollen taken from herbarium specimens.

<table>
<thead>
<tr>
<th>&quot;Section&quot;</th>
<th>Species</th>
<th>No. of samples</th>
<th>No. of plants</th>
<th>Width in μm</th>
<th>Length in μm</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Range</td>
<td>Arithmetic mean</td>
</tr>
<tr>
<td>Phleoides</td>
<td>microphyllum</td>
<td>10</td>
<td>7</td>
<td>18-27</td>
<td>22.23</td>
</tr>
<tr>
<td>Foliosi</td>
<td>foliosum</td>
<td>2</td>
<td>2</td>
<td>23-25</td>
<td>24.55</td>
</tr>
<tr>
<td>Villosi</td>
<td>villosum</td>
<td>10</td>
<td>10</td>
<td>22-29</td>
<td>25.23</td>
</tr>
<tr>
<td>Candidi</td>
<td>occidentale</td>
<td>11</td>
<td>8</td>
<td>24-33</td>
<td>26.41</td>
</tr>
<tr>
<td>Candidi</td>
<td>candidum</td>
<td>8</td>
<td>5</td>
<td>25-33</td>
<td>28.61</td>
</tr>
<tr>
<td>Ornati</td>
<td>obovatum</td>
<td>2</td>
<td>2</td>
<td>25-31</td>
<td>28.0</td>
</tr>
<tr>
<td>Ornati</td>
<td>searsiae*</td>
<td>4</td>
<td>4</td>
<td>27-35</td>
<td>30.27</td>
</tr>
<tr>
<td>Purpurei</td>
<td>tenuifolium</td>
<td>7</td>
<td>5</td>
<td>22-36</td>
<td>29.32</td>
</tr>
<tr>
<td>Purpurei</td>
<td>gattingeri</td>
<td>5</td>
<td>4</td>
<td>27-33</td>
<td>29.78</td>
</tr>
<tr>
<td>Purpurei</td>
<td>ar enicoa</td>
<td>7</td>
<td>5</td>
<td>27-35</td>
<td>30.49</td>
</tr>
<tr>
<td>Purpurei</td>
<td>tenue</td>
<td>4</td>
<td>3</td>
<td>27-35</td>
<td>30.95</td>
</tr>
<tr>
<td>Purpurei</td>
<td>purpureum</td>
<td>13</td>
<td>10</td>
<td>25-36</td>
<td>31.01</td>
</tr>
<tr>
<td>Purpurei</td>
<td>pulcherrimum</td>
<td>15</td>
<td>14</td>
<td>27-36</td>
<td>33.24</td>
</tr>
<tr>
<td>Purpurei</td>
<td>decumbens</td>
<td>1</td>
<td>1</td>
<td>33-36</td>
<td>34.91</td>
</tr>
</tbody>
</table>
Fig. 24. Pollen size and shape analysis of selected species of *Petalostemon*. Length of the horizontal line indicates the range of variation in width (upper line) and length (lower line). The central cross mark indicates the arithmetic mean for all grains sampled. The rectangle represents + or − one standard deviation.
possession of large, prolate pollen grains. 2.) The pollen size of *P. searlsiae* is interesting because this species has many characteristics which suggest that it is allied with the Purpurei -- most specifically with *P. tenuifolium* whose pollen size *P. searlsiae* closely approximates. The morphological basis for including the latter species in the Ornati rather than the Purpurei will be discussed later. 3.) Sections Phleoides, Foliosi and Villosi possess small subprolate pollen grains. Morphologically these sections are quite distinct from one another, yet they are unique among the *Petalostemon* in that they all possess a high leaflet number (15 or more).

I have also examined the pollen of most of the artificial hybrids that I have synthesized as well as that of a naturally occurring hybrid between *P. purpureum* and *P. pulcherrimum* (Table 4 *(Wemple 402, Marshall Co., Okla.)*). Usually pollen size of the hybrid is intermediate in size between that of either parent -- this intermediacy parallels that shown by the hybrids in other morphological characteristics. Seldom is the viability of the pollen substantially reduced except in the case of all *P. tenuifolium* hybrids, where the "abnormalities" -- size and shape variation and inviability -- of the *P. tenuifolium* parent appear to be emphasized. This variation was noted in crosses with all other species and seemed to hold true regardless of whether *P. tenuifolium* was used as the staminate or pistillate parent. Data is also presented on a
limited number of second generation hybrids, most of which show a high proportion of abnormal pollen grains.
Table 4. Pollen analysis of interspecific hybrids of *Petalostemon*. SSV indicates that size and shape variation was noted. Abnormalities are indicated in % of the sample that appeared abnormal. Asterisk (*) indicates a field collected hybrid between *P. purpureum* and *P. pulcherrimum* (Wemple 402 Marshall Co., Okla.)

<table>
<thead>
<tr>
<th>Female parent</th>
<th>Male parent</th>
<th>No. of samples</th>
<th>No. of plants</th>
<th>Width in μm</th>
<th>Length in μm</th>
<th>Abnormalities</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. candidum</em></td>
<td><em>P. occidentale</em></td>
<td>2</td>
<td>2</td>
<td>25-31</td>
<td>33-36</td>
<td>33.91 8%</td>
</tr>
<tr>
<td><em>P. tenuifolium</em></td>
<td><em>P. purpureum</em></td>
<td>4</td>
<td>3</td>
<td>29-33</td>
<td>36-47</td>
<td>42.77 SSV, 15-70%</td>
</tr>
<tr>
<td><em>P. purpureum</em></td>
<td><em>P. tenuifolium</em></td>
<td>1</td>
<td>1</td>
<td>31-36</td>
<td>40-51</td>
<td>44.91 5%</td>
</tr>
<tr>
<td><em>P. tenuifolium</em></td>
<td><em>P. pulcherrimum</em></td>
<td>1</td>
<td>1</td>
<td>29-33</td>
<td>44-47</td>
<td>45.64 --</td>
</tr>
<tr>
<td><em>P. tenuifolium</em></td>
<td><em>P. arenicola</em></td>
<td>14</td>
<td>13</td>
<td>25-35</td>
<td>33-47</td>
<td>42.91 SSV</td>
</tr>
<tr>
<td><em>P. arenicola</em></td>
<td><em>P. tenuifolium</em></td>
<td>1</td>
<td>1</td>
<td>25-33</td>
<td>40-46</td>
<td>40.36 SSV</td>
</tr>
<tr>
<td><em>P. gattinneri</em></td>
<td><em>P. tenuifolium</em></td>
<td>1</td>
<td>1</td>
<td>29-33</td>
<td>36-42</td>
<td>39.09 SSV, 20%</td>
</tr>
<tr>
<td><em>P. gattinneri</em></td>
<td><em>P. purpureum</em></td>
<td>2</td>
<td>1</td>
<td>25-31</td>
<td>36-44</td>
<td>36.29 SSV</td>
</tr>
<tr>
<td><em>P. purpureum</em></td>
<td><em>P. gattinneri</em></td>
<td>2</td>
<td>2</td>
<td>27-33</td>
<td>42-51</td>
<td>44.10 SSV</td>
</tr>
<tr>
<td><em>P. arenicola</em></td>
<td><em>P. gattinneri</em></td>
<td>1</td>
<td>1</td>
<td>29-31</td>
<td>38-44</td>
<td>42.54 --</td>
</tr>
<tr>
<td><em>P. arenicola</em></td>
<td><em>P. purpureum</em></td>
<td>2</td>
<td>2</td>
<td>29-35</td>
<td>42-51</td>
<td>46.36 --</td>
</tr>
<tr>
<td><em>P. arenicola</em></td>
<td><em>P. pulcherrimum</em></td>
<td>3</td>
<td>3</td>
<td>29-36</td>
<td>42-51</td>
<td>45.27 --</td>
</tr>
<tr>
<td>Female parent</td>
<td>Male parent</td>
<td>No. of samples</td>
<td>No. of plants</td>
<td>Width in μm</td>
<td>Length in μm</td>
<td>Abnormalities</td>
</tr>
<tr>
<td>---------------</td>
<td>----------------------</td>
<td>----------------</td>
<td>---------------</td>
<td>-------------</td>
<td>--------------</td>
<td>---------------</td>
</tr>
<tr>
<td><em>P. pulcherrimum</em></td>
<td><em>P. arenicola</em></td>
<td>3</td>
<td>3</td>
<td>29-36</td>
<td>32.24</td>
<td>40-53</td>
</tr>
<tr>
<td><em>P. purpureum</em></td>
<td><em>P. pulcherrimum</em></td>
<td>1</td>
<td>1</td>
<td>33-35</td>
<td>33.27</td>
<td>42-51</td>
</tr>
<tr>
<td><em>P. pulcherrimum</em></td>
<td><em>P. purpureum</em></td>
<td>2</td>
<td>1</td>
<td>31-36</td>
<td>33.18</td>
<td>36-45</td>
</tr>
<tr>
<td><em>P. purpureum</em></td>
<td><em>P. tenue</em></td>
<td>3</td>
<td>2</td>
<td>29-33</td>
<td>30.61</td>
<td>42-45</td>
</tr>
<tr>
<td>402*</td>
<td></td>
<td>3</td>
<td>1</td>
<td>31-36</td>
<td>32.91</td>
<td>47-56</td>
</tr>
<tr>
<td><em>P. tenuifolium</em></td>
<td>402*</td>
<td>1</td>
<td>1</td>
<td>29-33</td>
<td>31.09</td>
<td>40-47</td>
</tr>
<tr>
<td><em>P. purpureum</em></td>
<td>402*</td>
<td>2</td>
<td>2</td>
<td>29-36</td>
<td>32.73</td>
<td>42-47</td>
</tr>
<tr>
<td>402*</td>
<td><em>P. arenicola</em></td>
<td>1</td>
<td>1</td>
<td>29-33</td>
<td>30.91</td>
<td>47-53</td>
</tr>
<tr>
<td>(<em>P. tenuifolium</em></td>
<td><em>P. arenicola</em>) X</td>
<td>3</td>
<td>3</td>
<td>27-33</td>
<td>30.18</td>
<td>40-45</td>
</tr>
<tr>
<td><em>P. arenicola</em></td>
<td><em>P. gattingeri</em> X</td>
<td>2</td>
<td>2</td>
<td>33-35</td>
<td>34.73</td>
<td>40-45</td>
</tr>
</tbody>
</table>
THE GENUS PETALOSTEMON

Type species P. candidum Michx. Type material in P.


Generic description

Perennial, glandular-punctate herbs with many stems arising from a well developed taproot or caudex (Fig. 54F). Stipules subulate. Leaves usually with smaller leaves or reduced stem systems in their axils, odd-pinnate, with (3) 5—numerous leaflets; leaflets usually narrow to elliptical but sometimes broad and almost ovate, usually ± involute. Flowers in terminal, globose to cylindrical spikes, each flower subtended by a conspicuous bract which usually exceeds the length of the calyx in bud; the flowers of some species also with bracteoles flanking the base of the calyces. Calyx campanulate to tubular, 3.0—7.5 mm long (including lobes), sometimes oblique; the lobes deltoid to lanceolate or, less frequently, filiform plumose. Standard long-clawed, arising from a socket near the floral base, the blade oblong to cordate; the four other petals arising from the apex of the staminal tube, or slightly below, interdigitating with the 5 monadelphous stamens; claws inserted in prominent sockets;
blades strap-shaped to oblong, spreading from the floral axis. Free portions of the filaments usually diverging from the floral axis, equalling or exceeding the length of the androecial tube and usually subequal to the petal apices at anthesis. Ovary globose to elliptical, 2-ovulate; the style equalling or exceeding the petal apices and anthers shortly after anthesis. Pod ovate to lunate, 1 seeded; the styalr beak offset to the standard side of the calyx at maturity. The indehiscent legume falling enclosed in the calyx.

Distribution

Ranging from northern Mexico throughout much of the United States north to southern Canada. The greatest number of species is found in Texas. One complex extends from the Great Basin northward into the Pacific Northwest. Another is found in the southeastern states. The principal area in which *Petalostemon* is absent is the northeastern deciduous forest.

Key to the subgenera

1. Spikes subglobose, compact, disposed in a corymbose manner, surrounded by a series of oval to reniform, sterile bracts; calyx lobes filiform and plumose; flowers white; restricted to the southeastern states.

I. *Kuhnistera* page 63
1. Spikes various, rarely subglobose or corymbosely disposed, seldom with sterile bracts at the base of the spikes; calyx lobes deltoid or lanceolate; flowers variously colored; not restricted to the southeastern states.

II. Petalostemon page 78

I. Subgenus KUHNISTERA (Lam.) Wemple comb. nov.


Introduction

The three taxa composing subgenus Kuhnistera are united by the possession of three distinctive characteristics: 1.) subglobose, compact spikes surrounded by a series of oval to reniform, sterile bracts; 2.) spikes disposed in a corymbose manner; and 3.) filiform and plumose calyx lobes. None of these characteristics are unique within Petalostemon but their combination in this geographically restricted trio of species, clearly sets this subgenus apart. The plants are endemic to the southeastern Coastal Plain of southern Mississippi, Alabama, Florida, Georgia, South Carolina and North Carolina. Within this area they are found only on the more elevated, drier, sandy areas, locally called "sandhills." They are usually associated with pines and scrub oaks. Ecologically they are sympatric through part of their range with Petalostemon albidum and P. feayi. They are the only species of
Petalostemon with representation in the Carolinas.

Meiotic and mitotic preparations of P. caroliniense yield 7 and 14 chromosomes respectively, consistent with the rest of the genus (Table 2, Fig. 22, D, E). Pollen collected from P. caroliniense ssp. trifoliatum, (Isely & Wemple 9177), Holmes county, Florida, appeared typical of the genus, in length averaging 29 microns, in width 20 microns.

Key to the Species

1. Leaflets over 2 mm wide; stems with spherical, protuberant "glands" becoming more numerous toward the apex of the stem; limited to the Florida peninsula.

   1. P. adenopodium p. 64

1. Leaflets less than 2 mm wide, generally filiform; "glands" present on the stem but not spherical-protuberant; not limited to the Florida peninsula.

   2. P. caroliniense p. 72

Taxonomy

1. PETALOSTEMON ADENOPODUM (B. L. Robs. ex Rydb.) Wemple (Fig. 25)

   Petalostemon adenopodium (B. L. Robs. ex Rydb.) Wemple. Based on Kuhnistera adenopoda B. L. Robs. ex Rydb. [Improperly published as Kuhnistera adenopoda (B. L. Robinson) Rydberg. N. Am. Fl. 24: 136. (1919-1920)].

   Petalostemon corymbosum adenopodium B. L. Robs. M. S. in herb. Type in GH. (1).

**Description**

Plants lacking a prominent caudex, the root often red. Stems dark, glabrous and striate, 1 m or shorter, covered with spherical, protuberant secretory cavities ("glands") about 1 mm in diameter, increasing in abundance toward the stem apex. Leaves fascicled, less than 2 cm long with 3--7 elliptical leaflets, usually 2--3 mm wide and 6--8 mm long, paler green on top surface, often involute. Inflorescence corymbose with peduncles below the individual flower spikes lacking, the leaves gradually merging into involucral-like, oval to reniform, sharply acuminate, ciliate, sterile bracts. Calyx villous, tube 2--3 mm long, lobes plumose, 4.0--4.5 mm long. Corolla white, standard lanceolate, sometimes truncate, 0.8 mm wide, 3.5 mm long, equalling claw; apical petals lanceolate, sometimes truncate, blades 1.0 mm wide, 3.0 mm long, claw 1.2 mm long. Androecial tube 5--6 mm long, almost equalling tips of calyx lobes, stamen filaments 4.0 mm long, spreading at anthesis. Ovary 2.0 mm long, bearded on the distal 2/3, predominantly so on the upper surface; style 10.0 mm long bearded proximally over 1/2 its length.
Distribution and phenology

Restricted to the lower half of peninsular Florida. Limited to the higher, drier sandy areas. Often associated with turkey oak (*Quercus laevis* Walt.), long leaf pine (*Pinus australis* Michx.) and saw palmetto (*Serenoa repens* Small), a habitat similar to that occupied by *P. caroliniense* to the north. Geographically and ecologically sympatric in part of its range with *P. feayi*.

Anthesis from mid September to late November.

Nomenclature and observations

This species was first described by Rydberg (1919-1920) who based his name on a B. L. Robinson annotation label. The type sheet is a mixture of *P. adenopodum* and *P. caroliniense* ssp. *caroliniense*. Robinson identified both on the annotation label as respectively: "*P. corymbosum*, var. *adenopodum*, Rob. n. var." and "*P. corymbosum*, Michx. typical form." Rydberg's description is headed by: "2. *Kuhnistera* adenopoda (B. L. Robinson) Rydberg sp. nov.," giving Robinson full credit for the specific epithet even though it was not validly published. I have designated the citation as, "Rob. ex Rydb.," a

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1 A northern extension to the range is suggested by three collections from St. Johns county in northeastern Florida. All are collections of Mary C. Reynolds (1874-1877). The labels state St. Augustine, Florida. It is possible that this was her place of residence and not necessarily the location where the plants grew.
Fig. 25. Geographic distribution of the species of subg. *Kuhnistera*
procedure which is possibly not without question but seems the most logical course. Rydberg limits the species to the Tampa Bay Region of Florida's west coast, the location of the original Garber collection on which the name was based.

Small proposed the species *Kuhnistera truncata* based on an F. C. Hane collection at Earman, Florida, March 2, 1921, also citing other collections along the east coast of Florida at Jupiter, "many years ago," by C. Hitchcock. Small's discussion is confusing since he begins with an acknowledgement of Rydberg's *K. adenopoda* and then compares his species with *K. pinnata* (*P. carolinense*) rather than *K. adenopoda*. He comments on the differences in leaflet width and the more open inflorescence in his species, but attaches special emphasis to the truncate petals. He makes no explicit comparison with *K. adenopoda*. Had he done so, he would have found no essential differences. With regard to petal shape, I have examined petals of specimens throughout the range of *P. adenopodum* including several sheets annotated in Small's hand, "K. truncata." Fig. 26 shows examples of the variation found. There seems to be no correlation between petal conformation and distribution. In contrast to *P. carolinense*, the petal shape is quite different, as Small points out. It is possible that Small, in studying specimens from the east coast of Florida and presuming that Rydberg's species, *K. adenopoda*, was restricted to the west coast, cast around for a character on which to base a new species and seized on the apparent
variation in petal shape.

The poor representation of this species in major herbaria perhaps represents as much a paucity of collectors as a rarity of the plants (see Shinners 1964). During the course of two days collection across peninsular Florida, \textit{P. adenopodum} appeared common in its preferred habitat.

2. \textit{PETALOSTEMON CAROLINIENSE} (Lam.) Sprague

\textbf{Description}

Stems slightly branching, up to 1.1 m tall; moderately striate, glabrous with "glands" prominent but not protruding above the surface of the stem and not increasing in number toward the stem apex. Leaves fascicled, 1--2 cm long, bearing 3--13 linear-filiform, usually involute leaflets which are less than 0.9 mm broad. Inflorescence corymbose, simple or compound; peduncles below the individual flower spikes lacking, the apical leaves merging into several whorls of oval to suborbicular, ciliate-acuminate, sterile bracts. Flowers disposed in compressed spikes. Calyx villous, tube 2 mm long, lobes plumose-filiform, 3--6 mm long. Corolla white, standard lanceolate, cuneate at the base of the blade, 1 mm wide, 4 mm long, equalling the claw; apical petals similar to the standard but with claws only 1.0--1.5 mm long. Androecial tube 5 mm long, the free portions of the filaments 5--6 mm long. Ovary 2 mm long, the style 10 mm, both bearded.
Key to the subspecies

1. Leaflets 5–13; spikes arranged in a compound corymb; ranging through northern peninsular Florida, western Georgia, South Carolina and North Carolina.

   2a. *P. caroliniense* ssp. *caroliniense* p. 73

1. Leaflets 3; spikes arranged in a simple corymb; limited to southern Alabama, southern Mississippi, the panhandle of Florida and central Georgia.

   2b. *P. caroliniense* ssp. *trifoliatatum* p. 76

2a. PETALOSTEMON CAROLINIENSE SPP. CAROLINIENSE (Lam.) Sprague (Fig. 25)


   *Psoralea corymbosa* Poir. in Lam. Encycl. 5: 694-695. (1804). Based on *Petalostemon corymbosum* Michx.


Distribution and phenology

A common plant of the high, dry, white sand pine scrub. Ranging from central peninsular Florida, where it replaces the more southern *P. adenopodium*, through eastern Georgia and the Carolinas. Consistently associated with long leaf pine (*P. australis*) and turkey oak (*Q. laevis*) and, throughout its Florida range, with *Petalostemon albidum*.

Anthesis September to early November.

Nomenclature and observations

To my knowledge, the name *P. caroliniense* has never been used in this country; rather, the taxon has been referred to either *P. pinnatum* (Walt.) Blake or *P. corymbosum* Michx. The former lacks priority because the name was first published as *Anonymos pinnat.*, the *Anonymos* names are outlawed by Article 20 of the *Code of Botanical Nomenclature* (Lanjouw 1961) and the Blake combination was not made until 1915. The Lamarck epithet is therefore the first published and the combination by Sprague should be adopted.

Typification of *Kuhnistera caroliniensis* Lam. and *Petalostemum corymbosum* Michx. deserves comment. Lamarck precedes his description of the species with this paragraph:

En attendant que par un nouvel examen on ait confirmé & déterminé avec une précision convenable les vrais caractères de cette plante, nous en faisons ici une mention succincte d’après ce que nous apprend M.
which I translate as, "Until we have confirmed and determined with suitable precision by a new examination the true characters of this plant, we make of it here a brief mention according to what Mr. Walter tells us about it." Following this paragraph is an almost exact translation of Walter's description. It seems that Lamarck, even though using a new name, is basing it on Walter's description and therefore Walter's type specimen in the British Museum is the type for Kuhnistera carolinensiens. In the same manner, Michaux based P. corymbosum on the Walter name and therefore on the Walter type.

Subspecies carolinensiens is distinguished from subspecies trifoliatum by possessing more than three leaflets and having the spikes disposed in a compound rather than a simple "corymb." The range of the two is for the most part distinct, but they are sympatric in Franklin and Leon counties in the panhandle of Florida and in Richmond county in northeastern Georgia. Subspecies carolinensiens throughout its southern range usually has five to nine leaflets but specimens with a

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1The wording used by Lamarck suggests that this name could possibly be rejected as a "provisional name" (Article 34, Lanjouw 1961). I consulted several other botanists on this point but they were not of one accord. Two men prominent in nomenclatural matters, Dr. J. E. Dandy of Kew and Dr. H. W. Rickett of the New York Botanical Garden, were both of the opinion that the name is valid and cite several examples of similarly worded notes in Linnaeus' work. I concur with their viewpoint, but as Dr. Rickett stated, "The decision is a close one." (pers. comm. 1965).
higher leaflet number, 11-15, occur in the more northern part of the range, particularly South Carolina. Usually the leaflets are highly involute, presenting an almost filiform appearance. Three collections from South Carolina lack involute leaflets and the plants look remarkably different until one realizes that the leaflets are simply flat rather than tightly rolled. It is possible that these represent a geographic variant of this taxon. The northern populations also frequently show a less well developed inflorescence, some even possessing a simple "corymb" as found in subspecies trifoliatum.

2b. PETALOSTEMON CAROLINIENSE SSP. TRIFOLIATUM (Chapm.) Wemple (Figs. 25, 52C)

Petalostemon caroliniense ssp. trifoliatum (Chapm.) Wemple. Based on Petalostemon corymbosus var. trifoliatus Chapm.


Distribution and phenology

Limited to southern Mississippi, southern Alabama, the panhandle of Florida and extending northward through the interior of Georgia. Apparently occupying a similar habitat.
to that of subspecies *carolinense* but largely west of the latter. Associated with long leaf pine (*P. australis*) and turkey oak (*Q. laevis*) and ecologically sympatric in part of its range with *P. albidosum*. Geographically sympatric with *P. gracile* but occupying a different habitat. Anthesis from early September to late October.

As one travels from west to east through southern Mississippi, Alabama and the panhandle of Florida, a gradient in anthesis time is apparent; the more easterly plants bloom several weeks earlier than the western populations.

**Nomenclature and observations**

Chapman, in presenting variety *trifoliatus*, separates it from the typical *P. corymbosus* on the following characteristics: 1.) it is glandless or nearly so; 2.) it possesses 3--4 broadly ovate, acute bracts; 3.) the style is ciliate below the middle; 4.) the petals are acute; and 5.) the leaves are "mostly" trifoliate. To my observation, the two subspecies are indistinguishable in all the aforementioned characteristics except the last. Although Chapman did not cite a type or even a type locality, his numerous collections of this taxon (4-NY, 3-US, 3-MO) clearly indicate his understanding of it. I accept as a lectotype, his No. 6097, October 1897, Apalachicola, Florida (US 335288). A duplicate of this collection is at NY.

*Gatesia alabamensis* Bertol. was described from a plant
collected in Alabama and named in honor of the collector, Dr. Gates. The region of collection would indicate that it belonged in subspecies *trifoliatum* although the description does not indicate the leaflet number. A colored drawing following the article, plainly shows trifoliate leaves but a compound corymb. Throughout the range of subspecies *trifoliatum*, there are occasional individuals possessing compound corymbs. Their occurrence seems to have no geographic basis and they always possess trifoliate leaves. Assuming the accuracy of the artist, this is perhaps one of them. Since the type specimen was destroyed at Bologna during World War II (R. Savelli, pers. comm. 1964), this question may never be answered.

*Gavesia* appears to be merely an orthographic error, a substitution of a "v" for a "t." Walpers gives Bertoloni full credit for the original name but places it in synonymy.

II. Subgenus PETALOSTEMON Michx. Fl. Bor. Am. 2: 49. (1803)

**Key to the Sections**

1. Calyx glabrous throughout or villous ciliate on the lobes only (in *P. occidentale* and *P. microphyllum* puberulant overall); bracteoles usually present flanking the base of the calyces.

2. Mature stem leaves with 3--11 leaflets.
3. Calyx split dorsally to 1/2 its length; standard blade not lobed at base, the claw over twice as thick as the apical petal claws; limited in distribution to the southeastern United States.

   A. Carnei page 80

3. Calyx not slit dorsally to 1/2 its length; standard blade basally lobed, the claw the same diameter as the apical petal claws; not limited to the southeast.

4. Corolla rose-purple; known only from New Mexico.

   B. Prostrati page 125

4. Corolla white; not restricted as above.

   C. Candidi page 130

2. Mature stem leaves with more than eleven leaflets.

5. Corolla rose-lavender, apical petals not strap shaped; restricted to Tennessee and Illinois.

   D. Foliosi page 156

5. Corolla white, apical petals strap shaped; restricted to Texas and adjacent counties in Oklahoma.

   E. Phleoides page 164
1. Calyx densely pubescent, at least on the angles and lobes; bracteoles lacking.

6. Stems and leaves spreading pubescent to villous; leaflets 11–21; all species restricted to sandy soils.

F. Villosi page 173

6. Stems and leaves glabrous to glabrate (spreading pilose in P. obovatum); leaflets 5–11 (13); not all species restricted to sandy soils.

7. Leaves solitary, seldom fascicled; leaflets broad elliptical to almost ovate, seldom involute; spikes often subtended by sterile bracts; fertile bracts with scarious margins; calyces spreading sericeous-pubescent.

G. Compacti page 181

7. Leaves fascicled; leaflets linear, involute; spikes not subtended by sterile bracts; fertile bracts seldom with scarious margins; calyces with short appressed or rarely spreading pubescence.

H. Purpurei page 207

A. CARNEI

**Distinguishing characteristics**

Plants glabrous except for pubescence on margins and inner surfaces of the calyx lobes. Leaflets 3–9 (11).
Peduncles usually interrupted by sterile bracts below the spikes. Calyces flanked by a pair of bracteoles arising laterally from the subtending bract; calyx tube slit dorsally more than one-half its length. Corolla white or pink, the standard claw over twice as thick as the apical petal claws. Flowering in mid or late summer.

**Distribution**

Restricted to extreme southeastern Louisiana, southern Mississippi and Alabama, Florida and Georgia.

**Introduction**

The southeastern species, *Petalostemon gracile*, *P. albidum*, *P. carneum* and *P. feayi*, represent a relatively homogeneous section of the genus *Petalostemon*. Limitation of their distribution to the southeastern coastal plain, and possession of common morphological characteristics strongly suggests that this complex evolved from common ancestry and speciated in situ. My evidence supports the thesis that the group consists of four species, that *P. albidum* might have arisen as a consequence of hybridization between *P. gracile* and *P. carneum*, and that introgression between *P. albidum* and *P. carneum* is currently taking place. The data provide an explanation for the variability that is found in these three species as compared to the relatively homogeneous *P. feayi*. 
Ecology

*Petalostemon gracile* is limited to southern Mississippi, southern Alabama and the panhandle of Florida. It is commonly found in low grassy areas in association with uncut, long leaf pine (*P. australis*). On several occasions it was found growing in close proximity to *Sarracenia* bogs. It was never collected in disturbed habitats. *P. albidum* ranges down to Lee county in southern Florida and north-northwest into central Georgia. It is restricted to relatively dry, higher, often disturbed habitats -- cut over areas -- and particularly in association with turkey oak (*Quercus laevis*). It was in one such disturbed area that a "hybrid swarm" was found indicating introgression with *P. carneum*. *P. carneum* occurs throughout the Florida peninsula and southeastern Georgia. It is found in wet, low, undisturbed environments or in low areas where palmettos (*Serenoa repens*) have become the dominant vegetation. *P. feayi* is restricted to the white, dry sands of high pine woods, central Florida and southeastern Georgia.

Intermediacy of the range of *P. albidum* between that of *P. gracile* and *P. carneum* as well as its preference for a "hybridized habitat" in comparison with the older habitats of the latter two species suggests the hypothesis of hybrid origin of *P. albidum*. Verification was sought in the anatomical analyses that follow.
Anthesis time

In considering the trio of species, *P. gracile*, *P. albidum* and *P. carneum*, (Fig. 27) *P. gracile* has a very short flowering period, *P. albidum* a somewhat longer one and *P. carneum* an extended one. This is partially dictated by the growth habit of the species as well as by the southern extension of the range of the respective species. The major stem of *P. gracile* rarely branches; hence, there is seldom more than one terminal flower spike for each shoot. Anthesis of all the spikes on a plant begins almost simultaneously and thus the flowering period is of short duration. *P. albidum* has moderate development of axillary branches; after the main apex has flowered, the lateral branches subsequently bloom. Axillary branching is the rule in *P. carneum* and often a "pseudo-corymb" is formed by axillary spikes which surround the terminal one. This is also the case in *P. feayi*.

Although southern range extension, which prolongs the blooming period of certain species by allowing a longer frost-free growing period is important, genetically controlled axillary branching is probably the predominant causal factor for lengthening the flowering period in this section of *Petalostemon*. Evidence for this is found in the fact that most northern collections of *P. carneum* have as long a blooming period as the southern collections and exhibit an equal amount of axillary branching.
Fig. 27. Phenology and pollen measurements in section Carnei. Duration of flowering (bar graphs) as interpreted from herbarium sheets. The ordinate represents the number of collections. The smallest square (■) is one collection. The abscissa represents the months of the year. Pollen measurements (upper left) are in microns. The upper line represents the width of the grains and the lower line, the length. Length of the fine line is the total range of variation for the species; the heavy line represents plus or minus one standard deviation; the central, larger vertical line is the arithmetic mean; and, the smaller, lateral marks represent the range of variation of sample averages.
Cytology

Gametic chromosome number is uniformly $n = 7$ in the four species (Table 2, Fig. 22, A, C, F, H). While a determination on *P. feayi* has been previously reported (Turner 1963), those for the other three species are new. All counts were made from field collections and drawings were made of meiotic figures in pollen mother cells at pachytene, diakinesis, metaphase or incipient tetrad stages. Without exception, pairing was normal as was cytokinesis. Voucher specimens were deposited at ISC.

Pollen

Pollen size and shape proved valuable as diagnostic characters in other species of *Petalostemon* and data was obtained on the pollen of these southeastern species (Fig. 27). It is clear that pollen size and shape is of little value in separating these species; however, the similarity of the pollen is another indication of the closeness of their relationship.

Techniques for species determination

As a result of the familiarity gained during field work and herbarium study of the southeastern taxa, I sorted all the specimens into four stacks, each of which represented a putative species. I then analysed the character variations which allowed me to make such an intuitive separation. A
similar technique was utilized by Isely and Welsh (1960) in their study of *P. candidum* and *P. occidentale*. Their work differed to the extent that one individual utilized "taxonomic intuition" and the other, character analysis; thus avoiding possible "intuitive bias" when the analysis was conducted.

The material employed included 58 sheets of *P. gracile* representing 41 different collections, 80 sheets of *P. albidum* representing 52 collections, 183 sheets of *P. carneum* representing 127 collections and 109 sheets of *P. feayi* representing 72 collections. I chose 28 characteristics for study and from the data obtained, seven ratios were calculated. The characteristics were:

1. Stem striation.
2. Length of bracts on the peduncles.
3. *Length of leaf rachis.*
4. *Length of subtending internode of #3.*
5. Length of subapical leaflet.
7. *Length of peduncle.*
8. *Length of inflorescence.*
9. Width of inflorescence.
10. Degree of abaxial bending of bract tip.
11. Relative degree of axillary leaf clustering.
12. Presence of spherical secretory cavities (*"glands"*) at the apex of the peduncle.
13. *Degree of stem branching.*
15. Curvature of rachis and leaflets after drying.
16. Variation in stem ribbing below leaf.
17. Diameter of stem at base.
18. Length of bracts at anthesis.
19. Length of apical petal blade.
20. Length of apical petal claw.
22. Length of calyx tube.
23. Degree of bracteole pubescence.
24. Presence of bract "heel."
25. Degree of gynoecial pubescence.
27. Length of terminal rachis extension.
28. Exsertion of androecial sheath from calyx.
29. Maximum leaflet number.

Those characteristics with asterisks have been used by previous authors for distinguishing the species. However, the characteristics have been formerly used only in a generalized, comparative sense; they have not before been critically measured. The characteristics that are underlined were statistically analyzed. They were chosen because they showed distinctive means which distinguished the putative species. Before examining the analysis, each character deserves comment:
1. Stem striation

The degree of stem striation varied among these taxa. One-half of the *P. gracile* examined had smooth stems. Only a small proportion of the material of the other species lacked striate stems. Although an attempt was made to standardize the judgement of stem striation by observing the stem at a consistent distance from the base, the variations in striation patterns made objective analysis impossible. In general, the stems of *P. albidum* were coarsely striate, possessing less than ten major ribs around their circumference. The stems of *P. carneum* and *P. feayi* were usually finely striate possessing 15--25 low, rounded ribs.

2. Length of bracts on the peduncles

The bracts are not limited to the inflorescence proper but are, in part, scattered down the peduncle. These had never been used as characters in previous taxonomic treatments but I have found them most useful (Fig. 28, char. 2).

3. Length of leaf rachis, and

4. Length of subtending internode

A mature leaf, approximately one-third the distance from the stem base, was selected for measurement along with the internode immediately below it. Among the four species, there was significant variation in internodal length (Fig. 28, char. 4). *P. feayi* has the shortest internodes of the four species and *P. gracile*, the longest. This variation is seen in the more "leafy" appearance of the former species while *P.
gracile appears to be mainly stems. The other two species are intermediate in internode length and intermediate in "leafy" appearance. All species possess essentially the same length leaf, averaging between 13.5 and 15.0 mm long. Both characteristics were combined in the analysis (Fig. 28, char. 3/4).

5. **Length of subapical leaflet**, and
6. **Width of subapical leaflet**

Utilizing the leaf previously measured, one of the pair of leaflets immediately below the apical leaflet was measured. A subapical leaflet was measured in preference to a terminal leaflet because the terminal leaflet is often broken off on specimens. Although not statistically analyzed, these data are shown in the ideographs (Fig. 31).

7. **Length of peduncle**

Peduncle length varied among the putative species. *P. gracile* usually had the shortest peduncles and *P. albidum* was intermediate in this characteristic between *P. gracile* and *P. carneum* (Fig. 28, char. 7).

8. **Length of inflorescence**, and

9. **Width of inflorescence**

The spike continues to elongate as flowering progresses; hence, spikes with one-half their flowers open were always chosen for measurement. The most useful combination of these two measurements proved to be the product of the inflorescence length and the inflorescence width, which in essence is the silhouette area of a spike (Fig. 28, char. 8/9
and 8 x 9). Among these species, *P. carneum* possessed the largest inflorescence.

10. **Degree of abaxial bending of bract tip**

This was a subjective character chosen as a result of field observation of these taxa. The spikes of *P. gracile* often possessed recurved bracts, the tips were sometimes pointing directly toward the base of the plant. Abaxial bending was sometimes found in the bracts of *P. albidum* but never in *P. carneum*. This characteristic was rated on a three step scale: full bending, partial bending, or bracts with straight tips. It appears in the numerical analysis as characteristic No. 10 (Table 5, Figs. 29, 30).

11. **Relative degree of axillary leaf clustering**

In common with most species of *Petalostemon*, inhibition of axillary meristematic regions is not complete. The result is axillary leaf "clustering" or "fascicular leaf development". This condition varies from essentially no visible clustering to the development of an entire, dwarf, axillary branch system, within which, each axil has further clustering. The resulting visual appearance of such a plant is one of extreme leafiness. This characteristic was rated subjectively in three categories: no leaf clustering, some leaf clustering and extreme leaf clustering. While *P. gracile* consistently lacks clustered leaves, other species showed no variation -- they all possess axillary leaf clustering.
12. **Presence of spherical secretory cavities ("glands") at the apex of the peduncle**

Specimens were placed in one of three subjective categories: those with no glands visible at the apex, those with some glands and those with numerous glands. In general, *P. gracile* lacks glands immediately below the inflorescence. Only 6 out of 41 specimens examined had glands. *P. albidum* and *P. carneum* usually possess glands but those of *P. carneum* are usually larger and more protuberant than those of *P. albidum*. The majority of the specimens of *P. feayi* examined lacked glands.

13. **Degree of stem branching**

*P. carneum* and *P. feayi* both exhibit extensive stem branching. In the former species, branching usually occurs in the upper half of the stem while in the latter species, branches arise below as well as above. Most *P. albidum* specimens examined were branched above, but there were also ones lacking branching, the plant composed only of primary stems. *P. gracile* is usually unbranched.

The determination of this characteristic depends, to a large extent, on the age of the plant. Greenhouse studies indicate that young stems will not branch until they have nearly reached their maximum length. At this time, axillary buds become active and elongate. Thus, a specimen of a young plant will not necessarily indicate its ultimate branching pattern.
14. Growth habit

Growth habit is difficult to determine from herbarium specimens. Even when the whole plant is present, it is often manipulated by the collector so as to make it a more aesthetically attractive specimen. Objectivity in designating a specimen prostrate, decumbent, or erect is difficult to achieve. Often a determination can be made by noting the diameter of the stem, the thicker-stemmed plants being erect in growth habit. Herbarium studies, complemented by field experience, can perhaps provide a reasonable estimate of the differential growth of the species.

*P. gracile* with its thin stems is prostrate with the tips of the branches weakly assurgent. Since it grows in grassy areas, it obtains some support from the surrounding grass. *P. albidum* is variable in growth habit, a variation that provided the first clue that it might have had a hybrid origin. Sometimes it is prostrate with assurgent peduncles similar to those of *P. gracile*. The other extreme is an almost erect plant, the stems supporting themselves and the inflorescence. *P. carneum*, with its thick stems is erect, *P. feayi* is also erect but the entire plant is often hemispherical in appearance, the outermost branches making an angle of about 45 degrees with the ground. Often a part of the lower stem is completely prostrate, even at times underground. In this case, axillary branches arise from this "rhizome," bearing spikes at their apices. The "rhizome" usually develops a periderm and
is corky in appearance.

15. **Curvature of rachis and leaflets after drying**

This is almost an exclusive characteristic of the leaves of *P. carneum*. Over one-half the specimens examined had the rachis and leaflets curved.

16. **Variation in stem ribbing below the leaf**

Three patterns were found in these species. The first is a complete lack of vertical ribbing immediately below the leaves: 45% of the *P. feayi* specimens and 20% of those of *P. carneum*. A second pattern is characterized by three vertical ribs below the leaves: 50% of the material of *P. feayi*, 75% of *P. carneum*, 80% of *P. albidum* and 15% of *P. gracile*. Thirdly, a single vertical rib was characteristic of 85% of the *P. gracile* specimens. From an external examination, these ribs appear to be vascular bundles from which the epidermis has shrunk in drying. The central rib is always below the leaf axis. The two lateral ribs, if present, are on the stipule axes.

17. **Diameter of stem at base**

The diameter was measured at the point where the stem emerges from the ground. It proved a valuable distinguishing feature of the four species (Fig. 28, char. 17).

18. **Length of bracts at anthesis**

Bract length has been used in almost all species of *Petalostemon* as a taxonomic characteristic. It must, however, be employed with caution because the bracts elongate during...
anthesis. For example, mature bracts of *P. gracile* equal the calyx lobes at the base of the inflorescence but are shorter than the tube at the apex. This variation has apparently not been appreciated by previous authors. In an attempt to obtain consistency in determination, measurements were taken from spikes with one-half their flowers open and specifically, on bracts subtending flowers that had just undergone anthesis.

Bract length was found to be variable. *P. gracile*, *P. carneum* and *P. albidum* had bracts that varied in length from subequal to the calyx tube, to approximating or exceeding the lobes. On the other hand, the bracts of *P. feayi* are uniformly shorter than the calyx tube.

19. **Length of apical petal blade**, and

20. **Length of apical petal claw**

Total petal length, claw and blade inclusive, was similar for the four putative species — approximately 3.5 mm for *P. gracile*, 3.7 mm for *P. albidum*, 3.8 mm for *P. carneum* and 3.9 mm for *P. feayi*. However, the relationship between the length of the claw and blade varied and proved valuable in the separation of the four taxa. *P. gracile* possesses the shortest petal blades and the longest petal claws, the two being almost equal in length. *P. albidum* possesses longer blades and relatively shorter claws, *P. carneum* even longer blades and shorter claws, and *P. feayi* the longest blades and shortest claws. A ratio of petal blade length to petal claw length was calculated for each of the specimens examined (Fig.
21. **Length of ventral calyx lobe, and**

22. **Length of calyx tube**

Calyx measurements have often been used as key characteristics in *Petalostemon*. To avoid ambiguity, I have chosen the base of the ventral lobe to be the dividing line between tube and lobe, and all lobe measurements are of the ventral lobe. Calyx lobe length, tube length and total calyx length (sum of lobe and tube length) are presented in Fig. 28, chars. 21, 22 and 21+22.

23. **Degree of bracteole pubescence**

All species showed varying degrees of bracteole pubescence ranging from glabrous to extremely pubescent except for *P. feayi*, the bracteoles of which were consistently pubescent.

24. **Presence of bract "heel"**

This characteristic proved valuable to Isely and Welsh (1960) in their study of *P. candidum* and *P. occidentale*. However, it appears to be of little value in differentiating among the species herein under consideration. *P. gracile* lacks a well developed heel. The other species exhibit varying degrees of heel development.

25. **Degree of gynoecial pubescence**

*P. gracile* and *P. feayi* possess only glabrous ovaries. Barely a few long cilia at the base of the style are present. The ovaries of *P. albidum* and *P. carneum* are usually
pubscents; completely glabrous ovaries were not observed in *P. albidum*; about 25% were glabrous in *P. carneum*. Regardless of the degree of ovary pubescence, the style was consistently bearded in all species for at least the proximal one-third of its length.

26. **Width of the standard**

Standard width was characteristic of the species to the degree indicated in Fig. 28, char. 26.

27. **Length of terminal rachis extension**

The "rachis extension" is the length of rachis from the insertion of the petiolules of the distal pair of leaflets to the base of the petiolule of the terminal leaflet. This characteristic can be effectively used to separate *P. gracile* from the other species. *P. gracile* possesses an extension varying from 0.6--2.8 mm, whereas, the extension is short or lacking in *P. albidum*, *P. carneum* and *P. feayi*.

28. **Length of extension of androeclial sheath from calyx**

The androeclial sheath does not extend beyond the calyx lobes in *P. gracile*. It rarely exceeds the lobes in *P. albidum* and *P. carneum* (4% of the specimens of the former species and 10% of the specimens of the latter). Conversely, the androeclial tube equalled or exceeded the calyx lobes in 85% of the specimens of *P. feayi*.

29. **Maximum leaflet number**

Leaflet number was determined for *P. gracile*, *P. albidum* and *P. carneum*. If used in conjunction with other
characteristics, leaflet number can be useful in the identification of species. The maximum leaflet number in *P. gracile* is usually seven or nine; 65% of the material examined possessed the lower number. Leaflet number of *P. albidum* varied from three to seven. Only 2% of the specimens possessed three; 74% possessed five and 24% possessed seven. The maximum number of leaflets of *P. carneum* ranged from five to eleven. The frequency was as follows: five, 6%; seven, 28%; nine, 48%; eleven, 18%.

The wide range of leaflet number in *P. carneum* is interesting because those specimens with the leaflet numbers of five and seven are mostly southern in distribution, while those having eleven leaflets are largely northern.

**Analysis of measured characteristics**

The characteristics which proved useful in separating the species of this section are graphically presented in Fig. 28.

The isolation of *P. feayi* from the trio of *P. gracile*, *albidum* and *carneum* is consistently shown in all the selected characteristics. Not only is the arithmetic mean of a given characteristic often quite different, but the variation is always less as is the standard deviation. I interpret this to indicate the homogeneity of *P. feayi* as well as its remoteness from the other species.

In each of the 12 characteristics, *P. albidum* is found to be intermediate between *P. gracile* and *P. carneum*, but in
Fig. 28. Graphical analysis of selected characteristics in section Carnei. The numbers used are those of characters underlined on pp. 87--88. The thin line represents the total range of variation; the thick line, + one standard deviation; and, the central cross mark, the arithmetic mean. G = P. gracile; A = P. albidum; C = P. carneum; F = P. feayi
2. Peduncular bract length

4. Internode length

3/4. Rachis/internode length

7. Peduncle length

8/9. Inflorescence length/width

8 x 9. Inflorescence length x width
Fig. 28 (Continued).
17. Stem thickness

19/20. Petal blade/claw length

21. Calyx lobe length

22. Calyx tube length

21 + 22. Total calyx length

26. Standard width
almost all cases, the ranges overlap as do the standard deviations. It is evident that no single characteristic can be used to differentiate between the three species. Multiple characteristics must be used.

Using the technique followed by Isely and Welsh (1960), each of the characteristics was standardized so that most of the \textit{P. gracile} specimens would fall on one end of the scale and most of the \textit{P. carneum} specimens at the other. This was accomplished by dividing the total range of variation shown by all species for each characteristic into three parts and assigning the numbers 0, 1, or 2 to each part respectively. The dividing points were subjectively chosen following examination of the rough data. In general, each range contains approximately one-third of the total number of specimens studied, with a correction factor added to allow for the disproportionate number of specimens of each of the putative species. The ten characteristics chosen for analysis together with their subdivision ranges is shown in Table 5. To avoid redundancy, some of the characteristics previously analyzed were eliminated. Average values for each of the ten are shown in the polygonal graph (Fig. 29). This graph reiterates the fact that \textit{P. albidum} is intermediate in all characters. The values of all characteristics for each collection are then added producing a total "index" for each specimen or group of specimens from the same collection. This index would run from 0 for an
Table 5. Standardized, selected characteristics drawn from those listed on pp. 87-88. The total range of variation has been divided into 3 parts, arbitrarily numbered 0, 1, 2

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>Dividing points</th>
</tr>
</thead>
<tbody>
<tr>
<td>2. Length of bracts on peduncles</td>
<td>0 → &lt; 2.0 mm = 0</td>
</tr>
<tr>
<td></td>
<td>2.0 → &lt; 3.5 mm = 1</td>
</tr>
<tr>
<td></td>
<td>3.5 → 6.0 mm = 2</td>
</tr>
<tr>
<td>3. Ratio of length of leaf rachis to length of subtending internode</td>
<td>0.4 → &lt; 1.0 mm = 0</td>
</tr>
<tr>
<td></td>
<td>1.0 → &lt; 1.5 mm = 1</td>
</tr>
<tr>
<td></td>
<td>1.5 → 5.23 mm = 2</td>
</tr>
<tr>
<td>7. Length of peduncle</td>
<td>3.5 → &lt; 50.0 mm = 0</td>
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<tr>
<td></td>
<td>50.0 → &lt; 80.0 mm = 1</td>
</tr>
<tr>
<td></td>
<td>80.0 → 200.0 mm = 2</td>
</tr>
<tr>
<td>8. Length of spike x width of spike</td>
<td>36.0 → &lt; 80.0 mm = 0</td>
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<tr>
<td></td>
<td>80.0 → &lt; 125.0 mm = 1</td>
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<tr>
<td></td>
<td>125.0 → 272.0 mm = 2</td>
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<tr>
<td>10. Abaxial bending of bract tip</td>
<td>Maximum bending = 0</td>
</tr>
<tr>
<td></td>
<td>Moderate bending = 1</td>
</tr>
<tr>
<td></td>
<td>No bending = 2</td>
</tr>
<tr>
<td>15. Curvature of rachis and leaflets after drying</td>
<td>No curvature = 0</td>
</tr>
<tr>
<td></td>
<td>Partial curvature = 1</td>
</tr>
<tr>
<td></td>
<td>Full curvature = 2</td>
</tr>
<tr>
<td>17. Thickness of stem base</td>
<td>0.6 → &lt; 1.1 mm = 0</td>
</tr>
<tr>
<td></td>
<td>1.1 → &lt; 2.1 mm = 1</td>
</tr>
<tr>
<td></td>
<td>2.1 → 5.5 mm = 2</td>
</tr>
<tr>
<td>19. Ratio of length of apical petal blade to length of petal claw</td>
<td>1.0 → &lt; 1.4 mm = 0</td>
</tr>
<tr>
<td></td>
<td>1.4 → 2.0 mm = 1</td>
</tr>
<tr>
<td></td>
<td>&gt; 2.0 mm = 2</td>
</tr>
<tr>
<td>21. Total calyx length</td>
<td>2.5 → &lt; 3.1 mm = 0</td>
</tr>
<tr>
<td></td>
<td>3.1 → 3.65 mm = 1</td>
</tr>
<tr>
<td></td>
<td>&gt; 3.65 mm = 2</td>
</tr>
<tr>
<td>26. Width of standard</td>
<td>1.1 → &lt; 1.4 mm = 0</td>
</tr>
<tr>
<td></td>
<td>1.4 → &lt; 1.8 mm = 1</td>
</tr>
<tr>
<td></td>
<td>1.8 → 2.9 mm = 2</td>
</tr>
</tbody>
</table>
Fig. 29. Polygonal graph showing the average values for the characteristics enumerated in Table 5 for *P. gracile* (innermost line), *P. albidum* (middle line), and *P. carneum* (outer line). The center point of the graph is 0, the first cross mark is 1, and the peripheral cross mark is 2.
"ideal" \textit{P. gracile}, to 20 for an "ideal" \textit{P. carneum}. Fig. 30 shows the frequency of each of the index numbers in all the specimens studied. All the sheets tentatively identified as \textit{P. gracile} showed a species index of 0--5, those identified as \textit{P. albidum} 6--11, and those identified as \textit{P. carneum} 13--20. There was no overlap in the index number between putative species. This clearly shows that while the three species in question cannot be differentiated consistently by a single characteristic, that by applying several, they are completely separated.

One collection deserves specific comment — Isely and Wemple 9238M, 2 miles south of Old Town, Dixie county, Florida. The environment was a dry, sandy, disturbed area, probably an abandoned field — a typical habitat for \textit{P. albidum}. This particular population had every appearance of a classical "hybrid swarm." The growth habit of the plants ranged from prostrate-scrambling to almost erect and the flower color varied from white to pale pink. A mass collection was made and a species index calculated for each member of the collection (Fig. 30, the clear and stippled rectangles). The two individuals with an index, respectively, of 11 and 15, were pale pink in corolla color.

\textbf{Summary}

Four species are recognized in this southeastern complex. \textit{P. feayi} is distinct from the other three on the basis of
Fig. 30. Species indexes computed for *Petalostemon gracile*, *P. albidum* and *P. carneum*. Based on the total of the ratings of the 10 characteristics enumerated in Table 5. The white and stippled rectangles represent specimens from the mass collection, Isely and Wemple 9238M. The two stippled squares represent specimens from this mass collection whose flowers were pale pink.
several unique characters. The remaining three are differentiated easily by utilizing multiple characteristics. The intermediacy of *P. albidum* between *P. gracile* and *P. carneum* on all characteristics suggests that *P. albidum* is possibly of hybrid origin. Support for this hypothesis is also found in the habitat occupied by *P. albidum* -- disturbed areas, which possibly came into existence with the advent of man; the geographical distribution of *P. albidum*, intermediate between the putative parents; and, the discovery of introgressive populations. That *P. feayi* has not entered into active hybridization with the other three species is indicated by its uniformity in all measured characteristics.

The ideograms (Figs. 31, 32) summarize vegetative and floral differences between the four species.

**Key to the Species**

1. Flowers white; ranging from southern Mississippi through the panhandle of Florida.

2. Stems weak, usually less than 1.1 mm thick at the base; leaves remote, not fascicled, leaflets 7--9, usually 2 mm or more wide, rachis extension beyond the apical pair, 0.8 mm or greater; peduncles short, usually less than 50 mm, with bracts less than 2 mm long; buds with bract tips recurved; limited to the Florida panhandle and southeastern Georgia, southern Mississippi and southern Alabama.
Fig. 31. Ideogram summary of vegetative and floral differences between *Petalostemon gracile*, G; *P. albidum*, A; *P. carneum*, C; and, *P. feayi*, F. Black areas represent minimum dimensions while the entire rectangles or lines represent maximum dimensions. a. length and width of spike; b. length of peduncle; c. length of peduncular bract; d. length of internode; e. length of leaf rachis; f. length and width of subapical leaflet; g. thickness of stem base
Fig. 32. Ideogram summary of the floral differences between *P. gracile*, G; *P. albidum*, A; *P. carneum*, C; and *P. feayi*, F. Black areas represent minimum dimensions while the entire rectangles or lines represent maximum dimensions. a. length of calyx tube; b. length of ventral lobe; c. length of apical petal claw; d. length of apical petal blade; e. width of standard blade.
2. Stems stout, usually greater than 1.1 mm at the base; leaves close and fascicled, leaflets 5–7, usually less than 2 mm broad, rachis extension less than 0.8 mm; peduncles usually 50 mm or longer with bracts longer than 2 mm; buds with straight bracts; central and southern Georgia and the Florida peninsula.

4. P. albldum p. 119

1. Flowers pink; peninsular Florida and southern Georgia.

3. Spikes cylindrical; bracts longer than the calyx tube; anthers equalling petals at anthesis.

5. P. carneum p. 120

3. Spikes globose; bracts shorter than the calyx tube; anthers exserted beyond the petal apex.

6. P. feayi p. 124

3. PETALOSTEMON GRACILE Nutt. (Fig. 33)


Description

Root with strong napiform development from which radiate multiple, usually unbranched, weakly assurgent, usually non-striate stems, 3--6 dm long and 0.6--1.3 mm in diameter. Internodes at the middle of the stems 9--32 mm in length, usually longer than the leaves. Leaves solitary at the nodes, usually subtended by a single rib gradually fading basally into the round stem; rachis from 8--22 mm long, extending beyond the terminal pair of leaflets 0.7--2.8 mm. Leaflets on mature leaves 7--9, glabrous, 5.5--12.0 mm long, 1.2--3.8 mm broad, always less than 5 times as long as broad, elliptical to elliptical-oblanceolate. Peduncles 0.4--10.8 cm long, with sterile bracts up to 2.8 mm in length disposed at varying distances below the spikes. Spikes columnar, 6--15 mm long, 6--8 mm wide, about 1.5 times as long as broad. Bracts elliptical, equalling or slightly less than the lobes at anthesis, the tips usually recurved, a pair of subulate, often ciliate bracteoles arising from the base of each. Calyx tubular, split dorsally to more than one half its length; the tube 1.9--2.6 mm long, glabrous, glistening white, the rachis attachment point below the longitudinal calyx axis; ventral lobe 0.5--1.2 mm long, green, fleshy and pubescent on the inner surface and margins; glands apparent at the base of the lobes on drying. Corolla white, the standard shorter than the other petals and relatively narrow, the blade 1.1--1.9 mm wide, rounded at the apex; the claw 3--4 times as thick as the
Fig. 33. Geographic distribution of *Petalostemon gracile* and *P. albidum*
claws of the apical petals. Apical petals uniform in shape, the two medial petals inserted lower than the two lateral petals; claws 1.2--2.9 mm in length; blades 1.3--2.9 mm long. Staminal tube not exserted beyond the calyx lobes, filaments shorter than petals, anthers yellow. Ovary always glabrous, style bearded proximally to 1/3--1/2 its length, predominantly on the lower surface.

4. *Petalostemon albidum* (T. & G.) Small (Fig. 33)

_Petalostemon albidus* (T. & G.) Small Fl. SE. U. S. 630. (1903). Based on *Petalostemon carneum* f. albidum T. & G.


**Description**

Stems numerous, prostrate to erect, 6--10 dm long, 1.0--2.6 mm in diameter, usually subtended by three ribs; leaf rachis 7--22 mm in length, extension beyond the terminal pair of leaflets less than 0.8 mm; leaflets 3--7, commonly 5, involute, 5--12 mm in length, 0.9--2.0 mm wide, usually about six times as long as wide. Peduncles 5--120 mm in length with pronounced glands at the apex; peduncular bracts to 5.5 mm in length. Spikes columnar, 8--22 mm long, 6--9 mm in width. Bracts equalling or exceeding the calyx lobes at anthesis, lanceolate, usually with straight tips, the base flanked by
subulate bracteoles. Calyx tubular, glabrous except for inner surfaces of the lobes, entire calyx 2.7--4.0 mm long, the tube 2.1--3.0 mm long and the ventral lobe 0.5--1.1 mm long. Corolla white; standard with claw 2--3 times as thick as apical petal claws, blade wider than apical petal blades, 1.2--2.9 mm wide; apical petals with blades 1.8--3.3 mm long, claws 1.0--1.9 mm long; claws about one-half the length of the blade. Androecial tube seldom exserted beyond lobes, anthers yellow, usually equalling the petal apices following anthesis. Ovary always + bearded, the style bearded proximally from one-third to more than one-half its length.

5. PETALOSTEMON CARNEUM Michx. (Figs. 34; 51D, 1-3)


_Psoralea carnea_ (Michx.) Poir. in Lam. Encycl. 5: 694. (1804). Based on _Petalostemum carneum_ Michx.


Fig. 34. Geographic distribution of *Petalostemon carneum* and *P. feayi*
**Description**

Stems many, erect, 5--10 dm long, fine-striate, usually branched above, 1.5--5.5 mm thick; internodes 3--23 mm long. Leaves fascicled, the rachis 6.5--23.0 mm long, often curving when dried, extending less than 0.8 mm beyond the terminal pair of leaflets; leaves subtended by three stem ribs, or ribs lacking -- never a single rib; leaflets 5--11, usually 9, moderately involute, 5--11 mm long and 1--3 mm wide, usually about five times as long as wide. Peduncles from 11--200 mm long, usually glandular at the apex; peduncular bracts subulate, 0.8--6.0 mm long. Spikes columnar, 10--31 mm long and 7--10 mm wide. Bracts usually equalling lobes at anthesis, lanceolate with straight tips, their base flanked by subulate bracteoles. Calyx tubular becoming strongly ribbed upon drying, glabrous except for inner surfaces of the lobes and their margins, entire calyx 3.3--4.7 mm long, the tube 2.2--3.4 mm long and the ventral lobe 0.8--1.8 mm long. Corolla pink; the standard blade orbicular, emarginate and wider than the apical petal blades, 1.2--2.9 mm wide, the claw twice as thick as the claws of the apical petals; apical petal blades 1.9--3.9 mm long, the claws 0.7--1.7 mm long, less than one-half the length of the blade. Androecial tube often equalling the calyx lobes; anthers extended, equalling the length of the petals, yellow-orange at anthesis. Ovary usually bearded or at least slightly pubescent; style bearded proximally from one-third to more than one-half its length.
6. PETALOSTEMON FEAYI Chapm. (Figs. 34; 51D, 4)

_Petalostemon feayi_ Chapm. _Fl. S. U. S._ ed. 2. 615. (1883). Type in US. (1)(2).


**Description**

Stems numerous, 2--6 dm long, arising from a horizontal rootstock or caudex; the central stems erect, the peripheral ones reclining, the whole often forming a hemispherical clump; the lower portions of the stems often with a corky exterior, the upper portions branching, finely striate or smooth; internodes 4--16 mm long. Leaves fascicled, rachis 8--22 mm long, often curved when dried, extension beyond the terminal leaflet pair always less than 0.8 mm; ribs below leaves often lacking or three in number. Leaflets on mature leaves 7--9, usually 7, filiform, involute, often curved when dried, 5--13 mm long and 0.5--1.4 mm broad, usually ten times as long as broad. Peduncles 10--80 mm long, usually lacking glands at the apex; sterile peduncular bracts 0.8--3.2 mm in length. Spikes globose, 6--11 mm long and 7--10 mm wide, the lower flowers declined. Bracts shorter than the calyx tubes, narrowly lanceolate, strongly keeled, flanked at the base by a pair of narrowly lanceolate bracteoles. Calyx tubular, slightly gibbous dorsally, glabrous except for a slight ciliation on the inner surfaces of the lobes, 3.2--4.5 mm long, the tube 2.5--3.5 mm long and the ventral lobe 0.7--1.4
mm long. Corolla pink, rarely white; the standard wider than
the apical petals, orbicular, 1.4—2.8 mm wide, the claw 3—4
times as thick as the apical petal claws; blades of the apical
petals 2.2—3.6 mm long, the claws 0.9—1.8 mm long, about one-
half the length of the blade. Androecial tube almost always
exserted beyond the calyx lobes, the anthers exserted beyond
the apices of the petals, orange at anthesis. Ovary globular,
glabrous, the style lightly pubescent proximally to one-half
its length, occasionally glabrous.

B. PROSTRATI

**Distinguishing characteristics**

Stems prostrate, glabrous, covered with reddish-brown,
spherical glands; leaflets glabrous, cuneate-ovate; spikes
subsessile, becoming lax in fruit; bracts broad and glabrous
with scarious and ciliate margins, early deciduous; paired
bracteoles present; calyx glabrous except for ciliate lobes,
prominently glandular between the calyx ribs, the tube split
dorsally to over one-third its length; corolla rose-purple,
standard broad-cordate.

7. *PETALOSTEMON PROSTRATUM* Woot. & Standl. (Fig. 35)

Description

Stems prostrate, 2--6 dm long, round at the base becoming striate toward the apex, straw-colored, glabrous, covered with reddish-brown, spherical glands. Stipules subulate, 2.5 mm long or less, often curved. Leaves glabrous, solitary; leaflets 7--9 (11), inserted in the distal one-half of the rachis, 6 mm long, 3 mm wide, cuneate-ovate, finely gland-dotted below. Spikes subsessile, 35--90 mm long, 8--9 mm wide, becoming lax in fruit. Bracts glabrous, margins scarious, ciliate, 2.5 mm broad, precocious, exceeding the calyx lobes in bud, equalling them immediately prior to anthesis, then deciduous, leaving a prominent heel on the glabrous rachis. Paired, pubescent bracteoles flank the calyx, 1.3 mm in length. Calyx tube glabrous, 3.2 mm long, slightly ten-ribbed, with 3--7 protuberant, yellow, pellucid glands lying between the ribs, each gland 0.2--0.3 mm long and 0.1 mm wide; tube slit dorsally to over one-third its length, the margin of the slit ciliate; lobes lanceolate, short-ciliate at the margins and on the inner surfaces, the ventral lobe 1.3 mm long. Corolla rose-purple; standard suborbicular, strongly lobed at the base, 4 mm broad, 2.8 mm long; the apical petals 3.5--3.7 mm long, 1.2--2.0 mm broad, the claws 0.7 mm long. Androecial tube not exserted beyond the calyx lobes at anthesis. Ovary 1.8 mm long, 1 mm in diameter, slightly ciliate on the distal portion; style ciliate dorsally only at its proximal end, 8 mm long. Pod not exserted beyond the calyx lobes, slightly
Distribution and phenology

Albuquerque and Belen, New Mexico. Known only from these two locations in Bernalillo and Valencia counties. Maximum flowering time probably late August.

Observations

I have studied the type specimen (Winnie Howard 17 Albuquerque, New Mexico, 1900) and two other collections from the same locality (Rusby 6 September 1909; Rusby 8 September 1909). Wooton and Standley cite another specimen (Wooton 1 August 1906 Belen, New Mexico). To my knowledge these are the only collections of this species.

*P. prostratum* is very distinctive but shares many characteristics with *P. foliosum* and *P. sabinale*, viz.: glabrous stems, leaves and calyx tubes; paired bracteoles flanking the calyces; deeply, dorsally-slit calyces and lavender to pink corollas. The calyx glands of *P. prostratum* are similar in size, shape and color to those of *P. sabinale*. It is noteworthy also that all three species are restricted endemics, although widely separated geographically.

However, *P. prostratum* differs from the other two species in several features, among them: 1) prostrate growth habit; 2) lower leaflet number and obovate leaflets; 3) wide bracts with prominent, scarious margins; 4) suborbicular, prominently
Fig. 35. Geographic distribution of *P. foliosum, P. sabinale* and *P. prostratum*
lobed standard with a narrow claw; and 5) an elliptically shaped ovary. Therefore, I have not included *P. prostratum* in the Foliosi. Probably it is related to that group, but not to the same degree that *P. foliosum* and *P. sabinale* seem to be associated.

In the description of the species, the authors state the stamen number to be six. In all flowers that I have examined, the stamen number was five.

C. CANDIDI

**Distinguishing characteristics**

Stems glabrous; paired bracteoles, arising from the calyx attachment point on the rachis flanking each calyx; calyx not inflated, + strongly ten-ribbed, glabrous to slightly pubescent, the tube white, the lobes green with prominent glands at their base between the calyx nerves; corolla white, the standard strongly lobed basally and the claw the same diameter as the apical petal claws; ovary with characteristic teardrop-shaped glands on the proximal lateral surfaces.

**Distribution and ecology**

Wide ranging through the tall grass prairies of the central United States, southern Canada, across the short grass plains to the Rocky Mountains and south to Arizona, northern Mexico and Texas. Apparently adapted to a wide range of soil
types; calcareous prairie soils, rocky limestone soils, clays and sands.

P. candidum, occupying the tall grass prairies of the central United States and Canada, is gradually replaced to the west by P. occidentale and to the south by P. multiflorum. Ecological sympatry occurs, however, only between P. candidum and P. multiflorum. All three species are interfertile, but allopatry and spatial separation of populations are probably important factors limiting hybridization. Of the three, P. multiflorum is distinctive and easily recognized, whereas there has been little agreement among botanists regarding the characterization of the other species. Isely & Welsh (1960) reviewed the controversy in detail, illustrating how, with multiple characteristics, the two species may be delimited. The work is summarized by Isely (1962).

Key to the Species

1. Leaflets 9—13 (5 on depauperate specimens), uniform over the entire stem; spikes globose to ovoid, less than 1.5 cm long, entire inflorescence corymbose; bracts shorter than the calyx tube in bud and scarcely exceeding the tube at anthesis.

8. P. multiflorum p. 132
1. Leaflets 5—9; lower leaves often with larger leaflets than upper ones; spikes cylindrical, usually exceeding 1.5 cm, not corymbosely arranged; bracts exceeding calyx lobes in bud equalling or exceeding them at anthesis.

2. Rachis: elongating in fruit, separating calyces; calyx usually finely puberulous, strongly ten-ribbed.

9. P. occidentale p. 137

2. Rachis not elongating, calyces remaining close together even in fruit; calyx glabrous, ten-ribbed but with rounded ridges.

10. P. candidum p. 149

8. PETALOSTEMON MULTIFLORUM Nutt. (Figs. 36, 510)


Description

Plants with coarse, black root system terminating in a woody caudex, occasionally with short rhizomes. Stems many, 3--8 dm long, the central ones erect, the lateral ones almost horizontal often giving a hemispherical appearance to the entire plant; stems glabrous, round when fresh, drying striate above, pale straw color with prominent yellow to red glands;
much branched, especially in the upper one-half of the stem, the uppermost flowering branches usually leafless. Stipules lance-subulate, 1--2 mm long, chartaceous, usually fugacious. Mature leaf rachis 5--15 (25) mm long, never extended beyond the terminal pair of leaflets more than 0.5 mm. Leaflets (5) 7--13, linear-oblong or linear-oblanceolate, often obtuse or mucronate, 6--14 mm long and 2--3 mm wide; prominently gland-dotted only on the lower surface. Flowers disposed in numerous, short, usually globose spikes, 8--12 (25) mm long and 8--10 mm thick, terminating the many upper branches of each main stem. Spike subtended by a whorl of sterile bracts that persists even after fruits fall from the rachis; fertile bracts never exceed the calyx lobes in early bud and are usually shorter than the calyx tube at anthesis, 2.0--2.4 mm long, early deciduous, leaving a prominent "heel" on the rachis. Lance-subulate, ciliate, bracteoles arise laterally and abaxially from the calyx attachment point on the rachis in close proximity to the "heel," 0.1 mm wide at the base, 1.4--1.8 mm long. Calyx tube white, the base suffused with pink, drying straw-colored and strongly ten-ribbed, 2.2--2.6 mm long, 1.6--2.0 mm high; lobes green, deltoid, ciliate on margins, 1.0--1.4 mm long, terminating in a gland; prominent bronze glands between ribs at the base of the lobes. Corolla white, persistent, the standard suborbicular, deeply lobed at the base, 3 mm broad, 2.0--2.8 mm long, the claw 3 mm long; apical petals oblong, 2.2--2.8 mm long, 1.4--1.8 mm broad, the
claw 1.3--1.6 mm long. Androecial tube equalling the calyx
lobes at anthesis; filaments white; anthers pale yellow,
slightly exserted beyond petals. Ovary 1.3 mm long, 0.7--0.8
mm in diameter, slightly ciliate dorsally, otherwise completely
glabrous; 4--6 teardrop shaped protuberant glands are
located proximally on the sides of the ovary, the largest
above, the remainder decreasing in size below; pellucid when
fresh, drying bronze; style glabrous, inserted on the carpel
axis, equalling or slightly exceeding the anthers at anthesis.
Pod exserted from calyx in fruit, the beak directed upward
from the calyx axis. All parts of the plant producing a
pungent odor when crushed.

**Distribution and phenology**

Eastern Kansas south through central Oklahoma, central
and central-eastern Texas; one collection in Chihuahua, Mexico.
Limited to relatively dry, rocky prairies. Flowering begins
in mid May for the south Texas populations, mid June for those
in Oklahoma and mid July for those in Kansas, concluding in
early August.

**Observations**

This species is usually readily distinguished from *P.
candidum* and *P. occidentale* by the possession of many globose
spikes arranged in a corymbose manner and uniform leaves with
9--13 leaflets. Geographically, the range overlaps both with
Fig. 36. Geographical distribution of P. multiflorum
P. candidum and P. occidentale but, from my field experience, ecological sympatry occurs only with P. candidum. Although I have never seen these species growing in close proximity, there is evidence indicating occasional hybridization between the two. The putative hybrids possess elongated spikes and have bracts exceeding the calyx tubes, sometimes equalling the lobes at anthesis. The elongate spikes are terminal, whereas, the lateral spikes (those producing the corymbose pattern, characteristic of P. multiflorum) are often more globose. Two such collections are from the zone of sympatry: Wemple 396, Cotton Co., Oklahoma, (ISC); and Sizemore 270, Osage Co., Oklahoma, (OKLA). In both, spikes up to 25 mm long are common. These characteristics are matched by hybrids between P. candidum and P. occidentale I have synthesized in the greenhouse.

9. PETALOSTEMON OCCIDENTALE (Gray ex Heller) Fernald (Figs. 38, 51B)

Petalostemon occidentale (Gray ex Heller) Fernald


Description

Stems several, branching above, decumbent to erect, glabrous, 4-8 dm long; coarsely striate, often drying a glaucous, pale green. Stipules 3.0-4.5 mm long, drying brown, fragile. Mature leaf rachis, 10-20 (30) mm long bearing 5-7 (9) glabrous, gland dotted, elliptical-oblong or oblanceolate, often emarginate, involute leaflets, 5-10 (15) mm long, 2-4 (5) mm wide; often with larger leaflets at the base of the plant; the leaflet midrib is usually not prominent on the lower surface. Flowers disposed in a columnar spike which becomes
lax in fruit, 6--8 mm wide and up to 70 mm long; occasionally with a few short, sterile bracts at varying distances below the spike. Fertile bracts exceeding the calyx lobes in bud, deciduous prior to anthesis, usually leaving a short "heel" on the rachis. Bracteoles filiform, 1--2 mm long, slightly ciliate, inserted beside calyx attachment point on rachis, quite separate from the bract "heel." Calyx tube white, strongly ten-ribbed drying sharp-ribbed, not round-furrowed as in P. candidum; usually + pubescent between ribs, 2.3--2.9 mm long, 1.6--2.0 mm in diameter; lobes green, deltoid-lanceolate, ciliate at margins, the ventral lobe 1.0--1.3 mm long; prominent glands at base of lobes between ribs of calyx tube, drying bronze. Corolla white, standard 2.6--3.3 mm broad, 1.8--2.2 mm long, lobed at base, the claw 3.0--3.5 mm long; apical petals elliptical-oblanceolate, 2.5--3.0 mm long, 0.9--1.4 mm wide, the claw 1.1--1.3 mm long. Staminal tube exserted beyond calyx lobes at anthesis; anthers not extended to petal tips, pale yellow, drying yellow-brown. Ovary glabrous save for ciliate fringe on dorsal surface, 1.3--1.7 mm long, 0.8--1.0 mm in diameter: style glabrous, inserted slightly above carpel axis, 8--10 mm long, exceeding the petal tips. In fruit, the pod exceeding calyx, the beak directed upward, between dorso-lateral lobes.
Distribution and phenology

Southern Alberta, Saskatchewan and southwestern Manitoba, south throughout the short grass plains to western Texas, Durango, Arizona and southeastern Utah. Western representatives are always found at high altitudes, e.g. New Mexico, 6,000 ft. +, Arizona, 6,000 ft. +, Colorado, 4,500 ft. +. Adventive to the east in particularly xeric environments, e.g. the loess bluffs along the Missouri River at the Iowa-Nebraska border. Ubiquitous throughout its range except for the lower elevations to the west. It is found in sands, limestones and clays. Its aggressiveness is shown by its ability to colonize road cuts. Blooming time is from late May until early August, blooming first in the southern part of its range.

Nomenclature and observations

Except for the unverified virgatum to be discussed later, the epithet oligophyllum is the oldest applied to this taxon. It was not, however, elevated to the species level until two years after occidentalis was proposed, thereby losing priority. K. occidentalis Gray ex Heller is based on an unpublished Asa Gray name appearing on "Pringle's labels," P. candidus var. occidentalis. Fernald, in his later combination, Petalostemon occidentale, says:

... Heller definitely stated that he was deriving the name from one used on herbarium-sheets but unpublished by Gray. It seems proper, then, to cite
Gray as the originator of the name.

His combination was published as, *Petalostemum occidentale* (Gray) Fernald. According to currently accepted rules Fernald’s logic must be rejected since Gray’s epithet was not validly published. The proper name should be *P. occidentale* (Gray ex Heller) Fernald.

Since neither Heller nor Fernald designated a type specimen, I have selected as a lectotype, a C. G. Pringle collection labeled, "*Petalostemon candidus* Michx., var. *occidentalis*, Gray. Mesas around the Mustang Mts. 26 June 1884," (US 24508).

*Petalostemon gracile* Gray is *Fendler No. 135* from *Plantae Fendlerianae* (Gray 1849). One of this collection is at MO and it is clearly *P. occidentale*. I have not seen the type of *P. gracile* var. *oligophyllum* Torr. in Emory but according to Heller (1898):

The type, but unnamed, is in the herbarium of Columbia University. On a small slip of paper pasted upon the sheet is recorded in Torrey’s hand "Emory, Sept. 28th, 1846. Valley of Del Norte."

Heller continues by commenting that according to the journal this collection was made near Albuquerque, New Mexico. The Rydberg trinomial, *K. candida occidentalis* represents the first attempt to merge *P. candidum*, *P. occidentale* and *P. multiflorum* into a single species with three varieties. He cites no synonymy but lists 19 representative collections, all in NY. His publication of *P. diffusa* followed later the same
year and was said to be like *K. candida occidentalis,* "but prostrate, decumbent, or diffuse... *Petalostemon gracilis* Gray in Fl. Fendl. may belong here. Deuel Co., Rydberg 58." I have examined four collections labeled Rydberg 58, only two of which have labels indicating the same location, although all are from Deuel Co. Three are referrable to *P. occidentale* but the fourth is definitely *P. candidum,* the most western collection of that taxon. Rydberg does not include the epithet *diffusa* in *Flora of North America* (1919-1920).

*P. truncatus* Rydb. is based on Palmer 284, NY, collected at Tepehuanes, Durango. I have examined the type, an isotype at US, as well as three sheets annotated by Rydberg reassigning them to this taxon. The definitive characteristic of this species, according to Rydberg, is the presence of petals truncate at the base of the lamina. Had he examined petals from specimens collected throughout the range of *P. occidentale* he would have found that truncate petals are not an exclusive characteristic of plants from northern Mexico. With regard to petal shape I sampled specimens at random from this taxon (Fig. 37). The least truncate petals seen were from one of Rydberg's own collections (Rydberg 59, Deuel Co., Nebraska). The type location of *P. truncatus* is the southern-most spot on the distribution map.

*P. sonorae,* another Rydberg name proposed in the *Flora of North America* (1919-1920), is based on a Schott collection
Fig. 37. Variation in apical petals of Petalostemon occidentale throughout its range. A-C. Petals of specimens annotated in Rydberg's hand as P. truncatus. D-I. Petals of P. occidentale.
A. Pringle 1216, Guerrero, Chihuahua (US).
B. Pringle 1216, Guerrero, Chihuahua (NY).
C. Nelson 7248, below Pacheco, Chihuahua.
made during the Emory, Mexican Boundary Survey, No. 241. The location is shown on the distribution map as the most western Mexican collection. According to Rydberg, it is characterized by having: 1.) scattered leaves, 2.) long acuminate bracts exceeding the calyces in bud and in fruit, and 3.) compact spikes. I have examined the type and an isotype at NY and find them both to be well within the range of variability of *P. occidentale*. Both specimens have lost most of their upper leaves, the lower leaves, which are usually more scattered and larger, remain. The weak midrib, characteristic of *P. occidentale*, is clearly seen. The bracts barely exceed the calyx lobes in late bud and are usually lost prior to anthesis. There is evidence of some, although not excessive rachis expansion. T. H. Kearney recognized this taxon and five Arizona specimens are so labeled in US. On one (Peebles 5329) is the comment, "Related to *P. oligophyllus* and perhaps not sufficiently distinct. (THK)."

*Petalostemum virgatum* was included in the synonymy of *P. candidum* by Rydberg (1919-1920). Perhaps this placement was motivated by the title of Nees von Esenbeck's paper, "Botany of Missouri." From the description in the original publication, the specimen would seem to be *P. occidentale*. Particularly indicative of this is, "Calyx ... glaber aut pubescentia laxissima minutissimaque conspersus, compressus, ...." I have been unable to locate the Nees herbarium and thus have not seen a type specimen for this name. If the description is
verified by a type, the epithet has clear priority over all other names and should be adopted.

*Petalostemon occidentale* can be distinguished from *P. candidum* on the basis of multiple characteristics as previously discussed. Gross, visual characters, easily seen in the field are: 1.) a more diffuse, spreading growth pattern, 2.) a lower leaflet number with smaller leaflets and 3.) a spike that elongates following anthesis. *P. occidentale* is not as homogeneous a species as *P. candidum*. Variation appears chiefly in leaflet size and shape. Throughout most of its range, the leaflets are small. If large leaflets are present, they are restricted to the lower portions of the stems; however, in Colorado and Montana there are specimens possessing only large leaflets. This condition mimics the leaflet size found in *P. candidum* and has been partly responsible for the identification of some Rocky Mountain material as *P. candidum*. In the same general area where the broad leaflet forms are found, the more typical plants have also been collected. Variation is also seen in calyx pubescence. Many of the western specimens lack pubescence entirely. This is particularly evident in those from the southwest. The ribs of the calyx nerves are also less prominent in the western specimens and some have rather pronounced bract "heels." In short, many of the western specimens seem more "candidum-like" than those found in the zone of overlap of the two species. Superficially one might hypothesize that the difference in
Fig. 38. Geographic distribution of *Petalostemon occidentale*
morphology of the eastern species in the sympatric region might be a reflection of a genetic barrier, operating to prevent introgression with *P. candidum*. Such a situation, called a "reverse cline" (Creed *et al.* 1959 and Harper *et al.* 1961) has been postulated in the study of animal species. That such a hypothesis is not warranted in this case, is the fact that the two species, even when geographically sympatric are not at all ecologically sympatric. *P. occidentale* is restricted to xeric habitats while *P. candidum* grows in the richer more mesic prairie habitats. A better explanation for the greater variability of *P. occidentale* as compared to *P. candidum* might be varying environments over the range in which the former species grows. As indicated above, all the western populations of *P. occidentale* are high altitude forms. Undoubtedly these habitats have acted as selectors for certain phenotypes different from those at the lower elevations. The variance exhibited by *P. occidentale* is probably a reflection of a basic plasticity within its genetic makeup.

10. PETALOSTEMON CANDIDUM Michx. (Figs. 39, 51A, 54B)


Description

Stems few, arising from a woody caudex, 3--10 dm long, usually erect, moderately branching above; glabrous, striate, the protruding ribs drying white or pale green. Stipules white when fresh, drying straw-colored, persistent, subulate, 4--7 mm long. Leaves remote, glabrous, slightly fascicled, usually with not more than three small, inconspicuous, axillary leaves; rachis green, winged, often expanded just proximal to the petiololes forming a tubercle, always extended 1.0--3.5 mm beyond the terminal pair of leaflets; leaflets 5--9, elliptical to oblanceolate, 10--30 mm long, 2.5--7.0 mm wide, the lower surface dotted with small glands and possessing a prominent midrib when dry which usually terminates in a micro. Peduncles 5--10 cm long, interrupted by prominent sterile bracts, 1--2 cm long, scattered below the spikes. Flowers in compact, non-expanding spikes, 1--8 cm long, 7--9 mm wide, sweetclover scented. Bracts precocious and persistent, far exceeding the calyx lobes in bud, slightly exceeding them at anthesis; body 2.0 mm long, ciliate margined, expanded and prominently glandular below the acumen; acumen subulate, often curved abaxially, abscission leaving a prominent "heel" on the rachis; paired, subulate, ciliate bracteoles, 1.5 mm long, flank the base of each flower. Calyx tube neither strongly ten-ribbed nor pubescent, usually drying with smoothly rounded longitudinal furrows; white, suffused with pink at the base when fresh, drying to a
pale straw color, 2.0–2.5 mm long, 1.7–2.0 mm in diameter; lobes green, ciliate on margins, lanceolate, the ventro-lateral lobes often directed upward overlapping dorsal-lateral lobes; ventral lobe, 1.4–1.6 mm long; a pair of prominent glands, drying yellow to bronze, immediately below each lobe between the calyx bundles. Corolla white; standard lamina strongly concave and lobed basally, 2.2–2.5 mm broad, 2.0 mm long, the claw 3.0–3.2 mm long; apical petals oblong-oblanceolate, 2.2–3.3 mm long, 1.2–1.5 mm wide, slightly cuneate at base, the claw 1.8–2.2 mm long. Androecial tube not exserted beyond apex of calyx lobe, 3.5 mm long; filaments equalling or slightly exceeding the petal tips at anthesis; anthers pale yellow. Ovary globose, glabrous except for a tuft of cilia on dorsal surface, 0.7–1.2 mm long, 0.6–1.1 mm in diameter; teardrop-shaped glands prominent on proximal-lateral surfaces, smaller in size toward ventral side of ovary, drying dark colored; style exserted beyond petal tips soon after anthesis, 7.0 mm long. Pods exserted from calyx, the beak angled upward between dorso-lateral lobes, prominently glandular.

**Distribution and phenology**

A widespread species from southern Manitoba and Saskatchewan, eastern Dakotas, Minnesota and Wisconsin; south, to eastern Texas, Louisiana, Mississippi and Alabama. Occupying primarily prairie habitats, open woodlands and glades,
Fig. 39. Geographic distribution of *Petalostemon candidum*
occasionally adventive along roadsides. Replaced in the High Plains to the west by *P. occidentale*. *P. candidum* is ecologically sympatric with *P. purpureum* throughout most of its range; the two are frequently present on prairie remnants. Anthesis time is from mid May to late July, flowering proceeding south to north.

**Nomenclature and observations**

Many authors cite *P. candidum* (Willd.) Michx. on the basis of the earlier publication of Willdenow's *Species Plantarum*. As Isely (1962) points out (p. 120):

... since Michaux did not cite Willdenow (the contrary is in fact the case), his epithet would seem to be most properly considered a new name rather than a combination.

The correct citation should be *P. candidum* Michx.

It is probable that this species was introduced into Europe at the same time as *P. purpureum*. Both grow together in Illinois (the stated locale of the Michaux collections) and seeds of both were undoubtedly gathered and returned to Europe. In support of this hypothesis is a specimen from the Herbarier de Ventenat (G) which is labeled, "ex H. Gels." It was from a plant growing in the gardens of M. Gels that Ventenat described *P. purpureum* and it is likely that cultivation of *P. candidum* was attempted there also. A plausible explanation for Ventenat not including a report of both species in *Description des plantes nouvelles et peu connues, cultivées*
Isely & Welsh (1960) clarified the species status of *P. candidum* and *P. occidentale*. As they pointed out, the two are quite distinct when multiple characteristics are used for differentiation. My studies have corroborated their findings; however, I find no indication of any introgression in the sympatric zone of the two species. In fact, eastern specimens of *P. occidentale* (those sympatric with *P. candidum*) are more readily separated from *P. candidum* than are those collected farther west. Some of the western forms have many characteristics of *P. candidum* (e.g. broader leaflets and more glabrous calyces) but their habitats -- usually 5,000 ft. elevation and above -- are probably in part responsible for the apparent morphological convergence toward *P. candidum*. In the sympatric zone, the two species are not ecologically congruent. *P. occidentale* is always found in the more xeric habitats, whereas *P. candidum* is found in the mesic areas of rich prairie soil.

*P. candidum* and *P. multiflorum* are geographically sympatric over a great part of the range of the latter species. Habitat preference is almost identical and occasional inter-breeding apparently takes place. The rare, putative hybrids
found in herbarium collections match those I have synthesized in the greenhouse.

Despite the few intermediates resulting from hybridization, *P. candidum* is morphologically consistent for such a wide ranging species. It can readily be recognized by its upright growth habit, relatively few leaves but large leaflets, long, non-expanding, columnar spike with precocious and persistent bracts. The main exceptions in growth pattern are found to the southeast where habitats of heavy clay soils and glade environments have evidently acted as selective forces to shape a more decumbent-prostrate stem and in general, a small plant. Despite the reduced size and growth habit of these plants, their floral characteristics match those in other areas of the range.

D. POLIOSI

**Distinguishing characteristics**

Plants completely glabrous. Stems round below, becoming striate above. Leaves mostly solitary; leaflets 13--27. Spikes becoming lax at anthesis. Bracts lanceolate, scarcely expanded proximally, short ciliate on margins only, otherwise glabrous, far exceeding the calyx lobes in bud but early deciduous. Paired bracteoles present, flanking the base of the calyx. Calyx tube glabrous, ten-ribbed, gibbous dorsally and slit to almost one-half its length, slit margins ciliate as
are the lobe margins. Corolla pale lavender to rose; the standard broad, rounded-deltoid, its claw much thicker than the claws of the apical petals.

**Distribution and ecology**

Both species are rare and evidently restricted to specialized habitats in the Tennessee Basin and south central Texas. The northern species perhaps currently restricted to limestone glades; the southern species to "exposed rocks" and "limestone clefts" according to herbarium labels.

**Observations**

These two species, although widely separated geographically share many of the same characteristics, presumably indicating that they are closely related. Since both are highly restricted and rare, they possibly represent relic populations of formerly more widely spread taxa. They are both so distinct from the other species or groups of species of *Petalostemon* that it is unlikely that they arose as a result of relatively recent hybridization between more wide ranging species and persisted because of their ability to survive in specialized habitats. Possible distant relationship with *P. prostratum*, a rare endemic from New Mexico, is discussed under that species. Further collecting may possibly indicate that both are more widespread than currently known.
Key to the Species

1. Leaflets 20--29, elliptical; peduncles shorter than 3 cm; spikes compact; calyx tube not prominently gland-dotted; ovary covered with protuberant, spherical glands; Illinois and Tennessee.

11. P. foliosum p. 158

1. Leaflets 7--17, linear; peduncles 6--12 cm; spikes lax; calyx tube with numerous glands between ribs; ovary not glandular; Texas.

12. P. sabinale p. 161

11. PETALOSTEMON FOLIOSUM Gray (Figs. 35, 52D)


Description

Stems several, 3--8 dm long, branching above, smooth, glabrous, round at the base but becoming striate immediately below the spike. Internodes 1.0--1.5 cm long. Stipules subulate, 3--5 mm long, persistent, becoming sinuous when dried. Leaves 3.5--4.5 cm long, initially solitary at nodes ultimately becoming fascicled on older stems; leaflets 20--29, evenly spaced along rachis, not always paired; petiolules 0.5 mm long with a prominent gland on lower surface of the rachis.
at the point of insertion; blades 6--10 mm long, 2.5--3.5 mm wide, elliptical to elliptic-obovate, mucronate, finely gland-dotted; midrib very prominent on the ventral surface. Peduncles short, 1.5--2.5 cm, bearing scattered sterile bracts, 5--6 mm long. Spikes clustered, moderately compressed, cylindrical, 8--10 mm broad, 25--50 mm long. Bracts subulate, expanded in the center, about 5 mm long, far exceeding the calyx lobes in bud, becoming chartaceous and falling soon after anthesis. Subulate bracteoles flank the calyx, 0.5--1.0 mm in length. Calyx tube white, thin walled, 3.5--3.8 mm long, gibbous distally, narrowing proximally, slit dorsally to almost one-half its length, slightly oblique, laterally ribbed; rachis attachment point below the longitudinal axis of the tube; lobes deltoid, green, appressed pubescent on inner surface and margins, the ventral lobe 2.0 mm long. Corolla pale purple, the petals widely reflexed; standard ovate-emarginate, 3 mm wide, 2.5 mm long; claw 4 mm long, 0.3 mm thick (over twice as thick as claws of apical petals); apical petals strap shaped, 2.7 mm long, 0.8 mm wide, slightly truncate anteriorly, cuneate at base, the claw 0.8 mm long. Staminal tube 3.6 mm long, shorter than calyx lobes; filaments 4.0 mm long, the anthers bright red-pink prior to anthesis; pollen orange. Ovary spheroidal, 1.4 mm long, 0.9 mm in diameter, glabrous, covered with protuberant, spherical glands; style glabrous, 5.5 mm long. Pod gland-dotted, exserted slightly from calyx, the anterior portion directed upward between the dorso-lateral
Distribution and phenology

Known originally from northern Illinois and the Tennessee Basin, perhaps now restricted only to the latter area. The only collections in the last fifty years that I have seen have been from a limestone glade across from Stone River Park, two miles northwest of Murfreesboro, Rutherford Co., Tennessee, (DeSelma (Year) 1879; Sharp & Shanks 25455; and, Isely & Wemple 9420) and "U. T. Farm," Knox Co., Tennessee, (Lanher 20). Blooming time is from July to mid September.

Observations

The type sheet in the Gray Herbarium bears two collections, those of Truesdale (year) 1867, Kane Co., Illinois and Hatch (year) 1854, Nashville, Tennessee. Both are cited by Gray. A similar mixed sheet is at MO and a specimen of the Truesdale collection is at NY. There have been no collections from the intervening areas and as previously stated, a total of only four collections have been made in this century. The habitat of the "cedar glades" of the Tennessee Basin has been discussed under P. gattingeri, a species also endemic to these areas. My collection of this taxon (Isely & Wemple 9420) was late in the season and only a few axillary spikes remained in bloom. Seeds were collected and the plants grown and flowered in the Iowa State University greenhouse. They grew well in
our prairie loam potting soil and flowered readily. Observations of living plants and fresh flowers facilitated preparation of the above description. As with all other species of Petalostemon cultivated under greenhouse conditions, there appear to be no artifacts induced. Pressed specimens from the greenhouse appeared exactly like those collected in the field.

This taxon is quite distinct from any other. Its possession of many leaflets, long, precocious, subulate bracts, bracteoles and glabrous calyx seem to relate it to P. sabinale (Rydberg, 1919-1920, places them in the same section), but leaflet shape, peduncle length, calyx shape, texture, and glandlessness as well as a glandular ovary, set P. foliosum apart.

12. PETALOSTEMON SABINALE Wats. (Fig. 35)


Description

Stems many, unbranched, erect, 2--4 dm long, glabrous, slightly glandular, round at the base becoming slightly striate above. Stipules fugacious, 2--4 mm long, subulate, often
curved. Lower leaves solitary, the upper ones often with suppressed axillary branch systems; rachis 2.0–2.5 cm long, glabrous, glandular, extended beyond terminal pair of leaflets 0.8–1.5 mm; leaflets (?) 13–15 (17), linear, narrowed at the base, 9–13 long, 1.5–2.0 mm wide, pale green above, darker green and gland-dotted below. Peduncle glabrous, 6–9 (12) cm long, rarely bearing sterile bracts near the apex. Inflorescence an expanding spike, up to 5 cm long; rachis glabrous to glabrate. Bracts precocious, far exceeding the calyx lobes in bud, deciduous before anthesis, lanceolate, only slightly broadened at the base, short-ciliate on margins; paired, ciliate bracteoles 0.5–1.0 mm in length, flank the calyces. Calyx expanded-tubular, slightly ten-ribbed, 2.2–2.9 mm long, slit dorsally almost half its length, glabrous except for margins of dorsal slit which are short-ciliate; tube glandular at base of lobes with numerous, yellow, pellucid, protuberant glands 0.2–0.3 mm in length, 0.1 mm wide; lobes ciliate, the ventral lobe 0.8 mm long. Corolla rose to pale lavender (?); the standard rounded-deltoid, 3.0 mm long, 3.5 mm broad, slightly emarginate at apex, the claw 3.5–3.9 mm long, thicker than the claws of the apical petals; apical petals 3.5 mm long, 1.0 mm wide, the claws 1.0 mm long. Androecial tube exserted beyond tips of the lobes, 3.5 mm long; the free filaments 5.3 mm long. Ovary 1.4 mm long, 1.0 mm in diameter, only slightly short-ciliate on dorsal, distal surface; the style 8 mm long. Pod not exceeding calyx lobes but bent
upward between dorsal lobes, short ciliate on apical margins.

**Distribution and phenology**

Known from only five collections in Texas; Bandera, Brewster, Uvalde and Val Verde counties. Apparently blooming in mid May.

**Nomenclature and observations**

The epithet *luteolus* was a tentative name placed in parentheses on the label of the type specimen of *P. sabinalis* by Sereno Watson. Watson eventually rejected the name and published the species as *P. sabinalis*. Heller (1896) restored the epithet, in a sense, by commenting:

**Petalostemon luteolus** S. Wats., is *P. sabinalis* S. Wats. Although the name *luteolus* appears in Patterson's Check-List, it has no foundation, being a label name given to a specimen of *P. sabinalis*.

The affinities of *P. sabinale* are decidedly with *P. foliosum* as first suggested by Rydberg (1919-1920). Turner (1949, p. 165) indicates that it is, "Closely related to *P. stanfieldii* [P. *tenue*] and apparently intergrading with that species." I find no evidence to support this view. It is true that the range of the two species is contiguous and that the leaflet number is similar, but all other characteristics are decidedly different -- the two are quite remote morphologically.
It is possible that this species is more common than the paucity of collections indicate and could be "rediscovered." The type location, "entrance to Sabinal Canyon," is not readily accessible, but a 1944 collection (Cory 44424, Val Verde Co., Texas) 12 3/4 miles south of Loma Alta, Texas is apparently along a highway. I collected for a day in this area during mid June, 1962 but did not find the species. My efforts were probably too late in the season and perhaps an earlier visit would bring it to light.

E. PHLEOIDES

Distinguishing characteristics

Stems striate with protuberant, globose glands; leaflets 11-48, glabrous to pubescent, sessile or nearly so; spikes 1.3-6.7 cm long, often becoming sinuous, 5-9 mm wide; bracts linear, exceeding calyx lobes, often deciduous; paired filiform bracteoles present, flanking the calyces; calyx oblique, deeply slit and dorsally gibbous, the lobes very short; corolla white, the standard broad, the apical petals strap-shaped.

Distribution and ecology

Dry sandy areas of south and east Texas and adjacent Oklahoma.
Observations

This section is easily recognized by its white flowers, dorsally gibbous calyx, numerous leaflets and spherical, protuberant glands, to 0.3 mm in diameter. The glands, when ruptured, release a pungent, watery liquid that has a sharp, distinctive odor. *P. microphyllum* has been in greenhouse cultivation for over two years. It thrives and flowers freely when grown in Iowa prairie soil. All attempts at cross-pollination with other species of other sections have been unsuccessful; indicative, as is the morphology, of the distinctiveness of these species within the genus.

The treatment of this section is in large part based upon unpublished investigations of Wesley S. Jackson (1964). Prior to Jackson's study, *Phleoides* was conventionally considered to contain three species (Rydberg 1919-1920, Turner 1959), but their distinguishing characters were far from clear. On the basis of analyses of mass collections as well as field and herbarium studies, Jackson demonstrated the existence of two reasonably distinct taxa. Their diagnostic characteristics are presented in the following key.

**Key to the Species**

Calyx glabrous; leaves (0.7) 1.3--2.3 (3.8) cm wide, leaflets 11--26, usually under 21; peduncles usually possessing sterile bracts.

13. *P. phleoides* p. 166
Calyx pubescent; leaves (0.5) 0.6--1.5 (2.0) cm wide, leaflets 15--48, usually over 25; peduncles usually lacking sterile bracts.

14. *P. microphyllum* p. 168

13. **PETALOSTEMON PHLEOIDES T. & G.** (Fig. 40)


*Petalostemon aphleoides* Young. *Fl. Tex.* 221. (1873). (2).


*Dalea glandulosa* (Coult. & Fish.) Shinners. *Field and Lab.* 17: 83. (1949). Based on *Petalostemon glandulosus* Coult. & Fish.

**Description**

Multiple stems ascending from a rusty to deep red taproot. Stems 2--7 dm long, glabrous to slightly pubescent, striate, and glandular. Stipules 2.5--3.5 mm long, pubescent, subulate from a broad base. Leaves 2.1--6.7 cm long, 0.5--3.8 cm wide, glabrous to pubescent; leaflets 11--26, elliptical to obovate, 1.5--2.5 mm long, 0.4--1.0 mm wide. Peduncles 0.1--26.3 cm long, usually with scattered sterile bracts near the apex. Spikes dense, cylindrical, becoming lax and sinuous in fruit,
13–58 mm long, 5–9 mm wide. Bracts glabrate in the southern portion of the range, becoming more pubescent northward, exceeding the calyx lobes in bud, deciduous prior to anthesis. Bracteoles present, flanking the calyces, 0.6–1.0 mm in length. Calyx glabrous; the tube oblique, 2.2–2.6 mm long, slit more than one-half its length dorsally, glandular between the nerves; lobes 0.6–0.9 mm long, ciliolate on the margins. Corolla white; the standard blade cordate, 2.5–3.5 mm long, 2.5–3.5 mm wide, the claw 3–4 mm long; apical petals linear, 3.0–3.5 mm long, 0.6 mm broad, the claws 2.0 mm long. The staminal tube about 2.7 mm long, the free filaments 2.5–3.5 mm long; anthers orange. Ovary 1.0 mm long, glabrous; the style 5 mm in length, proximally pubescent on the upper surface for one-third its length. Pod obliquely obovoid.

**Distribution and phenology**

Eastern and southern Texas. Primarily confined to deep sands of pine and oak woodlands. Flowering from mid May to mid July, reaching a maximum the third week of June.

**Nomenclature and observations**

Although Rydberg (1919–1920) and Turner (1959) upheld separation of *P. phleoides* and *P. glandulosum*, merger of the two species was first proposed by Heller in 1896 (p. 123). Under *Kuhnistera phleoides*, he writes:
A comparison of the type of phleoides and a duplicate type of glandulosus, both of which are in the Columbia University Herbarium, clearly shows them to be identical. The oblique calyx is a marked character in this species.

Heller also indicated the general lack of pubescence of K. phleoides in his earlier remarks regarding K. microphylla. Jackson's detailed study of these species corroborates Heller's intuitive approach.

14. PETALOSTEMON MICROPHYLLUM (T. & G.) Heller (Fig. 40, 52B, 54C)


Dalea drummondiana Shinners. Field and Lab. 17: 83. (1949). Based on Petalostemon phleoides var. microphyllum T. & G.

Description

Stems arising from a deep, red taproot, 2--7 dm long, glabrous to pubescent, striate, with protruding, globose glands. Stipules 3--5 mm long, curved. Leaves 1.4--6.0 cm long, 0.5--1.8 cm wide, glabrous to pubescent (densely so on
Fig. 40. Geographical distribution of *Petalostemon phleoides* and *P. microphyllum*
young leaves); leaflets 15--48, elliptical to obovate, sessile or nearly so, 4--7 mm long, 1.5--2.0 mm wide. Peduncles 0.1--22.5 cm long, usually without sterile bracts near the apex. Spikes 5--103 mm long, 5--8 mm wide. Bracts exceeding the calyx in bud, often deciduous, linear to linear-lanceolate, 4--5 mm long, 0.3 mm wide with subulate to subulate-filiform tips, glabrous to pubescent. Paired bracteoles present flanking the calyx, 0.6--0.8 mm long, filiform. Calyx oblique; the tube 3 mm long, slit dorsally to more than one-half of its length, dorsally gibbous; the lobes short, the ventral lobe less than 1.3 mm long, ciliolate on the margins. Corolla white; the standard blade cordate, 2.5--3.0 mm long, 2.5--3.5 mm wide, the claw 3--4 mm long; apical petal blades linear to linear-oblanceolate, 2.5--3.5 mm long, about 0.7 mm wide, the claw 1.5--2.5 mm long. Androecial tube exsserted slightly beyond the tips of the calyx lobes. Ovary 1.4 mm long, 0.8 mm in diameter, ciliate on the proximal two-thirds. Pod obliquely obovoid.

**Distribution and phenology**

Northern and eastern Texas in the deep, dry sands of the Cross Timbers and Prairies, Blackland Prairies, and South Texas Plains vegetational areas (Gould 1962). North to Montague county, south to Nueces county and extending west to Taylor county, Texas. Also from Marshall county, Oklahoma. Flowering from late May to mid July, reaching a maximum during
the second week of June.

Observations

This is a variable species and Turner (1959) has suggested that two varieties are possibly represented. His conjecture was based on the more glabrous condition of the northern populations. Jackson confirms Turner's observations but states:

However, no reasonable cline can be observed. Further, no other morphological features seem to exhibit a north-south bifurcation. Thus at this time *Petalostemon microphyllum* is considered as one entity though a highly variable one. (Jackson 1964). He concludes his discussion with this paragraph:

From both field and herbarium experience, both species of the section are highly variable. Each is probably represented by individual colonies or populations with not much interbreeding from one colony to the next, thus each colony is highly individualistic.
F. VILLOSI

Distinguishing characteristics

Stems arising from a long, red, seldom branched taproot; stems and leaves villous, leaflets (9) 11--19 (21), less than 1.5 cm long; spikes lax, usually 5--12 cm long and less than 1 cm broad; flowers pale lavender, rose to almost white.

Distribution and ecology

Texas, northward to southern Saskatchewan, throughout the Plains area on sandy soil, sandhills and blowouts.

Key to the Species

1. Stems reddish, striate, spreading pubescent; leaves thinly pilose, leaflets 10--15 mm long; not possessing sterile bracts below spikes; standard broad, cordate; east Texas and western Louisiana.

15. P. griseum p. 174

1. Stems pale, striations usually concealed by villous investure; leaves densely villous, leaflets 8--11 mm long; sterile bracts straggling down peduncle below spike; standard oblong, truncate or rounded at the base; central or north Texas and northward.

16. P. villosum p. 179
15. PETALOSTEMON GRISEUM T. & G. (Fig. 41)


Description

Plants arising from a long, relatively unbranched, red taproot, which is up to 4 dm in length. Stems erect, reddish, finely striate, spreading ciliate but not villous; usually branched in the upper half, (4) 6--7 (9) dm tall, 4--5 mm thick at the base. Stipules subulate, dark, 5--6 mm long. Leaves 2--4 cm long; rachis extended beyond the terminal pair of leaflets 1--2 mm; leaflets (9) 11--13 (15), oblong-elliptical, mucronate, slightly pubescent on both surfaces, but predominantly so on the lower surface, 10--15 mm long, 2.7--4.2 mm broad, not always perfectly paired on the rachis. Spike subsessile; the peduncle a maximum of 3 cm in length, often with straggling flowers near the apex; spike lax, flowering at 4 cm in length and through further floral differentiation reaching a maximum length of 14 cm, becoming sinuous and nodding; (6) 7--9 mm in diameter. Bracts lanceolate, only slightly expanded proximally, exceeding the calyx in bud, usually falling prior to anthesis leaving a decided "heel" on the rachis. Calyx spreading-ciliate; the tube ten-ribbed,
clearly visible, pale, slit dorsally to almost one half its length, 2.0--2.2 mm long, 1.7--2.0 mm in diameter; ventral lobe 1.0--1.2 mm long, each lobe tipped with a minute gland. Corolla pale lavender; standard blade cordate, entire at the apex, 2.1--2.6 mm long, 2.5--2.8 mm broad, arching over the other floral parts, the claw 2.3 mm long; apical petals oblong to slightly oblanceolate, 2.3--2.6 mm long, 1.0--1.2 mm wide, the claws 0.5 mm long; medial petals inserted lower than the lateral petals on the staminal tube. Staminal tube 3 mm long, equalling the length of the free filaments; anthers pale yellow. Ovary villous except at the extreme proximal end, 1.0--1.3 mm long, 0.8 mm in diameter; style 4 mm long, ciliate only on the proximal one-fourth. Pod not exserted beyond the calyx lobes, villous, thick walled.

**Distribution and phenology**

Limited to east Texas and western Louisiana. Restricted to sandy soils. Flowering from late May to late June, reaching a maximum approximately the second week of June.

**Nomenclature and observations**

Torrey and Gray cite two collections, "Pine woods near the Sabine River, Dr. Leavenworth! Texas, Drummond!". Both are mounted on one sheet at NY. The Leavenworth specimen (two stems) is taken as the type.

Petalostemon griseum is very closely related to *P.*
Fig. 41. Geographical distribution of *Petalostemon villosum* and *P. griseum*
villosum; indeed, all of the identifying characteristics of
the former are found sporadically throughout the range of P.
villosum. The possession of a specific array of character-
istics in conjunction with allopatric distribution, however,
is the basis for considering P. griseum a distinct species.
Distinguishing between the two species in the field is
relatively simple: P. griseum has fewer stems, grows taller,
branches more profusely in the upper half and all spikes be-
come long and nodding in fruit. Most of these characteristics
cannot be readily transferred to herbarium sheets; thus, the
correlation of several "minor" characteristics must be used
for identification. In general, P. griseum 1) is less
pubescent, 2) has reddish stems, 3) possesses larger leaflets,
4) often has "straggling" flowers below the main body of the
spike, 5) has extremely long spikes and 6) has a broad,
cordate standard. In conjunction with the earlier flowering
time and the geographic restriction to west Texas and eastern
Louisiana, P. griseum can be recognized readily from herbarium
specimens.

These species cannot be separated, either in the field or
in the herbarium, on the basis of spreading or ascending
leaves, calyx length or spike width as proposed by previous
authors.
16. **PETALOSTEMON VILLOSUM** Nutt. (Figs. 4l, 52A, 54A)

Type in PH. (1)(2).

Based on *Petalostemon villosum* Nutt.


**Description**

Taproot seldom branched, red, 2--4 dm long, usually equalling the stems in length. Stems many, radiating or ascending, often branching near the apex, 2.5--3.5 (5) dm long, 3.5--5.0 mm thick at the base, densely villous, the pubescence often obscuring the stem surface. Stipules subulate, spreading-villous, 5--7 (9) mm long. Leaves fascicled, often crowded; rachis 1.5--3.0 (4.0) cm long, villous, bearing prominent, red "stipe-glands", 0.2 mm in diameter, below the petiolule insertions; the midrib always extended 0.5--1.5 mm beyond the terminal pair of leaflets; leaflets 13--19 (21), gland-dotted below, long, appressed pubescence on both surfaces, 8.5--11.0 (13) mm long, 2--3 (3.5) mm broad. Spikes subsessile and lax, the rachis expanding following anthesis, often becoming sinuous in fruit, 4.5--11.0 (15) mm long, 8--10 (11) mm in diameter; sterile bracts often spread along the short peduncle below the spike. Bracts exceeding the calyx lobes in bud, villous throughout their length, 4--6 mm long, 1.2--1.4 mm broad, the acumen 2--4 mm long, usually deciduous.
immediately following anthesis. Calyx ten-ribbed, the surface often obscured by dense, spreading pubescence; the tube 2.0—
2.4 mm long, split dorsally to one-third its length; the ventral lobe 0.9—1.4 mm long. Corolla lavender-purple to almost white; the standard blade never becoming erect and open but usually covering the other floral parts, 2.7 mm long, 2.0—2.5 mm broad, oblong to oval, sometimes truncate at the base, rarely cordate, often emarginate at the apex; the claw 2.3—2.5 mm long; apical petals obovate, 2.6—2.8 mm long, 1.0—1.2 mm wide, the claw short, 0.5 mm; medial petals inserted on the staminal tube lower than the lateral pair. Staminal tube 2.2 mm long, the free filaments 3.7 mm long; anthers yellow to yellow-orange, exceeding the petal apices at anthesis. Ovary spreading-ciliate on the distal two-thirds, 1.0—1.1 mm long, 0.8 mm in diameter, the style 4.5 mm long, ciliate dorsally from the proximal end to barely one-third its length. Pod spreading-villous, exserted beyond the calyx lobes at maturity, the distal end bending upward between the dorsal calyx lobes.

**Distribution and phenology**

Restricted to sandy soils, sand hills and blow-outs; ranging from southern Saskatchewan to northern Texas and from eastern Colorado to eastern Missouri. Flowering beginning in late June in the southern part of its range, mid July in its northern part; most flowering terminated by mid August.
Observations

This is a wide ranging yet homogeneous species with a specific habitat preference for deep sand. Despite its ecological requirements in the field, it appears to grow and flower well in the greenhouse even though potted in Iowa prairie loam. Color variations are seen in the field as well as under greenhouse conditions, the petal colors ranging from almost white to light purple. The colors occur randomly distributed in most populations I have seen. Variations in degree of pubescence as well as leaflet number also exist but appear to show no specific regional trends, indicative possibly of a genetic plasticity expressed as varying phenotypes. *P. villosum* is replaced in east Texas and western Louisiana by *P. griseum*, a species with which it shares many characteristics.

G. COMPACTI

Distinguishing characteristics

Root in most species a relatively unbranched taproot. Leaves solitary, seldom fascicled, the leaflets broad-elliptical to almost ovate. Spikes 1.0--2.0 cm in diameter with sterile bracts often found at the spike base. Fertile bracts concave, lanceolate to obovate with a strong midrib and scarious margins toward the proximal end, densely villous-sericeous, always exceeding the calyx lobes in bud and
equalling or exceeding them in fruit. Calyx usually thin-walled and ciliate, the lobes villous-sericeous. Petals often inserted slightly below the apex of the androeclial tube. Pod usually not exserted beyond the apex of the calyx lobes at maturity.

**Distribution and ecology**

Generally, plants of the west -- south Texas through the Short Grass Plains to western Nebraska and Wyoming and west to the Continental Divide in the Columbia Plateau, southward to Nevada, Utah and northern Arizona. Most species are found in sandy soils.

**Observations**

This is perhaps an unnatural grouping, yet there appear to be pairs or trios of species which form links, one with another, which eventually tie all of the species together. *Petalostemon obovatum*, a sand dwelling endemic of south Texas seems quite different from most species of *Petalostemon* but has several characteristics in common with the rare Short Grass Prairie species, *P. compactum*. The latter species shares common characteristics with *P. ornatum* of the Columbia Plateau in the Pacific Northwest. *P. flavescens* of southeastern Utah seems related to both *P. searlsiae* of Nevada, Utah and Arizona and *P. ornatum*, thus completing the circle of species.

*P. ornatum, P. compactum and P. flavescens* all possess
petals that are inserted slightly below the apex of the staminal tube. This characteristic is also shown by *P. tenuifolium* of the Purpurei group. This variation from true apical petal insertion is very slight -- observable only with 30x magnification or higher. The petals are much closer to the apex than in any species of *Dalea* I have examined.

**Key to the Species**

1. Calyx slit dorsally to one-half its length; calyx tube relatively thick, neither transparent nor long-ciliate, plants of the Great Basin.

2. Corolla purple; calyx oblique, ventral calyx lobe 1.0--1.4 mm long; rachis elongating, spreading the calyces in fruit, spike over 4 cm long; plants of Nevada, adjacent counties in California, N. W. Arizona and E. Utah.

   17. *P. searlsiae* p. 184

2. Corolla yellow or yellowish-white; calyx not oblique, ventral calyx lobe 1.5--2.5 mm long, spike remaining compact in fruit, less than 4 cm long; plants of S. E. Utah and adjacent N. Arizona.

   18. *P. flavescens* p. 191

1. Calyx not slit dorsally to one-half its length, calyx tube thin-walled, transparent, long-ciliate; plants of southern Texas, the High Plains or the Pacific Northwest.
3. Corolla purple; stipules less than 3 mm long, plants of central Nevada and the Pacific Northwest.

19. *P. ornatum* p. 194

3. Corolla yellow to yellowish-white; stipules longer than 3 mm, plants of the High Plains and southern Texas.

4. Stems and leaves glabrous; leaflets elliptical-acute; peduncles 5—15 cm long; inflorescence less than 1.2 cm thick; plants of the High Plains.

20. *P. compactum* p. 199

4. Stems and leaves pilose; leaflets broadly-obovate; peduncles 1 cm long or shorter; inflorescence thicker than 1.2 cm. Plants of S. Texas.


17. **PETALOSTEMON SEARLSIAE** Gray (Fig. 42)


Description

Stems numerous, glabrous, often decumbent at the base, 3–5 dm long, glaucous-green, conspicuously gland-dotted with red-brown protuberant glands, these more numerous and conspicuous toward the stem apex. Stipules lance-subulate, deciduous, 1–2 (3) mm long. Leaves glabrous, usually solitary at nodes; rachis 1.5–2.5 (3.5) cm long with prominent "stipel-glands" below the petiolule insertions, extension beyond terminal pair of leaflets seldom over 1 mm; leaflets 5–7 (9), 9–16 mm long, 2–6 (8) mm broad, oblong to slightly obovate, often emarginate with a gland at the apex of the midrib, glandular below, smooth above; margins only slightly involute, but leaflets often folding when pressed, the midrib bending abaxially, especially so toward the leaflet apex. Peduncles long, 10–20 cm, glabrous, often with a few sterile bracts straggling below the main body of the spike. Inflorescence an expanding spike, compact in bud, becoming lax in fruit; spike 3–4 cm at anthesis, expanding to 6.5–9.0 (13) cm in length, 8–11 (12) mm wide; rachis glabrous to moderately pubescent, becoming visible in fruit. Bracts deciduous as spike expands, rhombic-lanceolate to oblanceolate, sometimes abruptly-acuminate, usually gradually narrowing to the acumen which exceeds the calyx lobes in bud and equals or exceeds them at anthesis, usually abaxially reflexed in bud; distal portions usually ciliate, especially the margins, proximal portion usually glabrous, strongly clasping, slightly scarious
laterally; total length of the bract 3.2--4.2 mm, breadth 0.8--1.2 mm. Calyx tube ± ten-ribbed, campanulate, oblique, slit dorsally to one-half its length, the margins of the slit ciliate; tube glabrous to puberulent, drying rufous, 2.4--2.8 mm long, 2.0--2.5 mm in diameter, usually possessing several yellowish glands lying between the calyx bundles; lobes drying black, spreading-ciliate, especially on margins, ventrolateral lobes often directed slightly upward above the longitudinal calyx axis, leaving a gap between them and the ventral lobes, the ventral lobe 1.0--1.4 (2.0) mm long. Corolla rose-purple; standard blade rounded deltoid, sometimes slightly cordate, usually emarginate, 2.6--3.0 (3.2) mm wide, 2.7--3.1 (3.3) mm long; claw 3.0--4.0 mm long, emerging from the deep dorsal slit of the calyx; apical petals inserted at equal levels at the apex of androecial tube, blades oblong to slightly obovate, 3.3--4.2 mm long, 1.1--1.5 mm wide, claw 1.2--1.4 mm long. Androecial tube not exserted beyond the tip of the ventral calyx lobe at anthesis, 2.5--3.0 mm long; free filaments, 4.0--4.5 mm long. Carpel densely ciliate on distal half, especially on upper surface, 1.5 mm long, 0.8--0.9 mm in diameter; style inserted on the longitudinal axis of the ovary or slightly below, ciliate proximally for more than half its length, 4.0--4.5 mm long. Pod villous at the distal end, protruding from calyx at maturity, the beak projecting between the dorsal calyx lobes.
Distribution and phenology

Restricted to Nevada, western Utah, southeastern California and northwestern Arizona. An abundant species found in dry gravelly or sandy soil usually associated with sagebrush and juniper. Flowering beginning in late April, reaching a peak at mid May, ending by mid June.

Nomenclature and observations

Rydberg distinguished Petalostemon rothrockii from P. searlsiae on the following characteristics:

<table>
<thead>
<tr>
<th></th>
<th>P. rothrockii</th>
<th>P. searlsiae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaflets</td>
<td>Oblong or linear oblong, obtuse or retuse, thick, 1 cm long.</td>
<td>Oblong or oblanceolate, involute on margins, acute at each end, 10--15 mm long.</td>
</tr>
<tr>
<td>Spikes</td>
<td>Cylindrical or oblong, 1.5 cm long, 8--9 mm wide.</td>
<td>Cylindrical, 1--4 cm long, 1 cm wide.</td>
</tr>
<tr>
<td>Bracts</td>
<td>Broadly obovate, short-acuminate, dark, short-pilose or glabrous.</td>
<td>Rhombic-oblanceolate, acute or short-acuminate, glabrous.</td>
</tr>
<tr>
<td>Calyx</td>
<td>3.5 mm long, lobes equalling tube.</td>
<td>4 mm long, lobes shorter than tube.</td>
</tr>
<tr>
<td>Standard</td>
<td>Broadly oblong-rounded or retuse at apex, truncate or subcordate, 3.5 mm, claw 5 mm long.</td>
<td>Broadly cordate, emarginate at apex, 3 mm, claw 4 mm long.</td>
</tr>
<tr>
<td>Apical petals</td>
<td>Oblong, acute at base 3.5 mm long, claw 2 mm long.</td>
<td>Oblong or obovate, 3--4 mm long, claw 1 mm long.</td>
</tr>
<tr>
<td>Distribution</td>
<td>Southern Utah and Arizona.</td>
<td>Southern Nevada, Utah and northern Arizona.</td>
</tr>
</tbody>
</table>
On the basis of my observations, bract shape is the only characteristic that shows a consistent regional variation. All other characters seem to fluctuate throughout the range of the species and perhaps represent various phenotypic combinations. The majority of specimens from extreme southeastern Utah (Washington and Kane counties), however, consistently have broader bracts, indicative of possible incipient regional patterning within the species. I have critically examined these specimens and find no further correlating characteristics that distinguish them from others throughout the range. This variation does not warrant specific ranking, nor from a practical standpoint, does it deserve varietal status. Bracts are early deciduous in this taxon -- they are lost shortly after anthesis of each flower; hence, spikes collected just past flowering or in fruiting condition lack the necessary identifying characters. I am of the opinion that the conservative inclusion of this variant within the confines of *P. searlsiae* is the best course of action. It is interesting to note that the type sheet (GH) containing Miss Searls' specimen from the Pahranagat Mts., southeastern Nevada, also contains two southern Utah collections, Capt. F. M. Bishop, *year, 1873* and *Meehan year 1873*. The latter specimen possesses the broad bracts, characteristic of Rydberg's *P. rothrockii*.

*Petalostemon searlsiae* is clearly distinct from *P. ornatum* even though the range of the two species is contiguous. *P. searlsiae* can always be distinguished by the possession of
Fig. 42. Geographical distribution of *Petalostemon searlsiae*, *P. ornatum* and *P. flavescens*
an elongating spike 12 mm or less in diameter and a calyx slit
dorsally to one-half its length, the slit ciliate at the
margins. The calyx is neither thin and papery nor sericeous-
pilose as in *P. ornatum*; rather, it is thick, drying rufous,
glabrous or short-puberulant. *P. searlsiae* differs in so many
ways from *P. ornatum* that it is indeed unlikely that they are
closely related; however, their common relationship to *P.*
flavescens of southeastern Utah provides justification for
their inclusion in a common group, Compacti.

18. **PETALOSTEMON FLAVESCENS** Wats. (Fig. 42)

*Petalostemon flavescens* Wats. Amer. Nat. 7: 299-300.
(1873). Type in GH. (1)(2).

*Kuhnistera flavescens* (Wats.) Kuntze. Rev. Gen. Pl. 1:
192. (1891). Based on *Petalostemon flavescens* Wats.

**Description**

Plants with stems 2--4 dm long, usually spreading-ciliate
at base, becoming appressed-ciliate above, the entire stem
covered with slightly protuberant glands. Stipules subulate,
2--4 mm long, ciliate. Leaves usually solitary, the rachis
1.5--2.5 cm long, often conspicuously gland-dotted, extended
beyond the terminal pair of leaflets 1.0--1.7 mm; leaflets
5--7, elliptical to narrow-obovate, appressed-ciliate on both
surfaces, rarely glabrous, 10--13 (16) mm long, 3--6 (7) mm
wide, gland-dotted below, not above; often becoming con-
duplicately folded when dried, the midrib bending abaxially, the entire leaflet becoming falcate. Peduncle long, 7--15 (22) cm. Inflorescence a nonexpanding spike, 21--35 (55) mm long, 10 mm broad; rachis pubescent. Bracts narrow, lanceolate, only slightly expanded below the acumen, 5--8 mm long, 1.3--1.5 mm wide, exceeding the calyx lobes in bud, equalling or exceeding them at anthesis; proximal end "v shaped" in cross section, the midrib prominent, usually ciliate, margins glabrous and slightly scarious; distal portion flat, not concave or "v shaped," glandular, ciliate, narrowing to the acumen which is long-ciliate; small, paired, glandular bracteoles, 0.2 mm long, flank the base of the calyx. Calyx obviously ten-ribbed, the tube slightly thin-walled but not translucent, 2.6--3.0 mm long, streaked red, slit dorsally over one-half its length, the margin of the slit, ciliate, lobes lanceolate with ciliate, sometimes glandular margins, the ventral ones 1.5--2.5 mm long. Corolla yellow or yellow-white; standard oblong to rounded-deltoid, slightly cordate, emarginate at apex, 2.5--4.0 mm long, 1.5--3.8 mm broad, the claw 3.2 mm long; apical petals inserted at the same level but slightly below apex of staminal tube, oblong, cuneate at the base, 2.6--5.0 mm long, 0.9--1.7 mm wide, the claw 1.2--1.6 mm long. Staminal tube 2.9--4.5 mm long; free filaments 3.0--6.0 mm long; anthers pale yellow. Ovary elliptical, 1.5--2.3 mm long, 0.8--1.2 mm in diameter, ciliate on distal half, mostly ventrally; style 6.0--8.0 mm long, ciliate dorsally from
proximal end to half its length. Pod villous, not exerted beyond the calyx lobes at maturity.

**Distribution and phenology**

Rocky, sandy areas in southeastern Utah and northeastern Arizona. Apparently a very restricted and seldom collected species endemic to this area. Blooming time from late April to early June reaching a maximum in late May.

**Observations**

Petalostemon flavescens is highly variable for such a geographically restricted species. Vegetative pubescence varies from entirely glabrous to spreading-villous below and appressed-pubescent above. Floral parts also vary widely in size, and shape. Standard shape fluctuates from oblong (quadrilateral, as described by Watson for the type) to rounded-deltoid. One specimen examined (Holmgren & Goddard 9990, San Juan Co., Utah) possesses a highly glandular calyx with large spherical, translucent glands on the margins of the lobes -- strikingly different from others of the species.

Notwithstanding the individual variations, this species seems distinct and quite separate from others of this group. The closest affinities appear to be with *P. searlsiae*. The moderate pubescence (not long, sericeous-pilose cilia), glandular bracts, relatively thick-walled, dorsally split
calyx and the more oval ovary are characteristics in common. Similarity between the two species was noted by Jones (1895, p. 631) who wrote: "Petalostemon flavescens Watson seems to be a white flowered form of P. Searlsiae. I can see no other valid difference." Jones' remarks are reflected by Rydberg (1919-1920) following his description of P. flavescens: "(Perhaps not distinct from P. Searlsiae)." Despite this warning, Rydberg places P. flavescens in his "section" Compacti while placing P. searlslae in Ornatii.

P. flavescens is distinct from P. searlslae on the basis of at least four characteristics. They are: 1.) possession of a nonexpanding spike; 2.) a yellow-white to white corolla contrasted with the purple corolla of P. searlslae; and 3.) longer calyx lobes. Petalostemon flavescens also shows certain characteristics in common with P. ornatum and P. compactum. The petals of P. flavescens are inserted slightly below the apex of the staminal tube and the villous pod is not exserted beyond the apex of the calyx lobes at maturity. It seems reasonable, therefore, to include all these species in a single group, Compacti.

19. PETALOSTEMON ORNATUM Dougl. in Hook. (Fig. 42)


Dalea ornatum (Dougl.) Eaton. Man. Bot. for N. Am. 120. (1833). Based on Petalostemum ornatum Dougl.


Description

Plants with reddish colored roots giving rise to numerous, glabrous, green-glaucous stems, 3--5 dm long, often corky below, moderately striate on lower portions, strongly striate above, dotted with slightly protuberant brown-red glands which are most pronounced and numerous at the stem apex. Stipules short, lanceolate, 1.2--2.2 (3.0) mm long. Leaves solitary at nodes; rachis to 4.0 cm in length, margined and glandular with prominent "stipel-glands" immediately below each petiolule insertion; rachis always extended 1.5--3.0 mm beyond the terminal pair of leaflets. Leaflets 5--7, varying in shape from broad-elliptic or broadly obovate to orbicular, 11--25 mm long, 6--12 mm broad, often emarginate, pale green and smooth above, gray-green and ± prominently glandular below. Peduncles 2.5--10.0 cm long, usually at least one-fourth the total stem length; sterile bracts lacking below the inflorescence. Inflorescence a compact, non-expanding spike 12--16 mm broad and to 57 mm long in fruit, usually conical in bud; rachis
varying from glabrous to extremely pubescent. Bracts lanceolate, exceeding the calyx lobes in bud, equalling or exceeding them at anthesis, 0.8—1.8 mm wide, 4.0—5.6 mm long; proximal one-half clasping calyx, possessing a strong midrib and scarious lateral areas, usually glabrous but sometimes with a ciliate midrib; distal one-half flat, green, drying black, often with scattered glands, sericeous-long-ciliate, cilia to 1.5 mm long. Calyx tube campanulate, thin-walled often + transparent with dark colored vascular bundles, 2.6—3.8 mm long, covered with long appressed trichomes, often with rows of glands visible between vascular bundles; calyx lobes deltoid, green — drying black, 1.2—2.0 mm long, sericeous, cilia to 1.8 mm in length. Corolla pale lavender; the standard 2.4—3.0 mm wide, 2.7—4.0 mm long, the base often slightly cordate, the apex entire or moderately emarginate, claw 4.5—6.0 mm long; apical petals oblong to slightly ob lanceolate, often inserted slightly below the apex of the androecial tube, the central pair inserted lower than the lateral pair, 3.5—4.7 mm long, 1.4—2.1 mm wide, the claws 1.2—1.7 mm long. Staminal tube about 4.5 mm long, the free portion of the filaments 4.0—5.5 mm; anthers yellow. Carpel bearded, predominately so dorsally although + pubescent over entire distal one-half; ovary 1.8—2.2 mm long, 1.0 mm in diameter; style inserted on the carpel axis, 8.0 mm long, ciliate dorsally from the proximal end to about one-half its length. Pod not exserted from calyx tube at maturity,
pubescent distally, glabrous proximally, the style remnant directed upward between dorso-lateral lobes of calyx.

**Distribution and phenology**

Limited to the Columbia Plateau (Fenneman 1938) and adjacent areas to the south; within this geologic area to the "Sagebrush Steppe, *Artemesia-Agropyron Association*" (Küchler 1964). Found on bluffs, rocky hillsides and slopes on sands, sandy clays. Flowering period from early May to early July, peaking during the first week of June.

**Nomenclature and observations**

The type specimen is in GL and is labeled in what I take to be Hooker’s hand:

*Petalostemon macrostachyum* Torrey

* P. *macrostachyum* Torrey

* ornatum* Douglas

North W. Coast Hooker*

It bears no other markings which correlate with Douglas' collection data -- "Frequent in the arid prairies near the Blue Mountains of Lewis River, North West America."

I have included within the delimitation of *P. ornatum*, Hydberg’s taxon, *P. lagopus*. I have seen the type at NY as well as an isotype at US. Although collected far to the south (western Nevada, Truckee Pass, Washoe Co.) of the presumed distribution of *P. ornatum*, it is indistinguishable, morphologically, from the more northern collections. To my knowledge
this southern distribution is represented by only two collections. Rydberg (1919-1920) separated the two species as follows:

"Bracts lanceolate, long attenuate, much exceeding the buds or calyces.


Bracts broadly obovate, abruptly acuminate, scarcely exceeding the buds or calyces.

40. *P. lagopus*, Idaho, Nevada & western Utah"

Among the plants examined from Washington and Oregon are to be found all shapes of bracts from narrow-lanceolate to rather broadly obovate, abruptly acuminate ones. Broad, short bracts, thus are not limited to the southern range. A further argument supporting merger of the two species is ecological.

A finger of the "Sagebrush Steppe, *Artemesia-Agropyron* Association" extends south into western Nevada from the Columbia Plateau (Küchler 1964). Due to its southern occurrence, this material has been confused with *P. searlsiae* (Porter 1957). Specific differences between the two species are more fully discussed under *P. searlsiae*. 
Petalostemon compactum (Spreng.) Swezey (Fig. 43)


Description

Plants with relatively few stems branching from an orange-red taproot, 3—5 dm tall, erect, branching above, glabrous, pale straw colored with prominent, slightly protuberant brown-red glands. Stipules 2.0—3.5 (5.5) mm long, subulate from a deltoid base. Leaves glabrous, 3.0—4.5 mm long; rachis extended 2—5 mm beyond terminal pair of leaflets; large "stipel-glands" often present immediately below the petiolule insertions; leaflets 7—9 (11), elliptical, acute, to 25 mm long and 6 mm wide, usually four times as long as wide; pale green and nonglandular above, gray-green and glandular-punctuate below, the glands generally restricted to areas near the margin or midrib. Peduncles 8—13 (15) cm long; glands protuberant, most numerous and pronounced near the apex. Inflorescence a non-expanding, compact spike beginning anthesis when 2 cm long but through further floral differentiation, attaining a length of 8—10 (12) cm with a breadth of 1.0—1.2 cm. Rachis 3 mm in diameter, densely spreading-villous, the
cilia immediately below flowers retrorse; frequently with a
whorl of sterile bracts at the base of the spike. Fertile
bracts exceeding calyx lobes in bud and at anthesis, narrow-
lanceolate with a prominent midrib proximally, 6--8 mm long,
0.5 mm wide, pubescence, spreading villous-sericeous, covering
the surface distally, restricted to midrib proximally espe-
cially pronounced at margins, the trichomes 1.5 mm long; calyx
tube thin walled and relatively transparent, 1.8--2.2 mm long;
vascular bundles drying red-black, visible through sericeous
indument; lobes equalling tube, 1.6--2.2 (2.4) mm long, often
not visible through the dense, spreading, cilia covering them.
Corolla yellow-white (bluish in New Mexico ?); standard 1.8--
2.2 mm long and as broad, rounded-deltoid, slightly cordate,
the anterior margin often crenate; apical petals 2.0--3.2 mm
long, 0.5--0.8 mm wide, oblong; claws 1.5 mm long, inserted
just slightly below the apex of the staminal tube, all at the
same distance from the floral base. Androecial tube 3.0--3.2
mm long; free filaments 3.0--3.4 (4) mm long. Ovary ellipti-
cal 1.8--2.2 mm long, 0.7--0.9 mm in diameter, long-ciliate
on distal one-half; style 4.0--4.5 mm long, ciliate dorsally
from the proximal end to one-third its length; stigma not
exserted beyond anthers. Pod not exserted beyond the apices
of the calyx lobes at maturity.
Distribution and phenology

Widely distributed but infrequent on the Great Plains from southwestern South Dakota to central New Mexico and west Texas. Apparently growing in a variety of habitats -- sandhills, rocky slopes and knolls. Flowering time is sporadic, as early as late May and as late as late September. Maximum flowering is in mid to late July. The southern populations do not seem to flower earlier than those in the more northern part of the range.

Nomenclature and observations

The nomenclatural problems involved in the adoption of *P. compactum* (Spreng.) Swezey are discussed by Isely (1962). In summary, the Sprengel description is inadequate and the Sprengel herbarium was broken up in the 1860's and the portion assumed to possess the sought after material destroyed during World War II. *P. macrostachyum*, published two years subsequent to the Sprengel name is clearly identifiable but has not been used by twentieth century botanists due to its relegation to synonymy by both Swezey and Kuntze. As to why Swezey and Kuntze placed the Torrey name in synonymy is not clear -- neither offer an explanation. Isely concludes that it is probable that either of the two could have had access to the Sprengel specimens or at least information about them on which to base their decisions.

It is apparent that this taxon and *P. ornatum* are related.
Both possess similar bract and calyx pubescence, thin transparent calyces with red-black vascular bundles, petals inserted slightly below the apex of the androeial tube, elliptical carpels and pods not exserted beyond the calyx lobes. The relationship of these two taxa was first suggested by Heller on an annotation label placed on a New Mexico collection of *P. compactum* (Vasey 1881, Albuquerque). It reads: "Seems to be intermediate between *K. ornata* and *K. compacta*.

The corolla color of fresh material is said to be white to yellowish-white. When dried, the petals appear pale yellow. One collection from New Mexico (Ripley & Barneby 8347) seems to possess lavender petals. Close examination, however, shows it otherwise to fit clearly within the circumscription of *P. compactum*. An indication that the corolla color is not merely an artifact of drying is that Barneby assumed it to be *P. tenuifolium* -- a purple species. Although corolla color cannot be ascertained on the Vasey specimen it was perhaps corolla color that partially prompted Heller's comment.

21. PETALOSTEMON OBOVATUM T. & G. (Figs. 43, 54E)


Fig. 43. Geographical distribution of *Petalostemon compactum* and *P. obovatum*
Description

Plants arising from a long, relatively unbranched, yellow-red taproot. Stems 4--5 dm long and to 6 mm thick at the base, decumbent and unbranched below, erect and often branched above, spreading pilose throughout their length. Stipules 4--7 (10) mm long, lanceolate from a broad base, spreading pilose. Leaves 3--4 (4.5) cm long, often deciduous on lower portions of stems; rachis extended beyond distal pair of leaflets 2.5--4.5 mm; leaflets (7) 9--11, 10--13 mm long, 5--8 mm wide, obovate, obtuse or emarginate at apex, appressed ciliate on both surfaces. Peduncles short or essentially nonexistent, a maximum of 1 cm long. Inflorescence a compact spike showing no rachis elongation in fruit but increasing in length due to apical floral differentiation following anthesis of lower flowers (spike then about 4 cm long), reaching a maximum of 8--10 cm in fruit, 1.4--2.0 (2.4) cm in diameter; inflorescence subtended by a whorl of sterile bracts. Fertile bracts concave, obovate, about 8.0 mm long, 3.3 mm wide, conspicuously glandular on the abaxial surface, pilose, spreading-ciliate, the trichomes 2.0 mm long; bract body 4.5 mm long, gradually tapering to an acumen 3.5 mm long, the tip drying dark red-brown; entire bract exceeding calyx lobes both in bud and in fruit; proximal portion of bract strongly "v-shaped"; margins scarious. Calyx tube transparent, spreading-villous, 2.2--2.5 mm long, the vascular bundles drying red, clearly visible through the dense pubescence; lobes plumose, equalling
or exceeding tube, subulate from a broad base, 2.0--3.0 mm long, the sinuses rounded between lobes. Corolla yellowish-white; standard 3.0--3.3 mm long, 1.6--1.8 mm wide, somewhat rectangular, truncate or slightly emarginate at apex, surpassing other floral parts following anthesis; claw 3.8--4.7 mm long; apical petals 2.8--3.4 mm long, 1.0 mm wide, rounded-oblong to obovate, the claws 0.6 mm long, inserted at the apex of the staminal tube. Androecial tube 4.6--5.0 mm long, the filaments 2.5--3.0 mm long, not spreading from longitudinal floral axis, the pale yellow anthers equalling the stigma in exsertion. Ovary 1.6--1.7 mm long, 1.0--1.1 mm in diameter, densely villous in its entirety, the cilia especially prominent distally; style 5 mm long, ciliate only at the very proximal end. Pod spreading villous, not surpassing calyx lobes at maturity.

**Distribution and phenology**

Restricted to the "deep sands" (Gould 1962) of south Texas, usually growing in association with *Dalea emarginata*. Flowering from early April to mid July.

**Nomenclature and observations**

The publication of Moricand's *Plantes nouvelles d'Amérique* was spread over the years 1833--1846. There is no indication in the paper itself as to the dates of publication of the various parts. The exact date of publication of pp. 65--66 is
1839, according to Rickett and Stafleu (1961), thus confirming that found in Heller (1896). The epithet *agastachya* is therefore a later homonym.

This species is unique in that it sets seeds freely even in the absence of insect pollinators. The free filaments are very short and do not diverge from the longitudinal floral axis as in all other species. At anthesis, the style is shorter than the anthers but gradually elongates, passing through the pollen masses held by the filaments and anthers thus effecting pollination. Another unique characteristic is the long, plumose calyx lobes, reminiscent of those found in subgenus *Kuhnistera*. *P. obovatum* seems most closely allied with *P. compactum*. Both share: 1) indeterminate spike growth with flowers developing apically while fruits are falling from the rachis below; 2) clustered sterile bracts at the base of the spike; and 3) a densely villous-sericeous calyx with transparent tube and dark colored vascular bundles.

**H. PURPUREI**

**Distinguishing characteristics**

Leaves with (3) 5--9 (13) leaflets. Bracts and calyces with \( + \) appressed, usually short pubescence; calyces lacking prominent ribbing; corollas purple; anthers orange-yellow.
**Distribution and ecology**

Restricted to the Great Plains and Prairies. None extend west of the Continental Divide and few penetrate into the Gulf Coastal Plain. Most appear to be calciphilic, growing either on limestone substrates or calcareous prairie soils.

**Observations**

Even though some species characteristically have leaves with a maximum number of leaflets greater than 5, penta-foliolate leaves predominate in this group. Trifoliate leaves are generally found only near the stem tips or stem bases (first formed leaves). Bract and calyx pubescence is short, often appressed, but sometimes spreading. Most species possess bracts that are glabrous except for a transverse belt of appressed cilia immediately below the base of the acumen, but in others, the bracts are uniformly pubescent. Calyx pubescence is uniform in some species but varying degrees of "balding" also occur. The extreme condition is reached in *P. pulcherrimum*, in which only an appressed fringe of hairs is found on the lateral margins of the calyx tube. In all species, the calyx is seldom prominently 10-ribbed, the vascular bundles supplying the lobes seem deeply imbedded within the tissues of the calyx wall and show little sclerification. *P. tenuifolium* shows moderate ribbing but it is generally concealed by the typical spreading pubescence of this species. All taxa possess a purplish corolla with a range between
species from pale lavender through blue to red-purple. There seems to be little variation within a single species and populations appear quite uniform in this characteristic. Compatibility tests carried on over the past three years have shown that all species of the complex are interfertile, furthermore, the progeny show no abnormal meiotic divisions or reduction in viable pollen.

There can be discerned three morphological units within the complex which are marked by variations in calyx shape. One group, perhaps the most generalized, is represented by *P. purpureum*, the most wide ranging species of the complex. This species possesses a tubular calyx of intermediate length (2.5–4.0 mm). The bract bodies are invested with a transverse belt of cilia, the remainder of the bract is glabrous.

*P. gattingeri*, *P. tenue*, *P. arenicola*, *P. tenuifolium* and *P. reverchonii* form another group, all possessing short (2.0–3.0 mm) campanulate calyces and narrow spikes. Generally the lobes are longer in relation to the calyx tube than in the other two groups. Even though uniform in major characteristics, there is considerable diversity within this group. For example, *P. gattingeri*, *P. reverchonii* and *P. tenuifolium* all possess a rachis that elongates following anthesis, while both *P. tenue* and *P. arenicola* retain a compact spike even in fruit. There is also variation in calyx pubescence, from the spreading investure of *P. tenuifolium* to the retrorse cilia of *P. tenue*. Although leaflet number is quite homogeneous in
this group, the unusual, high leaflet number of *P. reverchonii*
sets it quite apart from its associates. *P. tenuifolium* seems
to represent the closest link to the *P. purpureum* tubular
calyx form in closely resembling some of the "molle-pubescens"
specimens of the western range of *P. purpureum*. The latter
show a slight tendency for rachis elongation and short, almost
campanulate calyx tubes, but retain all the other *P. purpureum*
characters. On the other hand, *P. tenue*, even though specialized in the possession of retrorse pubescence, seems related
in certain characteristics to the last unit of the complex,
which is represented by *P. decumbens* and *P. pulcherrimum*.
These two species have long, tubular parchment-like calyces
which are basally rounded-deltoid in cross section and possess
short, incurved lobes. The dorso-lateral lobes arise from
flat surfaces and the three ventral lobes from the hemispheric-
cal lower part of the tube. The calyx of *P. tenue* is simi-
larly shaped. Calyx pubescence is limited in both species:
in *P. pulcherrimum*, it consists of a fringe along the lateral
angles, in *P. decumbens*, of a distal-lateral fringe plus
generalized pubescence toward the base of the calyx. Both
species have glabrous ovaries or nearly so, a condition also
found in *P. tenue*.

Hybridization in field populations of *Petalostemon* is
apparently rare. I have observed it only in *P. decumbens*, *P.
pulcherrimum*, and *P. purpureum*, and then only in the con-
tiguous southeastern Oklahoma counties: Marshall, Bryan,
Choctaw and McCurtain. Hybridization between *P. decumbens* and *P. purpureum* was studied in Bryan, Choctaw and McCurtain counties during the summers of 1963 and 1964. Field recognition of the presumed hybrid swarms proved to be simple. Flower color variation ranged from characteristic blue of *P. decumbens* to the red-purple of *P. purpureum*. Bract shape varied from the precocious, long, abaxially bent *P. decumbens* type to the short, subulate-tipped bract of *P. purpureum*. Peduncle length varied from the very short or non-existent one of *P. decumbens* to the long, graceful peduncle of *P. pulcherrimum*. Sixteen mass collections were made during the two growing seasons. Analysis of eight will be presented here.

Although 20 characteristics were examined only 11 were used in the analysis presented. The ordinate of the graphs is the product of the calyx tube length and the ventral lobe length. The product provided a better graphic separation than the sum of the two or total calyx length. The abscissa is a composite scale of two variables, pubescence of the ovary and pubescence of the style. "Whiskers" are added for bract length, degree of development of the typical *P. purpureum* appressed-ciliate belt on the bract, peduncle length, rachis extension beyond the last pair of leaflets, inflorescence width and leaflet number. Lastly a subjective evaluation of calyx pubescence is presented. If the calyx was entirely appressed-pubescent as in "typical" *P. purpureum*, the circle is left clear. If the "typical" *P. decumbens* pubescence
pattern was present, with two prominent, lateral ciliate bands with a slight amount of intermediate ciliation at the base, the circle was blackened. Proportions of black and white indicate value judgements of hybridity. This judgement was made prior to graphing and thus has some degree of objectivity.

Figure 44 shows an analysis of eight mass collections illustrating hybridization between *P. purpureum* and *P. decumbens*. The first two (412 and 571) are pure populations of the two species in question; the others show varying degrees of introgression. Mass collections 604 and 605 show quite different population structures yet they were collected in the same area but from different sides of the highway. I do not believe that the striking differences are due to non-random selection because the two were quite different visually at the collecting site; rather, since pollinators move from one contiguous flower to another, the highway may have been a major isolation factor from the standpoint of pollination.

Some time was spent in the area in 1964 observing and photographing the pollinators: Hymenoptera, Lepidoptera and some Diptera. These insects seemed to show no preference between the variants in the swarms. As previously indicated, I have synthesized hybrids between these species in the greenhouse and they match the intermediates found in field collections and show no reduction in fertility. All of the swarms were roadside populations -- growing in relatively disturbed habitats created by man. It is probable that in these environments the
hybrids compete successfully with the parents, and being fully fertile, persist.

Hybrids between *P. pulcherrimum* and *P. purpureum* were observed in Marshall county and studied by means of mass collection techniques. Three collections (59 specimens in all) were made in the vicinity of Madill, Oklahoma during the summer of 1963. All were from roadside populations which appeared intermediate between the two species in leaflet number, peduncle length and spike size. Twenty characteristics in all were studied and data is presented on twelve of them. Graphical analysis of these three mass collections in addition to two mass collections from adjacent areas of relatively pure populations of the putative parents is presented in Fig. 45.

Crosses between the two species synthesized in the greenhouse were morphologically identical with the intermediates seen in the field. The greenhouse progeny were fully fertile, underwent regular meiosis and set seeds normally. The swarms are evidently potentially self-perpetuating in an appropriate environment that allows the hybrid to compete on an equal basis with both parents. These conditions are apparently fulfilled only rarely in nature.

Voucher specimens of all the mass collections were deposited in ISC. They were selected to represent the wide variation range of each swarm and are so labeled.
Fig. 44. Graphic analysis of putative hybrid populations involving *P. purpureum* and *P. decumbens*.

412 and 571. Relatively pure populations of *P. purpureum* and *P. decumbens*.

579, 421-2, 424, 594, 604 and 605. Hybrid populations.

412. Wemple 412, 4.2 miles W Bokchito, Bryan Co., Oklahoma

571. Wemple & Jackson 571, 2½ miles W Soper, Choctaw Co., Oklahoma

579. Wemple & Jackson 579, 3 miles W Bokchito, Bryan Co., Oklahoma


424. Wemple 424, 3 miles E Hugo, Choctaw Co., Oklahoma

594. Wemple & Jackson 594, 3 miles W Ft. Towson, Choctaw Co., Oklahoma

604. Wemple & Jackson 604, 5 miles W Idabel, S side US 70, McCurtain Co., Oklahoma

605. Wemple & Jackson 605, 5 miles W Idabel, W side US 70, McCurtain Co., Oklahoma

The ordinate is the calyx length. The abscissa is the gynoecial pubescence, the first abbreviation representing the condition of the ovary, the second, the condition of the style. BEARD, bearded; CIL, ciliate; GLAB, glabrous.

The degree of darkening of the circle represents a subjective estimate of the degree of "decumbens-like" calyx pubescence.
<table>
<thead>
<tr>
<th>Trait</th>
<th>Categories</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bract Length</td>
<td>&lt; Lobes, SL &gt; Lobes, &gt; Lobes</td>
</tr>
<tr>
<td>Purpureum Belt</td>
<td>Strong, Moderate, Weak</td>
</tr>
<tr>
<td>Peduncle Length</td>
<td>&gt;20 mm, 5-20, &lt;5</td>
</tr>
<tr>
<td>Rachis Extension</td>
<td>0-0.5 mm, 0.51-0.99, &gt; 1.0</td>
</tr>
<tr>
<td>Inflorescence Width</td>
<td>10-11 mm, &lt;12, 12-13, 14-15</td>
</tr>
<tr>
<td>Leaflet Number</td>
<td>3, 7, 9</td>
</tr>
</tbody>
</table>

**Beard Cilium Glabrous Pubescence**

- **Gynoecial Pubescence**
Fig. 44 (Continued).
Fig. 44 (Continued).
BRACT LENGTH
PURPAREM BELT
PETER LOUNT LENGTH
RACHIS EXTENSION
INFLORESCENCE WIDTH
LEAFLET NUMBER
CALYX LENGTH
BEARD BEARD
CALIL CIL
GLAB CIL
GLAB GLAB
GYNODICAL PURESCE
Fig. 44 (Continued).
Fig. 45. Graphic analysis of putative hybrid populations involving *P. purpureum* and *P. pulcherrimum*.

412-717. Relatively "pure" populations of *P. purpureum* (lower left) and *P. pulcherrimum* (upper right).

402, 403 and 406. Hybrid populations.

412. Wemple 412, 4.2 miles W Bokchito, Bryan Co., Oklahoma
717. Wemple & Jackson 717, 7 miles E Navasota, Grimes Co., Texas
402. Wemple 402, 3 miles NW Madill, Marshall Co., Oklahoma
403. Wemple 403, 1 mile SE Madill, Marshall Co., Oklahoma
406. Wemple 406, 6 miles SW Madill, Marshall Co., Oklahoma

The ordinate is bract length relative to the calyx tube and ventral lobe. The abscissa is gynoecial pubescence, the first abbreviation representing the condition of the ovary, the second, the condition of the style. BEARD, bearded; CIL, ciliate; GLAB, glabrous.

The degree of darkening of the circle represents a subjective estimate of the degree of "pulcherrimum-like" calyx pubescence of each specimen.
Key to the Species

1. Rachis elongating following anthesis, the raceme becoming lax; bracts fugacious, evenly pubescent, the cilia not restricted to a narrow, transverse, appressed band at the base of the acumen; calyx evenly pubescent with short, spreading indument.

2. Leaflets 9--11 (13); stems less than 2 dm tall; rare, known only from type locality, Hood Co., Texas.

   22. *P. reverchonii* p. 227

2. Leaflets 3--9; stems longer than 2 dm; not restricted as above.

3. Leaflets 3--5; stem base and apex of long peduncle with dense spreading pubescence; bracts 2 mm broad or more; north Texas and adjacent areas.

   23. *P. tenuifolium* p. 232

3. Leaflets 7--9; stem glabrous at base becoming slightly ciliate above, usually densely ciliate at apex of the short peduncle; bracts less than 2 mm broad; central Tennessee, northwest Georgia and Alabama.

   24. *P. gattingeri* p. 237

1. Rachis not elongating following anthesis, the raceme remaining compact; bracts persistent, not evenly pubescent, the pubescence restricted to a narrow, transverse,
appressed band at the base of the acumen; calyx often unevenly pubescent, the cilia ± appressed.

4. Pubescence on distal 2/3 of calyx tube restricted to two bands of appressed cilia on lateral angles; spikes at anthesis usually 12 mm or more in diameter; leaflet number 7--9; restricted to southeastern Oklahoma and Texas.

5. Bracts shorter than calyx lobes at anthesis; leaflets less than 3 mm wide; peduncles 4 cm or longer; east-central Texas and adjacent counties in southern Oklahoma.

25. *P. pulcherrimum* p. 243

5. Bracts equalling or exceeding calyx lobes at anthesis; leaflets wider than 3 mm; peduncles 3 cm or less, spikes often subsessile; restricted to southeastern Oklahoma and southeastern Texas.

26. *P. decumbens* p. 252

4. Pubescence on distal 2/3 of calyx tube not restricted to lateral bands; spikes at anthesis usually less than 12 mm in diameter; leaflet number usually 5, rarely 7; not geographically restricted as above.

6. Plants ± pubescent with stems longer than 3.5 dm, usually branching above; peduncles
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short, less than \( \frac{1}{4} \) the length of the stems; spikes at anthesis 10 mm in diameter or wider; widespread from Canada to north Texas and Illinois to Colorado.

27. *P. purpureum* p. 255

6. Plants usually completely glabrous with stems shorter than 3.5 dm, usually unbranched above; peduncles long, usually exceeding \( \frac{1}{4} \) the length of the stems; spikes at anthesis narrower than 10 mm; restricted to Texas and the Llano Estacado.

7. Proximal calyx pubescence retrorse, directed toward the rachis; ovary glabrous or nearly so; central and east-central Texas.

28. *P. tenue* p. 263

7. Proximal calyx pubescence antrorse, directed away from the rachis; ovary bearded; Llano Estacado.

29. *P. arenicola* p. 271
Petalostemon reverchonii Wats. (Figs. 46, 53E)


Description

Stems multiple, arising from a stout rootstock, 1--2 dm long, + densely appressed-pubescent, striate, with three prominent ribs below each leaf. Stipules persistent, subulate, to 3 mm in length. Leaves glabrous to glabrate, fascicled, bearing 9--11 (13) linear-elliptical, involute leaflets 5--8 mm long, 1.5 mm wide, glabrous, pale, and nonglandular above, slightly ciliate, darker, and prominently glandular below. Peduncles short, less than 10 mm in length. Inflorescence an expanding spike originating as a subglobose bud, attaining 7 cm in fruit, 1 cm thick. Bracts fugacious as rachis elongates, precocious, becoming shorter than calyx lobes at anthesis, pubescent over the entire distal portion, the cilia not restricted to a narrow band, ciliate-fringed on proximal margins. Calyx tube campanulate, evenly short-spreading -- to slightly appressed-pubescent, 2.2 mm long, 2.4 mm in diameter; ventral lobe 1.8 mm long. Corolla deep pink or reddish, standard not lobed at base nor emarginate at apex, 2 mm wide, 2 mm long; apical petals oblong, 2.5 mm long, 0.9 mm wide.
Ovary slightly pubescent distally and ventrally, style inserted above the longitudinal axis. Pod developing ventrally and distally, pushing up between dorso-lateral lobes in fruit.

**Distribution and phenology**

Known only from the type locality, Comanche Peak, Hood Co., Texas. The two (three?) collections were made in June, the one labeled *5 June 1900* by H. Eggert, is in bud; the other, simply labeled *June* by J. Reverchon, 1882, has some spikes initiating anthesis and some in full fruit.

**Nomenclature and observations**

According to the description, the type collection was, "-- On the rocky top of Comanche Peak, in western Texas; J. Reverchon. June 1882 (n. 36)." I have seen two collections labeled *No. 36*. I accept as the type the specimen in GH; the other, an isotype, is at SMU. There are three additional Reverchon sheets also labeled Comanche Peak, June 1882 but numbered 1273, in NY, MO, and US. It is possible that there was a discrepancy in Reverchon's numbering system. For the present these sheets are assumed to be topotypes. The last collection of this taxon was in 1900 by H. Eggert (MO). This specimen, collected 5 June 1900 is in bud, clearly showing the precocious development of the bracts. The Reverchon specimens are, for the main part, fully in fruit but do possess small, secondary, axillary spikes at anthesis. There are few flowers
on the latter spikes but the corolla color is retained. The corolla dimensions used in the description were extrapolated from a floral drawing on a Reverchon, 36 sheet in NY. The drawing of the calyx on that sheet is quite accurate and I have assumed the same to be true of the corolla. I have compared this artist’s drawings on other sheets with my own observations and found them consistently accurate.

*P. reverchonii* represents somewhat of an enigma. It fits clearly within this section of the genus on all characters except leaflet number and the possession of pubescent stems while having relatively glabrous foliage. It has the elongating rachis characteristic of *P. tenuiolium*, yet the restricted bract pubescence and oiliation of *P. arenicola*. It is clearly related to the latter two species as well as *P. tenue* on the basis of calyx shape. Its location is within the current geographic range of *P. tenue* and apparently occupies the same "ecological niche." Evidence for this is given by Shinners (1949b), who says:

This is one of the most highly restricted endemics in north Texas. Comanche Peak is a massive, flat-topped outlier capped by one of the resistant limestone formations which make up the Edwards Plateau farther south and west. On the Edwards Plateau, the Comanche Peak limestone lies beneath other beds, but is exposed at many places in the intervening 'Lampasas Cut Plain' and elsewhere. Quite possibly the actual range of
Fig. 46. Geographical distribution of *Petalostemon tenue*, *P. tenuifolium* and *P. reverchonii*.
Dalea Reverchonii is greater than known at the present.

The "Lampasas Cut Plain" of which Shinners speaks is a portion of that area occupied by the eastern distribution of P. tenue.

Turner (1959, pp. 165-166) comments, "It is close to P. purpureum and P. pulcherrimum but seems to have a combination of characters that mark it distinct. However, detailed study of the entire P. purpureum complex may necessitate a change in its status." My study does not indicate that any change is in order regarding the status of P. reverchonii -- it is distinctive but appears to belong clearly in the P. purpureum complex.

It is quite possible that P. reverchonii is no longer extant. Unlike P. sabinale, also a very rarely collected Texas endemic, P. reverchonii is not indigenous to a relatively remote, inaccessible area. Considering the close proximity to major botanical institutions, it seems unlikely that this species would not be collected if it was still in existence.

23. PETALOSTEMON TENUIFOLIUM Gray (Figs. 46, 53A)


**Dalea tenuifolia** (Gray) Shinners. *Field and Lab. 17*: 84. (1949). Based on *Petalostemon tenuifolius* Gray.

**Description**

Stems moderately striate, 2--5 dm tall, often branching above, slightly pubescent overall, with dense spreading cilia (to 0.5 mm long) prominent at the stem base and again just below the inflorescence. Stipules subulate, dark, to 5 mm long. Leaves fascicled; leaflets linear, 3--5, slightly ciliate at margins, involute, often curving when dried. Peduncles variable in length, 0.9--12.5 cm, elongating in age. Bracts precocious, exceeding the calyx lobes in bud, usually deciduous by anthesis, concomitant with rachis elongation; not clasping calyx at base nor strongly keeled, 2 mm broad or greater at expanded portion, 2.5--3.0 mm long, narrowing gradually to the dark, subulate acumen, 0.7--0.9 mm long; entire surface evenly pubescent; anterior edge rounded, ciliate-fringed. Inflorescence globose in bud, becoming columnar; rachis elongating following anthesis, the raceme becoming lax and often sinuous, up to 10 cm long, 7--10 mm wide. Calyx ten-ribbed, often barely visible through spreading pubescence of hairs up to 1 mm long; tube campanulate, 2.4--2.8 mm long; dorso-lateral lobes deltoid, ventro-lateral and ventral lobes lanceolate, the latter 1.7--2.0 mm long. Corolla violet to purple; standard blade 2.0--2.2 mm long, 2.0--2.3 mm wide, strongly auricled, the claw 2.2--3.3 mm long;
apical petals inserted slightly below the apex of the staminal tube in prominent sockets, the blades 3.0—3.5 mm long, 1.0–1.5 mm wide, squared at the base but not auricled, claws 0.7–1.3 mm long. Anthers extended slightly farther than petal apices; pollen a bright yellow. Ovary 1.9–2.2 mm long, 0.8–1.1 mm in diameter, densely bearded on the distal one-half, the beard most prominently developed ventrally; pubescence continuing distally on the dorsal surface of the style for slightly over one-half its length; style inserted above the longitudinal axis of the carpel and in fruit directed upward at a 45° angle due to ventral development of the pod.

**Distribution and phenology**

Southwestern Kansas, southeastern Colorado, northeastern New Mexico and the panhandles of Oklahoma and Texas. Growing in rocky limestone soils usually in unprotected areas. Initiating anthesis in early May but not reaching maximum until early June, then tapering off until late July. A few collections have been made even later in the season, perhaps flowering at this time due to late season rains.

**Nomenclature and observations**

A single type sheet bearing specimens representing all the names that have been applied to this taxon is in GH. The primary label at the lower right hand corner reads, "*Petalostemon tenuifolius* n sp., Dr. J. T. Rothrock, No. 81,"
Explorations and Surveys West of the 100th Meridian, Corps of Engineers, U. S. Army, Expedition of 1874." Four specimens on the right side of the sheet (an entire branch, composed of five stems, and three separate stems) are mounted over the penned inscription, "Crossing of Red River, Arkansas, Dr. Newberry." At the upper left hand corner of the sheet is a handwritten note signed by T. C. Porter reading:


All of this coincides with Gray's complex type citation in the description as, "-- Arkansas, at the crossing of Red River, Dr. Newberry; New Mexico, Mr. Dieffendorfer (ex T. C. Porter), J. T. Rothrock."

That this sheet also contains material referable to a type of P. porterianus Small, is less clear. Small names no type nor does he cite specimens. He merely states, "On prairies, Arkansas, Summer." Further, there is apparently no material in NY annotated by Small as P. porterianus. The principal clue then is that the name suggests a Porter collection or at least one on which Porter supplied the information. Apparently of this mind, Rydberg (1919-1920) supplies
typification somewhat by stating at the close of his description, "Type locality: 'Leavenworth, Arkansas, to El Paso, Texas.'" I take this to mean a designation by Rydberg of this specimen. In corroboration is a pencilled arrow pointing to a stem below Porter's note on the subject sheet, followed by, "P. porterianus Small", signed "PAR" in Rydberg's hand. Inasmuch as Rydberg's interpretation is plausible and the specimen is consistent with Small's description, acceptance of this specimen as the type seems reasonable.

The primary difference among the specimens on this intricate sheet is that the calyx ribs are slightly more prominent on that presumed to represent P. porterianus than that of P. tenuifolium. This, in fact, was the main criterion on which the separation of the two was originally based. My experience has indicated that throughout the range of P. tenuifolium the calyx is ribbed, but spreading pubescence often obscures this fact. The specimen on the left of this sheet (that representing P. porterianus) is more mature; the spikes have lost their bracts and the calyces some of their pubescence: therefore, the calyx ribbing is easily visible. The other differences stated by Small and amplified by Rydberg are well within the range of P. tenuifolium as I understand it.

The range of P. tenuifolium is the southern part of the Llano Estacado and west into northeastern New Mexico. In parts of its range it is sympatric with P. purpureum and P. arenicola. It can readily be distinguished from both by its unique
rachis elongation and spreading pubescence at the stem base.

The habitat preference of *P. tenuifolium* is on the mesa tops, the limestone cap rocks of the Llano Estacado. This contrasts with the habitat preference of *P. arenicola*, the sandy stream beds dissecting this area, and that of *P. purpureum*, the relatively rich but rare prairie soils of this general area.

*P. tenuifolium* is the only species in section Purpurei showing petal insertion slightly below the apex of the staminal tube. This characteristic is considerably more common in section Ornati. In all other characteristics, however, *P. tenuifolium* clearly fits into the Purpurei. The occurrence of this presumed "daleoid" characteristic in two sections of *Petalostemon* (and among species clearly *Petalostemon* on the basis of other characters) strongly suggests that this type of petal insertion is a secondarily derived feature. There is no indication of affinity with those *Daleae* with subterminal petal articulation.

24. *PETALOSTEMON GATTINGERI* (Heller) Heller (Figs. 47, 53F)


**Description**

Root black, massive and highly ramified, usually branching laterally immediately below the caudex. Stems many, branched, 2–4 dm long; glabrous and round at the base, becoming slightly ciliate and striate above, usually drying to a pale, straw color; outer ones usually prostrate, inner ones erect, plants forming low growing mats. Stipules subulate, 5–7 mm long, persistent and drying straw colored. Leaves fascicled, the major leaf often with two minor trifoliate axillary leaves, occasionally an entire compressed branch system; mature leaf rachis to 20 mm in length bearing 7–9 narrow-lanceolate leaflets which are 10–14 mm long, 0.9–2.3 mm wide, usually near 1 mm, the wider leaflets restricted to leaves at base of stem; leaflets moderately involute, drying pale green above, darker below with small, red glands visible only on the lower surface. Peduncles short, less than 3 cm, often lacking; apex becoming densely ciliate. Inflorescence an expanding columnar spike often becoming sinuous in fruit, 70 mm in length, never exceeding 10 mm in width. Bracts precocious, far exceeding the calyx lobes in bud and equalling or slightly exceeding them at anthesis, fugacious as spike expands; body 1.5 mm long, elliptical, not tightly compressing calyx at base; bract pubescence evenly spreading over distal surface, not restricted to a narrow belt; distal-lateral margin fringed, the proximal end glabrous; acumen subulate, to 6 mm, often ciliate and recurved abaxially, especially in bud. Calyx tube
campanulate, 10-ribbed, 2.0--2.6 mm long, evenly, densely pubescent; trichomes 0.7 mm long, drying silvery over the pale rust colored tube; lobes evenly ciliate, lanceolate, often spreading away from longitudinal calyx axis, the ventral lobe 1.7--2.5 mm, green color persistent through drying. Corolla pale to deep purple; standard blade 2.3--2.6 mm wide, 1.4--2.0 mm long, deltoid, not auricled at base, the distal margin entire; claw 3.0--4.0 mm long; the apical petal lamina oblong-elliptical, 3.0--3.4 mm long, 1.3--1.4 mm wide, the claws 1.2--1.3 mm, cuneate at lamina base. Androecial tube 3.2 mm long, not exserted beyond calyx lobes; filaments 5.0--5.5 mm, purple, exserted beyond petal apices; anthers yellow-orange with lateral dehiscence lines bright red; pollen a bright orange. Ovary 1.2 mm long, 1.0 mm in diameter, strongly bearded on the distal-ventral two-thirds, the style 8.0 mm, bearded dorsally and proximally, 1/3 to 1/2 its length.

Distribution and phenology

Central Basin of Tennessee, northwestern Georgia and northwestern Alabama. Restricted to glade environments. Initiating anthesis in early May, reaching a peak at the middle of that month and gradually decreasing. Flowering may, however, continue to early August, due to secondary, axillary blooming.
Nomenclature and observations

Although Heller, in naming the species in honor of Dr. A. Gattinger, did not single out a specific sheet, he did comment that, "Some of his [Gattinger's] specimens are in Curtiss' North American Plants, no. 565." I have seen five sheets so designated, (SMU, TENN, GA, 2--US). By far the best specimen is at US and I designate it as the lectotype, US 24537.

P. gattingeri is an element of a flora endemic to the Cedar Glades of Central Tennessee and adjacent areas. The glades are a part of the Central or Nashville Basin (Quarterman 1950) and occur where the usual rolling upland pastures and alluvial farm lands are eroded away exposing horizontal layers of Lebanon limestone and Ordovician sediment. These strata are impervious to water and at certain times of the year are submerged. Some drainage is accomplished through small sink holes and vertical fissures which fill with soil allowing growth of clumps or rows of trees or larger shrubs. The strata themselves are often covered with a thin layer of soil varying up to one foot in depth. It is in this substrate than P. gattingeri grows. Quarterman classified P. gattingeri as a "characteristic species" i.e. it was found in over 80% of the glade areas she examined. Nostoc commune Vauch. and Aristida longispica Poir. were the only other two species to be so recognized, but the glades contain numerous other endemics. Quarterman presents two hypotheses to explain the characteristic flora of the glades: 1.) "The occurrence
Fig. 47. Geographical distribution of Petalostemon gattingeri and P. arenicola
of both wet and dry extremes must limit the number of species capable of living in glade areas" and 2.) "Restriction of certain species to glades is probably also affected by their inability to compete with mesic species in more favorable habitats."

Dolomitic limestone glades also occur in east central Missouri and many of the same species are found on these glades but Petalostemon gatteringi is not among them. I have collected *P. purpureum* from one such glade in the Missouri Botanical Garden arboretum, Franklin county, Missouri (Wemple 478). This plant appeared no different from the typical prairie form of *P. purpureum* elsewhere in Missouri.

Under greenhouse culture, the matted growth habit of *P. gatteringi* remains constant as do all the distinctive floral characters. Progeny grown from field collected seeds were uniform, growing and flowering with no special care beyond that given to other species of Petalostemon.

25. PETALOSTEMON PULCHERRIMUM (Heller) Heller (Figs. 48, 53H)


Description

Stems many, usually robust, varying from erect to decumbent, 3.5--7.5 dm in length, usually smooth near the base, becoming striate in upper portions; red "glands" apparent on dried stem, 1 mm in diameter, flush with surface; three vertical ribs below leaf axes not obvious on lower parts of stems but becoming apparent above; glabrate to moderately pubescent, usually more pubescent at apex of peduncle. Stipules subulate-setaceous, 3--5 mm in length. Leaves fascicled, seldom more than three trifoliate leaves in axils; leaflets 3--7, the terminal one to 26 mm long and 3 mm at widest point, elliptical, slightly involute; glandular and ciliate below, non-glandular and glabrous above. Peduncles 4--15 cm long. Inflorescence a columnar, non-expanding spike, 15--35 mm long, 11--14 mm wide. Bracts not precocious, never exceeding calyx lobes even in bud; acumen 0.6--1.2 mm long, subulate, drying black, always shorter than the calyx lobes and usually as
short as the tube itself at anthesis; body, 2.5--3.0 mm long, not markedly expanded distally, pubescence restricted to a transverse belt of appressed cilia immediately below the acumen and a ciliate fringe along the margin toward the rachis, strongly clasping the calyx throughout its length. Calyx tubular, dorso-lateral surfaces flat, ventral surface curved; tube glabrous, white, drying to a pale, thick, parchment-like surface save for two bands of appressed cilia along lateral margins, silvery, drying rufous; entire calyx tissue infiltrated with a gum, which dries to a shiny red, often showing through to the outside as red streaking; tube 3.2--3.9 mm long and 1.9--2.4 mm in diameter; lobes pubescent, especially on margins, incurved and valvate in bud, opening slightly at anthesis, usually flared in fruit, dark green, drying reddish on the outer surface, remaining green on the inner, the ventral lobe 1.0 to 1.6 mm long; extruded red gum lobelets ca. 0.1 mm long scattered along margins. Corolla blue to lavender-purple, the standard suborbicular and slightly lobed, 2.5--2.9 mm wide, 2.7--2.8 mm long, the claw 4.0--4.5 mm; in fresh flowers the claw is parallel to the staminal tube until just below the blade whence it reflexes upward at 90°; the apical petals oblong, sometimes slightly obovate, 3.1--4.2 mm long, 1.2--1.4 mm wide, the lateral pair with claws offset to one side, in the fresh flower arching up above, and lateral to, the medial pair; claws 1.0--1.4 mm long. Staminal tube exserted beyond the calyx lobes; filaments purple when fresh,
anthers bright orange, exceeding the apical petals, the longitudinal dehiscence lines deep red. Ovary completely glabrous, 1.3–1.7 mm long, 0.8–1.2 mm in diameter; style usually completely glabrous, occasionally slightly ciliate dorsally on the proximal third, inserted slightly below the longitudinal axis of the ovary, never exceeding the exsertion of either petals or anthers, pigmented purple distally. Pod developing mostly ventrally and distally, the proximal tissues of the style persisting as a dorsally directed beak.

Distribution and phenology

Restricted to rich, blackland prairies and associated areas in east-central Texas and adjacent counties in southern Oklahoma. Occurrence in western Texas (Hudspeth County) and New Mexico (Socorro County) is documented by only one collection each, possibly representing introductions. Primary flowering time is from mid May to early June.

Nomenclature and observations

Adolf Scheele in "Beitrage zur Flora von Texas" (1848) was the first to apply a name to this species. His description is lucid and concise, clearly setting it apart from P. violaceum (P. purpureum). Unfortunately, his name, P. virgatum, had been pre-empted nine years earlier by Nees von Esenbeck and is now in synonymy under P. occidentale. It is probable that Asa Gray, the next person to deal with the
nomenclature of this taxon did not realize that Scheele's name was a later homonym. Gray's work has been discussed in detail by Heller (1901). The following is but a brief review.

Gray in *Plantae Lindheimerianae* (1850) stated in a footnote (p. 176):

*Petalostemon virgatum*, Scheele, in *Linnaea*, 21, p 461, is plainly the No. 42, *Pl. Lind.* [of Lindheimer] and No. 137, *Pl. Fendl.* [of Fendler], viz. a pubescent variety of *P. violaceum*, perhaps connecting that species with *P. decumbens*.

I have examined the three sheets comprising *Lindheimer 42* (GH) and they are clearly *P. pulcherrimum* (Scheele's *P. virgatum*). The single sheet, *Fendler 137*, is definitely not the same species but rather it is what Gray described -- "a pubescent variety of *P. violaceum*" -- *i.e.* *P. purpureum*. In short, Gray misinterpreted Scheele's concept of *P. virgatum*, or perhaps as Heller (1895) put it, "...Dr. Gray very much underrated the excellent work of Scheele, refusing, at least for a time, to recognize some very good species which he described."

In *Plantae Wrightianae* (1852), Gray actually published *P. violaceum* var. *pubescens* but further compounded nomenclatural problems by writing (p. 46):

Burke sent to Sir Wm. Hooker dwarf specimens of this variety, and from the Black Hills of the Platte both Burke and Gordon have sent others, with densely pubescent leaves and even tomentose stems, which I cannot otherwise distinguish from this species.

This discussion presents two nomenclatural problems. First, Gray's citation back to his preceding publication, Plantae Pendlerianae (1849), is incorrect because there, under No. 137, Gray has: "P. violaceum Michx. Fl. 2. p. 50. t. 37. f. 2: -- a pubescent variety; the calyx very silky-villous. Five miles west of Las Vegas, New Mexico; August." This is not a valid publication of a new variety. Secondly, his use of the Scheele name as a synonym follows that in his Plantae Lindheimerianae discussion, but he cites the Burke and Gordon specimens as representatives of this new taxon. I have examined one of Burke's sheets (NY, unnumbered, Snake River Country) and it fits into the general range of variation of P. purpureum. Even though Gray obviously intended this name for the extremely pubescent forms of P. purpureum, still, according to nomenclatural practice, the name P. violaceum var. pubescens is legally based on the description of P. virgatum Scheele.

Heller published Kuhnistera pulcherrima as a nomen novum in 1895 and based it on P. virgatum Scheele. Following the description he speaks of his finding the plant and recognizing its individuality from other purple flowered species and naming
it a "n. sp.", the designation that occurs on his widely

Four years later (1899) Heller transferred K. pulcherrima
to Petalostemon along with three other species originally
placed in Kuhnistera. In the July, 1901 issue of Muhlenbergia,
Heller made a final transfer of his species to P. pubescens
(A. Gray) Heller, listing P. violaceum var. pubescens A. Gray.,
P. virgatum Scheele, K. pulcherrima Heller and P. pulcherrimum
(Heller) Heller, as synonyms. He concluded with this sentence:

This beautiful species has been burdened with much
synonymy mainly by the writer, who may perhaps be
pardoned for not earlier understanding the true
place of publication of the first available name,
when viewed in the light of the preceding article.

Unfortunately Heller's publication appeared one month after
the publication by Aven Nelson of P. pubescens (Bot. Gaz. 31:
395. 1901, June) and so it too, is a later homonym.

Petalostemon pulcherrimum is readily recognized by four
characteristics: 1.) long peduncles, 2.) a long tubular calyx
with short lobes, 3.) a glabrous calyx tube except for the
ciliate bands on the lateral margins, and 4.) short bracts.
The growth pattern is variable and ranges from decumbent to
erect. This variation was first thought to be due to hybridiza-
tion with P. decumbens but analysis shows decumbent material
clearly to be P. pulcherrimum. Hybridization with P. purpureum
has been previously discussed.
Fig. 48. Geographical distribution of Petalostemon decumbens and P. pulcherrimum
P. decumbens

P. pulcherrimum
26. PETALOSTEMON DECUMBENS Nutt. (Fig. 48, 53B)


Description

Stems many, arising from a prominent caudex, usually decumbent and apically ascending, occasionally erect, partially supported by adjacent vegetation, 2--5 dm long, glabrous and smooth at base becoming slightly pubescent and striate above. Stipules 4--6 mm long, subulate, never thicker than 0.5 mm at base. Leaves fascicled with seldom more than two trifoliate leaves in axes of major leaves. Leaflets 7--9, elliptical, 17--25 mm long, 3.0--4.6 mm wide, rarely involute, the tip subulate; rachis extended beyond distal pair of leaflets 0.5--3.5 mm. Peduncle short, often lacking, never over 3 cm long. Inflorescence a columnar, non-expanding spike, 14--36 mm long, 13--16 mm wide. Bracts long-acuminate, exceeding the calyx in bud and at anthesis; body 2.8--3.5 mm long, neither strongly clasping nor sharply narrowing at base, lateral margin often scarious; entire bract glabrous save for a small triangular area of appressed cilia at widest part; body gradually tapering distally to a narrowly lanceolate acumen, 4--7 mm long, often reflexing abaxially. Calyx tubular, deltoid in cross-section with a rounded base; tube generally glabrous except for two bands of appressed cilia along lateral
margins which traverse the entire length of the calyx and general appressed pubescence between the bands on the proximal 1/3 of the tube; tube 3.6--4.3 mm long, 2.2--2.6 mm in diameter; lobes pubescent, incurved, valvate in bud, barely opening at anthesis, ventral lobe 2.0--2.7 mm long. Corolla blue to blue-purple; standard blade oval-deltoid, strongly concave, not basally lobed, 2.3--2.7 mm wide at base, 2.4--3.0 mm long, the claw 5--6 mm long; apical petals oblong, often slightly lobed at the base, 3.5--4.0 mm long, 1.2--1.5 mm wide, the claw 1.0--1.4 mm. Staminal tube not exserted beyond the calyx lobes; filaments tinged blue-purple, exceeding petals; anthers orange, the dehiscence line bright red. Ovary glabrous, 1.5--1.7 mm long, 0.9--1.1 mm in diameter; style usually glabrous, occasionally slightly ciliate, roseate at tip, exserted slightly beyond anthers soon after anthesis. Pod developing by enlargement of the ventral-distal portions of the ovary, the style base persisting as a beak on the legume.

**Distribution and phenology**

Distribution bicentric. Northern populations found in counties of southeastern Oklahoma and adjacent counties in northeastern Texas. Southern population center is in southeastern Texas. Restricted to calcareous soils with underlying horizontal limestone strata -- glade conditions. Flowering from mid April to early June, reaching a maximum in early May.
Nomenclature and observations

Nuttall's definitive description (1834) concludes, "On the plains of the Red River, Common, Flowering in June." The specimen at Philadelphia is labeled in Nuttall's hand, "Arkansas." Adjacent to the name *P. decumbens* is an asterisk, Nuttall's designation for a new species. The asterisk, however, is in pencil, not ink, as is the rest of the label. A specimen in the New York type collection is labeled in Nuttall's handwriting with the location, "Red River." It too has an asterisk but in ink of the same type as the rest of the label. It is a better specimen than the one at PH which has lost most of its leaves. A third Nuttall specimen at Cambridge labeled, "Arkansas Red River" lacks an asterisk. Presumably these three sheets were in Nuttall's possession when he prepared his description and were subsequently distributed. It seems best to choose the specimen at NY to be the lectotype on the basis of, 1.) the distinguishing asterisk matching the rest of the label, 2.) the exact locality as in the description and 3.) the quality of the specimen.

The distributional pattern of this species is unique, the two disjunct areas being separated by over 200 miles. The soil types, however, are very much alike, both calcareous in nature. The southeastern counties of Oklahoma possess other restricted species e.g. *Leavenworthia aurea* Nutt. and *Lesquerella angustifolia* (Nutt.) Wats. (Cruciferae). Rollins (1956, 1963) attributes the limited range of *L. aurea* to the
thin soil with underlying horizontal limestone strata — a
glade condition. This species, also bicentric in its distribu-
tion, has been collected in San Augustine county, Texas —
within 50 miles of the southern distribution of *P. decumbens*.
It is probable that the habitat dictates the distribution of
*L. aurea* and *P. decumbens* in the same manner.

Hybridization between *P. decumbens* and *P. purpureum* in
southeastern Oklahoma has already been discussed.

27. PETALOSTEMON PURPUREUM (Vent.) Rydb. (Figs. 49, 53C)

Gard. 1: 238. (1900). Based on *Dalea purpurea* Vent.

Type in G. (1)(2).

(1802). Original material in B. (1)(2).

(1803). Original material in P. (1)(2).

*Psoralea purpurea* Poir. in Lam. Encycl. Meth. 5: 694.
(1804). Based on *Dalea purpurea* Vent.

*Petalostemon violaceum* var. *pubescens* Gray. (Quoad mate-
rial in part non citation) Smith. Contr. Knowledge 3:
46. (1852). Based on *Petalostemon virgatum* Scheele.

Vall. 329. (1892). Based on *Dalea purpurea* Vent.

(1900). Original material at NY. (1)(2).

(1901). Holotype in RM. (1)(2). Not *P. pubescens*
(Gray) Heller (1901) which is *P. pulcherrimum*. 


Petalostemon purpureum f. pubescens (Gray) Fassett. (Quoad concept non basionym) Rhodora 38: 96. (1936). Based in part on P. violaceum var. pubescens Gray.


Petalostemon purpureum var. pubescens (Gray) Boliv. (Quoad concept non basionym) Nat. Canad. 87: 43. (1960). Based on P. violaceum var. pubescens Gray.

Description

Root black with multiple stems arising from a prominent caudex. Stems usually erect, 2--8 dm tall, ± pubescent, generally branching near the top, striate with three prominent vertical ribs immediately below each leaf. Stipules subulate, glabrous, reaching a maximum of 8 mm, drying dark, often fugacious. Leaves prominently fascicled, each leaf bearing at least two trifoliate leaves in its axil and often an entire compressed branch system; nodes usually close together giving the plant a dense, leafy appearance. Leaf rachis extending to 3 cm bearing 3--5 (?) linear, strongly involute leaflets, 6--20 mm long and 0.8--2.0 mm wide; the proximal pair inserted in
the distal 1/3 of the rachis; petiolules usually ciliate even in otherwise glabrous material; lower surface, when dried, dotted with small, dark glands and often pubescent, the upper surface nonglandular and glabrous. Peduncle short, usually less than 1/4 the entire height of stem, usually more pubescent above than below. Inflorescence a compressed, non-expanding, columnar spike, usually at least three times as long as wide, 30--70 mm long, 10--15 mm in diameter. Bracts persistent and precocious, exceeding the calyx in bud but usually shorter than the lobes at anthesis; acumen dark, subulate, often pubescent; bract body expanded distally and covered with a characteristic transverse band of appressed cilia, glabrous and contracted proximally, tightly clasping the calyx base, the calyx ± tubular, 2.5--4.0 mm long, not conspicuously ribbed, usually entirely covered with appressed, silvery pubescence; the three lower lobes often incurved toward the calyx axis, the ventro-lateral pair often overlapping the dorso-lateral lobes; the ventral lobe 1--2 mm long, all lobes green tipped, sometimes becoming bald but the margin always ciliate. Corolla varying from pale purple to a deep red-purple, standard globose and concave, often with prominent auricles flanking the claw, the blade 1.4--2.4 mm in diameter, the claw 3.4--4.0 mm; apical petals spreading at anthesis, the blades oblong, 2.5--3.0 mm long, 0.8--1.0 (1.5) mm wide. Staminal tube equalling or exceeding the calyx lobes; filaments tinged purple with the anthers exserted beyond the petals; the
pollen orange. Ovary spherical or slightly elliptical, bearded on the distal-ventral one-half, the dorsal surface bald; style arising on the longitudinal axis of the ovary, bearded proximally and dorsally 1/3 to 1/2 its length, usually exserted beyond the anthers soon after anthesis.

**Distribution and phenology**

Throughout the short grass plains and prairies of southern Canada and the United States. North to south: from southern Alberta, Saskatchewan and Manitoba, to eastern New Mexico, central Oklahoma and Arkansas; scattered in isolated colonies in Louisiana, Mississippi and Alabama; in Texas along the Red River Valley and rarely into the Black Belt Prairie region. East to west: from central Indiana to Montana, central Wyoming and central Colorado.

Anthesis: northwest, mid June to early August; southwest, late May to late July; northeast, late May to mid August; southeast, mid May to early June.

**Nomenclature**

*Petaloastemon purpureum* was observed and collected by Michaux in Illinois and introduced into Europe in 1794. Verification of this date is given by Ventenat (1800) and by a label affixed to one sheet of Willdenow's original material at B: "ab Ann. 1794." The Ventenat name appeared in, *Description*
des plantes nouvelles et peu connues, cultivées dans le jardin de S. M. Cels, and he made good use of the unusual opportunity of studying an American plant growing on European soil. His description and accompanying drawing are superior. His collection is currently housed in the Herbarium Delessert, Conservatoire et Jardin Botaniques, Geneva. In the collection are two specimens, one clearly marked "Dalea N. Sp. purpurea Hort. Cels," the other, "Dalea purpurea Vent. H. C. -- violacea W. Petalostemum violaceum Michx." I take the former to be the typus.

The Willdenow collection at Berlin-Dahlem possesses three sheets referable to Willdenow's Dalea violacea which appeared in Volume III of Species Plantarum, the name attributed to Michaux. Michaux's original material is in Paris. Dr. A. Lourteig kindly sent me two specimens representative of the material in the Herbarium Richard. They are both of one species but differ in degree of pubescence, a common variation seen throughout the range of P. purpureum.

The problems involved in typification of Petalostemon violaceum var. pubescens Gray has been discussed under P. pulcherrimum. In summary, Gray's variety is P. pulcherrimum as to citation, but his material included both P. purpureum (Fendler No. 137) and P. pulcherrimum (Lindheimer No. 42). Both P. purpureum f. pubescens (Gray) Fassett and P. purpureum var. pubescens (Gray) Boiv. are based on the Fendler specimen. Petalostemon mollis Rydb. is based on four collections.
I have seen duplicates of Canby, Snowy Mts., 1882 from Montana at NY. The specimens are very pubescent plants, practically lacking a peduncle, possessing leaflets only slightly involute making them seem quite wide in comparison to other members of the species. In addition, the apical petals are uncommonly wide and represent the measurements in parentheses in the descriptions of these structures. A similar phenotype also occurs in southeastern Colorado but possesses a prostrate-assurgent habit, and has received the name P. pubescens A. Nels. The holotype for the Nelson name is at RM and an isotype at NO. Both of these forms of P. purpureum are apparently rare. I have seen only six sheets including the types which fit the description of P. pubescens and only the two sheets referrable to the Rydberg "species."

Rydberg in his portion of Flora of North America (1919-1920) created P. standleyanus for the moderately pubescent purple species found in New Mexico. I have studied the holotype and it falls within my delimitation of P. purpureum. It most closely resembles the more pubescent forms found in Colorado and Wyoming, particularly regarding petal size and calyx length.

Observations

Petalostemon purpureum is variable with respect to amount of pubescence. Truly glabrous individuals are rare but they are found throughout the entire range of the species. Most
specimens are pubescent at least on the petiolules and the lower surface of the leaflets. The greatest number of extremely pubescent plants is found in the northwestern part of the range and Colorado to New Mexico. However, glabrate or completely glabrous specimens are not lacking in these areas. For example, A. Hayden, July 1929, Ft. Collins, foothills, is represented by two sheets (ISC 101400, 101735). One specimen is moderately pubescent, the other is glabrous. Close examination of both indicates, however, that in all other respects, the two entities are identical. Collections from Montana indicate that the specimens from higher elevations are generally low in stature but a wide range of pubescence is exhibited. Pubescence variations in the Canadian specimens parallel those found in the United States. Towards the west, there is an increase of pubescent forms, yet in the same areas where the "mollis" forms are found, there are glabrate ones. A collection from the extreme northwestern part of the range in Alberta is almost glabrous [G. H. Turner, 17 (NY)].

Disposition of extremely pubescent, broad-leafed variants -- P. pubescens A. Nels. and P. mollis Rydb. is difficult. From my herbarium study of these taxa, they seem more deserving of elevated rank than any other variation in the extensive P. purpureum complex. Harrington, in his comparatively recent "Manual of the Plants of Colorado" (1954), relegates P. pubescens A. Nels. to the subspecific level and comments, "Intergrades with the typical form." -- a comment presumably
based on field experience. Lacking personal field experience in this region, I am adopting a conservative approach and considering the two as phenotypic extremes of an inherent polymorphism in this widespread species. The names are relegated to synonymy.

A cinereous or silvery-pubescent condition of the calyx and rachis is characteristic of *P. purpureum*. The rachis pubescence is usually carried to slightly below the inflorescence. The calyx tube is always invested with appressed, to slightly spreading pubescence but "balding" of the lobes occurs sporadically throughout the range. It is most common in specimens from Arkansas and Missouri, especially those collected in the vicinity of Kansas City but it is also found as far north as Wisconsin. This variation accounts for the reports of the occurrence of *P. pulcherrimum* north of Texas and southern Oklahoma. My studies indicate that this is no evidence for introgression with any other species. Calyx pubescence variation does not seem to be of sufficient significance to justify nomenclatural recognition.

The growth habit of certain southeastern specimens of *P. purpureum* is different from that in other parts of the range. Several collections from Arkansas, Louisiana and Alabama are decumbent or prostrate. With this is coupled the possession of extremely small leaves and small flower spikes. In all other respects, i.e. floral characters, these plants can not be excluded from *P. purpureum*. They are generally limited to
specific habitats, for example, "glades" or chalky-marl soils. The holotype of *P. purpureum* f. *arenarium* Gates, a sand dwelling "ecotype" from Illinois possesses many of the same characteristics. Perhaps there has been phenotypic convergence between these widely separated populations since both grow in rather unusual environments for the species.

The normal leaflet number for *P. purpureum* is 3—5. In the five leaflet form, the proximal pair of leaflets are invariably inserted on the distal one third of the rachis. Specimens possessing seven leaflets are rare but scattered throughout the range of the species from such widely disparate locations as Lucas Co., Iowa; El Paso Co., Colorado; and, Blaine Co., Oklahoma. Of the over 800 specimens of *Petalostemon purpureum* I have examined, only ten were found to have seven leaflets.

Hybridization between *P. pulcherrimum* and *P. decumbens* and *P. purpureum* has been discussed previously.

28. *PETALOSTEMON TENUE* (Coult.) Heller (Figs. 46, 53D)


Fig. 49. Geographical range of *Petalostemon purpureum*

Dalea tenuis (Coult.) Shinners. Field and Lab. 17: 84. (1949). Based on Petalostemon violaceus var. tenuis Coult.


Dalea purpurea var. tenuis (Coult.) Shinners. Field and Lab. 21: 165. (1953). Based on Petalostemon violaceus var. tenuis Coult.

Description

Stems many, branching above, 2.0--5.5 dm tall, pale, moderately striate with three prominent vertical ribs below the nodes, usually glabrous but occasionally evenly glabrate; center stems erect, peripheral ones often almost parallel with the ground. Stipules setaceous, dark, to 4.5 mm in length. Leaves fascicled; nodes close, producing a leafy appearance; leaflets 3--5 (7), the proximal pair inserted in the distal one-third of the rachis, prominently gland-dotted below and often moderately ciliate. Peduncles long, 3--18 cm, from 1/5 to 1/2 total length of the stem, usually glabrous, rarely pubescent immediately below the spike. Inflorescence a compact, non-expanding spike, often conical in bud, becoming columnar in fruit, 12--44 mm long, 7--11 mm in diameter; rachis pubescent; bracts precocious but at anthesis equal to or shorter than the lobes, body 2.4 mm long, the dark acumen 1.3--2.2 mm long, a slight pubescent band at broadest part of bract body
(about in the middle of the whole bract), usually with a ridge of cilia along the back toward the rachis; from the transverse belt of cilia proximally, the margin of bract is fringed; base of bract neither clasping the calyx nor sharply tapered; entire bract persistent even after mature fruit falls from rachis. Calyx tube campanulate, 2.0--3.5 mm long and 2.0--2.9 mm in diameter, invested with retrorse hairs, all pointed toward base of calyx; pubescence most strongly developed on the lateral ribs; lobes often bald but with ciliate margins; dorso-lateral lobes large, deltoid, arising from flat surfaces of the tube; ventro-lateral and ventral lobes lanceolate, arising from hemispherically curved surface of the tube; ventral lobe 1--2 mm long; in bud, lobes incurved and valvate, scarcely opening at anthesis. Corolla purple; standard auri-cled, not emarginate at apex, 2.1 mm long, 2.2 mm wide, broadly deltoid; apical petals 1.1--1.5 mm wide and 2.3--3.6 mm long, auricled at base, the claw 0.5 mm long. Stamens bright orange, extended as far as the petal tips. Ovary glabrous save for a few cilia distally and dorsally in some specimens, never bearded ventrally, 1.1--1.9 mm long, 0.6--1.0 mm in diameter, usually less than twice as long as high; style inserted on the longitudinal ovary axis, bearded dorsally for one-half its proximal length. Legume ventral surface developing more than dorsal so that in fruit the beak (remnant of style) is offset dorsally.
Distribution and phenology

Limited to the eastern Edwards Plateau in Texas and adjacent areas to the east; north and south from Wise to Bexar county, east and west from Coryell to Irion county, Texas. Always found in rocky, limestone soil. Common along roadsides. Anthesis beginning in early May, reaching a peak in early June, ceasing by early July.

Nomenclature and observations

The primary unifying characteristics of this species are its distribution and habitat preference, and the possession of retrorse pubescence on the calyx tube. The latter character is unique in the genus.

This taxon has been known as *P. stanfieldii* Small, but it must yield priority to the earlier *P. tenue* (Coult.) Heller. Both types fall within the circumscription of this species as I understand it. The type specimen of *P. violaceum* var. *tenuis* Coult. is in US; No. 23346, Santa Anna, Coleman Co., Texas. G. C. Nealley, 1889. A photograph is also at NY. The Coulter interpretation is not without flaws. Following a brief description he states:

Santa Anna (Coleman county). Apparently the form referred to in *Pl. Fendl.* under No. 138. The species is an exceedingly variable one, but the above variety is so distinct that it seems to deserve a name and description.
I have seen Fendler No. 138 (MO) and it is clearly a *P. tenuifolium* with expanding spikes and spreading pubescence.

In the transfer of Coulter's variety to species level, Heller (1896) makes this pertinent comment:

This is a very good species, quite distinct from the *Petalostemon violaceous*, which has been made a dumping ground of various red-flowered species which are not at all related to it. This species is much more closely related to *Reverchonii* than to *purpurea*. With this I concur.

In his description of *Petalostemon stanfieldii*, Small does not name a type, merely listing the distribution as, "On plains or prairies, Texas." There is a specimen in the J. K. Small collection at NY labeled, "Type," in what I take to be Small's handwriting. It was collected by S. W. Stanfield, *Summer 1896 at San Marcos and vicinity." Rydberg (1919-1920) apparently accepted this specimen as the type because he indicates, "Type locality: San Marcos, Texas."

The type specimen of *Petalostemon grothii* is at GH. I have also studied an isotype from US, No. 717748. Although collected in fruit, it is without doubt *P. tenue* as herein described. MacBride comments on the persistence of the bracts (visible only in fruit) which is unique among purple species. The collecting site is within the range of *P. tenue*, also.

Shinners (1949) transferred both *P. tenue* and *P. stanfieldii* to *Dalea*. Under the latter name he included *P.*
pulcherrimum (Heller) Heller and its synonymy. In 1953 he removed *P. pulcherrimum* and renamed it *Dalea helleri* Shinners. In the same paper, passing almost unnoticed in the body of the paragraph, is a retraction of his acceptance of *Dalea tenuis* (Coulter) Shinners, relegating it to a variety of *Dalea purpurea*. He based the combination on the type specimen at US, which he saw. He states:

Considerably resembling *D. helleri* is *D. purpurea* Vent. var. *tenuis* (Coulter) Shinners, comb. nov. ..., which has the calyx tube pubescent throughout with more or less appressed hairs instead of loose or spreading ones as in var. *purpurea*. *D. purpurea* var. *tenuis* is known from Coleman and Taylor counties; ....

*P. tenue* is limited in its distribution to the eastern Edwards Plateau, its escarpment and outliers. It possesses many characteristics in common with *P. arenicola*, but differs sharply from that species in its distribution, habit preference and the unique characteristic of retrorse calyx pubescence. This can best be observed in a dried specimen because when fresh, the trichomes are silvery-transparent and difficult to see. It is particularly apparent at the base of the calyx.

Two other species have ranges which overlap that of *P. tenue*. They are *P. pulcherrimum* and *P. purpureum*. *P. tenue* can usually be differentiated visually on the basis of size, being smaller than the other two species both in stature and
spike size. It also has a habitat preference decidedly different from that of P. pulcherrimum in that it is found in rocky limestone areas whereas P. pulcherrimum is characteristically found in black calcareous soils in this region of Texas.

29. PETALOSTEMON ARENICOLA Wemple (Figs. 47, 50, 53I, 54D)

Petalostemon arenicola Wemple sp. nov.
P. tenuifolium authors pro parte
P. purpureum authors pro parte

Description

Petalostemon arenicola Wemple, sp. nov. Caules e basi (raro superne) ramosi glabri vel glabrati 2--4 (5) dm alti striati. Stipulae subulatae fragiles usque 5 mm longae. Folia fasciculata; foliola 3--5 (7) linearia arcte involuta. Pedunculi caules 1/5--1/2 aequantes; spicae compactae non producentes 2--5 cm longae 6--9 mm latae. Bracteae non amplexicaules nec basi constrictae, cum margine apicali ciliato et cum vitta pubescente prominente transversa in parte expansa; acumen atratum sub anthesi calycis lobis brevius. Calycis tubus campanulatus 2.0--2.9 mm longus, lobi 1.0--1.5 mm longi cum pilis appressis raro demum glabrati. Corolla purpurea. Ovarii apex et venter barbati; stylus dorso barbatis per mediam proximam.
Typus, ISC (Wemple 319).

Plants lacking a prominent caudex; tap root long, pale yellow, 2—4 (5) dm tall, spreading, glabrous or glabrate, striate, prominently 3-ribbed below nodes; branching from the base, seldom above. Stipules subulate, drying dark brown, fragile, to 5 mm in length. Leaves fascicled, primary leaves bearing at least two axillary trifoliate leaves; leaflets 3--5 (7) all inserted in the distal 1/3 of the rachis, linear, strongly involute. Peduncles usually long, 1/5--1/2 the stem length, glabrous. Inflorescence a compact, non-expanding spike 20--500 mm long, 6--9 mm wide; bracts precocious, exceeding the calyx lobes in bud, shorter than lobes in flower; bract body 2.2--2.8 mm long at anthesis, not constricted toward base nor strongly clasping calyx; bearing an appressed, transverse belt of cilia below the dark, brown-black base of the acumen, a ridge of pubescence often extending proximally down the back of the bract; distal edge of the bract fringed-ciliate, cilia often extending out onto the acumen; acumen 0.7--1.4 mm long, drying black-brown. Calyx campanulate, 2.0--2.9 mm in length, 2.1--2.7 mm in diameter at mouth, bearing appressed, anteriorly directed, evenly distributed pubescence; dorso-lateral lobes deltoid and straight, the ventro-lateral and ventral lobes subulate and incurved; ventral lobe 1.0--1.5 mm long, villous-ciliate, seldom balding. Corolla purple, widely opened at anthesis; standard blade 2.2--2.8 mm
across at widest point, 1.8—2.0 mm long, strongly auricled, claw 2.2—2.6 mm long; apical petals oblong, 2.4—3.2 mm long, 1.2—1.6 mm wide, the claws 0.7—1.1 mm. Filaments usually exceeding petals in length, anthers yellow-orange; pollen a bright yellow. Ovary bearded ventrally on distal 1/2, more than twice as long as its diameter (1.2—1.5 mm long, 0.5—0.7 mm in diameter); style arising from above the longitudinal axis of ovary, bearded dorsally on the proximal end to 1/2 its length.

Distribution and phenology

Southwestern Nebraska, eastern Colorado, southwestern Kansas, the panhandles of Oklahoma and Texas and eastern New Mexico. Limited to deep sands of the Llano Estacado, on dunes, blowouts and riverbottoms. Flowering in early July in the northernmost part of the range, early June to early July for the southern part. Texas collections of flowers at anthesis have been made as early as May 1, and as late as August 31. The majority of the collections, however, are as previously stated. The exceptions are probably caused by droughts or early rains typical of the unpredictable rainfall in north Texas.

Discussion

This new species is distinctive both in appearance and in habitat preference from the other purple species of Petaloste-
mon growing in the south central United States. Throughout its range, which is almost precisely the geological delimitation of the Llano Estacado (Fenneman 1938), it is found only in the stream beds, which dissect this massive limestone plateau and stream-associated dunes and blowouts. My field studies indicate that it is never found on the caprock nor partially down canyon walls but only in the sand of the river bottoms. In the southern part of its range it is geographically sympatric with *P. tenuifolium*. Ecologically the two are quite isolated, however, because the latter species is restricted to the caprock, penetrating only part of the way down the valley walls.

The overlapping distribution, and morphological similarity of *P. arenicola* and *P. tenuifolium* has resulted in previous confusion; however, the two are distinguishable morphologically as well as ecologically. The typical *P. tenuifolium* pubescence pattern (the stem base and the apex of the peduncle pubescent) is never found in *P. arenicola*. The apex of the peduncle is almost always glabrous in the latter species. One of the easiest field recognition features differentiating the two species is that of rachis elongation. As the spike matures, following anthesis, in *P. tenuifolium*, it elongates, often becoming sinuous. That of *P. arenicola* never elongates following anthesis. Accompanying spike elongation in *P. tenuifolium* is loss of the bracts, whereas, the bracts are retained in *P. arenicola*. The bracts of the latter species
are never pubescent over their entire surface, nor are they as wide as those of *P. tenuifolium*; additionally, they are ciliate along the distal margin. The two species differ to some degree in calyx pubescence. This feature is a difficult key character, but *P. tenuifolium* has a more spreading calyx pubescence while that of *P. arenicola* is more appressed. The ovary at anthesis is linear in *P. tenuifolium* often being three times as long as the diameter, while in *P. arenicola* it is usually about twice as the diameter. The style is axial in *P. tenuifolium* but decidedly above the longitudinal axis of the ovary in *P. arenicola*.

Material of *P. arenicola* has also previously been referred to *P. purpureum*. The two taxa are quite distinct even though their geographical ranges slightly overlap. The simplest, yet perhaps the most effective characteristic to separate the two species is spike width — the width of a spike at anthesis or shortly thereafter, calyx lobe to calyx lobe. *P. arenicola* has spikes narrower than 10 mm while *P. purpureum* has spikes wider than 10 mm. It was this differentiation that Turner (1959) utilized to exclude *P. purpureum* from the panhandle of Texas. Concommitantly, he broadly defined *P. tenuifolium* to include *P. arenicola*. *P. arenicola* seldom exceeds 3.5 dm in stem length, while *P. purpureum* is taller; in addition, the stems of the latter species are usually branched above resulting in numerous spikes from each major stem, while branching is uncommon in *P. arenicola*. *P. purpureum* possesses relatively
short peduncles while *P. arenicola* has longer peduncles, usually 1/4 the length of the stems. The peduncle apex is glabrous in *P. arenicola*, while almost always pubescent in *P. purpureum*. Bract pubescence differs between the two species in that the ciliation often extends rearward of the transverse appressed belt in *P. arenicola* while the entire proximal area of the bract is glabrous in *P. purpureum*. In addition, the expanded, distal end of the *P. arenicola* bract is ciliate giving it a "fringed" appearance. Lastly, the ovary instead of being almost spherical with the style extending from the center of the ovary as in *P. purpureum*, is elliptical in *P. arenicola* -- at least twice as long as its diameter with the style protruding from the dorsal surface, not the center.

Another species that could be confused with *P. arenicola* is *P. tenue*. The two are separated in range by almost 100 miles but are similar in stature and gross appearance. They are readily distinguished by calyx pubescence. On *P. tenue* the pubescence is always retrorse, that is, pointing rearward toward the axis of the rachis. In *P. arenicola* the pubescence is oriented in the typical manner, pointing away from the axis of the rachis. A further difference is the glabrous or slightly ciliate ovary of *P. tenue* while in *P. arenicola*, the ovary is bearded distal-ventrally.

The differentiational characteristics of *P. arenicola* and the other purple species discussed above are summarized in Table 6.
Greenhouse hybridization experiments indicate that *P. arenicola* and *P. tenuifolium* are freely compatible. In fact, in attempted crosses, seed set was unusually high and the hybrids themselves while intermediate in all characteristics were fully fertile. Why do the two species not hybridize in nature? They are seldom separated by more than 1/2 mile, one on the valley floor, the other on the mesa, yet I have seen no hybrids in the field or sheets of any putative hybrids in the herbarium. It is possible that the pollinators of the two are different or that the pollinators are localized, either remaining in the valleys or on the mesas. Another possibility is that the hybrids, while growing vigorously in the greenhouse are less well adapted to the available habitats than the parents in nature, and their survival is limited.
Table 6. Character comparisons between *P. arenicola*, *P. tenuifolium*, *P. purpureum* and *P. tenue*.

<table>
<thead>
<tr>
<th>Character</th>
<th><em>P. arenicola</em></th>
<th><em>P. tenuifolium</em></th>
<th><em>P. purpureum</em></th>
<th><em>P. tenue</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant height</td>
<td>&lt; 3.5 dm</td>
<td>&lt; 3.5 dm</td>
<td>&gt; 3.5 dm</td>
<td>&lt; 3.5 dm</td>
</tr>
<tr>
<td>Branching</td>
<td>below</td>
<td>below</td>
<td>above</td>
<td>below</td>
</tr>
<tr>
<td>Vegetative pubescence</td>
<td>glabrous-glabrate</td>
<td>dense below &amp; above</td>
<td>glabrate to pubescent</td>
<td>glabrous-glabrate</td>
</tr>
<tr>
<td>Peduncle length</td>
<td>usually long</td>
<td>long</td>
<td>short</td>
<td>long</td>
</tr>
<tr>
<td>Spike width</td>
<td>&lt; 1 cm</td>
<td>&lt; 1 cm</td>
<td>&gt; 1 cm</td>
<td>&lt; 1 cm</td>
</tr>
<tr>
<td>Spike elongation</td>
<td>none</td>
<td>much</td>
<td>none</td>
<td>none</td>
</tr>
<tr>
<td>Bract pubescence</td>
<td>transverse belt + back rib. Ant. ciliate fringe</td>
<td>uniform</td>
<td>transverse belt only + back rib. Ant. ciliate fringe</td>
<td>transverse belt + back rib. Ant. ciliate fringe</td>
</tr>
<tr>
<td>Calyx pubescence</td>
<td>appressed antrorse uniform</td>
<td>spreading antrorse uniform</td>
<td>appressed antrorse uniform</td>
<td>appressed retrorse uniform &quot;balding&quot;</td>
</tr>
<tr>
<td>Ovary shape</td>
<td>2 x long as high</td>
<td>3 x long as high</td>
<td>1-1½ x long as high</td>
<td>1-1½ x long as high</td>
</tr>
<tr>
<td>Ovary pubescence</td>
<td>bearded</td>
<td>bearded</td>
<td>bearded</td>
<td>glabrous</td>
</tr>
</tbody>
</table>
Fig. 50. Type specimen of Petalostemon arenicola Wemple. Deposited in ISC
280

**Eulophomya longiflora**

- **5**, 5 mi. south on road, east side of Sumas Rd.
- Long, yellowish tips on soft, pubescent samara.

**From:**

**N.Z.**

- **Col. Sample 319**
Fig. 51. Floral parts and seeds of members of section Candidi (A--C) and Carnei (D).

Seeds and ovary drawings x15, other drawings x5. A. *P. candidum*. 1. lateral view of flower 2. ovary 3. seed 4. and 5. two views of a teratological stamen-petal. The teratology is bilateral -- exactly one-half petal, one-half stamen. B. *P. occidentale*. 1. lateral view of flower. 2. ovary 3. seed. C. *P. multiflorum*. 1. lateral view of flower. 2. seed. 3. standard -- slightly folded at the center of the blade due to the concave nature of the lamina. D. *P. feayi* and *P. carneum*. 1. lateral view of flower of *P. feayi*. 2. standard of *P. feayi*. 3. apical petal of *P. feayi*. 4. seed of *P. carneum*.
Fig. 52. Floral parts and seeds of selected species of sections Villosi, Phleoides, Foliosi and subg. Kuhnistera.

Seed drawings x15, other drawings x5.

Fig. 53. Floral parts and seeds of species in section Purpurei.

All floral drawings except I are x5. All seeds and the petals in I are x15.

A. *P. tenuifolium*. 1. lateral view of flower 2. seed 3. androecium and gynoecium, standard removed 4. carpel 5. bract.

B. *P. decumbens*. 1. lateral view of flower 2. seed.

C. *P. purpureum*, seed.
D. *P. tenue*, seed.
E. *P. reverchonii*, seed.
F. *P. gattingeri*, seed.
G. *P. tenuifolium* X *P. gattingeri*. 1. legume 2. fruit.

H. *P. pulcherrimum*, seed.

I. *P. arenicola*. 1. standard (folded in the center due to concave shape) 2. apical petal.
Fig. 54. Representative species of Petalostemon (A--E). The caudex of a seedling of *P. candidum* (F).

A. *P. villosum*
B. *P. candidum*
C. *P. microphyllum*
D. *P. arenicola*
E. *P. obovatum*
EXCLUDED SPECIES

All are annuals referable to Dalea (see pp. 14-31).


and


According to Kearney & Peebles (1960, p. 440):

_Petalostemon pilulosus_ [sic] Rydb. was described from a specimen collected by Nealley (No. 237), probably in the Rincon Mountains, Pima County. The type appears to be a form of _Dalea albiflora._

I have not seen the type.
ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to Dr. Duane Isely for his suggestion of the problem, his advice and encouragement during the course of the investigation. I would also like to express my thanks to Dr. Richard Pohl, Curator of the Herbarium for his helpful suggestions and to Dr. Nels R. Lersten for his encouragement and aid in the anatomical investigations of the genus.

I am grateful to Dr. G. B. Van Schaack of the Missouri Botanical Garden for his helpful suggestions in literature research and herbarium locations and Dr. L. H. Shinners of Southern Methodist University for his preparation of the Latin diagnosis for P. arenicola.

I am indebted to the National Science Foundation which supported me as a Summer Research Fellow and a Regular Graduate Fellow during the entire course of my research.

Finally, I wish to express my deep thanks to my wife, Mary, whose constant aid and encouragement resulted in the completion of this work.
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Kuntze, O. 1891. Revisio generum plantarum. Liepzig, Germany, Arthur Felix.


Turner, B. L. 1959. The legumes of Texas. Austin, Texas, Univ. of Texas Press.


APPENDIX

Cited Specimens

Petalostemon adenopodium -- specimens examined


Petalostemon albidum -- specimens examined


Petalostemon arenicola -- specimens examined

State unknown: County unknown. Wood, no date or number (NY).

Colorado: Cheyenne. Ripley & Barneby 10164 (NY). Las Animas. Rogers 6002 (US). Lincoln. Marsh 9 July 1907 (US). Yuma. Eggleston 15169 (MO); Osterhout 4017 (RM); Osterhout 4052 (RM); Piemeisel 1511 (US); Shattz 593 (US); Shantz & Piemeisel 1459 (US).


Petalostemon candidum -- representative specimens examined

CANADA

Manitoba: Love & Love 5627, W of Brokenhead (US); Fowler 6 July 1887, Brandon (US).

Ontario: Denike 577, Ingolf (NY).

Saskatchewan: Ledingham & Yip 2244 (ISC); Bourgeau year 1857-8 (NY).

UNITED STATES

Alabama: Colbert, Isely 3741 (ISC); Greene. Harper 3426 (NY, US); Sumter. Crawford & Harvill 1133 (TEX).
Arkansas: Baxter, Demaree 30835 (ISC, SMU, TEX); Benton, plank year 1899 (NY); Boone, Demaree 3218a (SMU); Carroll, Iltis 4868 (OKLA, SMU, TENN); Conway, Demaree 37154 (SMU); Fulton, Demaree 30803 (ISC, SMU, TEX); Garland, Demaree 23203 (ISC, NY, OKLA, SMU, TENN); Logan, Demaree 17680 (NY, SMU); Lonoke, Demaree 22358 (NY, SMU); Marion, Demaree 30915 (ISC, OKLA, SMU, TEX); Pulaski, Merrill 39 (FSU); Saline, Demaree 22254 (NY, SMU); Washington, Demaree 3183 (TEX).

Illinois: Champaign, Reynolds 566 (US); Cook, Babcock 15 June 1871 (US); Dupage, Umbach 4 July 1896 (RM); Hancock, Mead August 1844 (NY); Henderson, Patterson, Oquawka (NY); Kane, Eldredge 18 July 1888 (ISC); Macon, Clokey 2395 (NY, OKLA, RM); Menard, Hall July 1863 (NY); Ogle, Waite 3 August 1885 (DUKE, US); Peoria, Chase 3186 (ISC, NY); St. Clair, Herzog, year 1878 (NY); Winnebago, Bebb year 1867 (NY).

Indiana: County unknown, Umbach 5728, Millers (ISC); Umbach 20 August 1898, Clarke (US); Stuart 7 July 1900, Elston; Cass, Friesner 9740 (DUKE, GA, NY, SMU, TENN); Newton, Friesner 22885 (FLAS, KY, TEX); Vigo, Evermann year 1889 (US).

Iowa: Adair, Morrill 144 (ISC); Allamakee, Shimek 13 August 1917 (ISC); Appanoose, Davidso, 6520 (ISC); Black Hawk, Carver year 1854 (ISC); Boone, Isely 5262 (OKLA, US); Buchanan, Bode 13 August 1919 (ISC); Buena Vista, Pammel 31 July 1908 (ISC); Carroll, Hayden 3446 (ISC); Cerro Gordo, Shimek 29 July 1922 (NY); Chickasaw, Spiker 12 July 1926 (ISC); Clarke, Pammel 26 September 1924 (ISC); Clay, Hayden 7666 (ISC); Clayton, Shimek 19 August 1922; Crawford, Isely 4194 (ISC); Decatur, Anderson 1 August 1903 (ISC, RM); Delaware, Shimek 18 July 1928 (ISC); Des Moines, Pammel 948 (ISC); Dickinson, Thorne 12996 (US); Cherokee, Pammel 5 September 1920 (ISC); Dubuque, Pammel 16 August 1907 (ISC); Emmett, Cratty July 1895 (US); Fayette, Fink 218 (US); Fremont, Gleason 9296 (NY); Guthrie, Monson 2547 (ISC); Hamilton, Pammel 29 July 1927 (OKLA); Hancock, Hayden 3442 (ISC); Hardin, Jones August 1876 (NY, US); Harrison, Schumeyer 1875 (US); Howard, McDill 289 (ISC); Humboldt, MacBride 1898 (ISC); Ida, Pammel July 1896 (ISC); Iowa, Shimek 12 July 1913 (ISC); Jasper, Bruggen 587 (FLAS); Johnson, Shimek 14 July 1923 (NY); Jones, Isely 5903 (ISC); Kossuth, Martin 95 (ISC); Linn, Shimek 2 July 1921 (ISC); Louisa, Shimek 24 August 1926 (ISC); Lyon, Shimek 27 August 1932 (NY); Mills, Morrill 976 (ISC); Mitchell, Tuttle 10 (ISC); Monona, Shimek 19 July 1909 (ISC); Muscatine, Shimek 14 July 1911 (NY); O'Brien, Hayden 3450 (ISC); Osceola, Monson 2290 (ISC); Palo Alto, Hayden 4033 (ISC, NY); Pocahontas, Monson 2577 (ISC); Pottawatomie, Clawson 309 (ISC); Poweshiek, Russell 712551 (TENN); Sac, Monson 2620a (ISC); Scott, Shimek 8 August 1927 (ISC); Shelby, Shimek 24 August 1913 (ISC); Sioux, Hayden 4040 (ISC); Story, Wingo 191 (SMU); Warren, Bruggen 1255 (SMU); Webster, Churchill
2109 (ISC); Winnebago, Monson 2861 (ISC); Winnesheik, Holway 43 (ISC); Woodbury, Gleason 9334 (NY); Worth, Shimek 25 August 1928 (ISC); Wright, Shimek 9 August 1919 (ISC).

Kansas: Bourbon, Hubert 3761 (OKLA); Cherokee, Rydberg & Imler 273 (NY); Douglas, Chamney 5 (SMU); Franklin, Welsh 662 (ISC); Geary, Wemple 295 (ISC); Harvey, Biltmore 17 June 1896 (NY, US); Labette, McGregor 16986 (SMU); Linn, Isely 7449 (ISC); Pottawatomie, Marsh 1720 (SMU); Reno, Smyth 36 (US); Riley, Norton 95 (NY, RM, US); Saline, Demaree 29374 (ISC, SMU, TEX); Sedgwick, Bartley 1128 (ISC, NY).

Kentucky: County unknown, Short year 1842 (NY); Logan, Braun 3539 (NY); Lyon, Eggleston 4835 (NY); Nelson, Wharton 5574 (KY); Trigg, Baker 17 (FSU).

Louisiana: Acadia, Shinners 2363 (SMU); Calcasieu, Cocks 5 November 1912 (NO); LaSalle, Shinners 23985 (SMU); Natchitoches, Ware 24 June 1956 (SMU, TEX); Rapides, Ball 622 (ISC, NY, US).

Minnesota: Big Stone, Gleason 9436 (NY); Brown, Isely 8169 (ISC); Cass, Fammel 70 (ISC); Chicago, Taylor August 1892 (RM); Clay, Solheim 255 (RM); Clearwater, Grant 3003 (NY, US); Hennepin, Schuette 1. 39. 43. (NY, US); Kittson, Johnson 463 (ISC, NY); Nicollet, Ballard July 1892 (RM, US); Ottertail, Chandonnet 26 July 1911 (RM); Ramsey, Brown 53-44 (ISC); Redwood, Isely 8150 (ISC); Rice, Goldsmith 101 (NY); St. Louis, Lakela 2585 (NY, SMU); Sherburne, Isely 6352 (ISC, SMU); Stevens, Moore & Huff 19066 (SMU); Todd, Schuster 27 June 1947 (FSU); Winona, Hase 24 July 1882 (NY).

Mississippi: Clarke, Harper 3241 (NY, US); Lee, McDougall 1702 (US); Newton, Kral 9002 (FSU); Oktibbeha, Mohr 17 June 1892 (NY).

Missouri: Franklin, Mason 1 (TEX); Greene, Redfearn 3738 (FSU); Jackson, Bush 457 (US); Lewis, Gleason 9237 (NY); Livingston, Sparling 1110 (ISC); Ozark, Palmer 34747 (US); Phelps, Kellogg 111 (NY); St. Louis, Letterman year 1880 (ISC, NY, TEX); Stone, Isely 7004 (ISC); Sullivan, Gleason 9263 (NY); Taney, Isely & Wemple 9010 (ISC).

Nebraska: Adams, Barnhart 465 (NY); Buffalo, Rydberg 58 (NY); Cass, Morrison 1111 (US); Deuel, Rydberg 58 (NY); Hall, Isely 6084 (ISC, NY); Knox, Clements 2699 (US); Lancaster, Webber July 1888 (NY); Pawnee, Mohler 26 June 1941 (ISC); Webster, Tolsted 411023 (ISC).

North Dakota: Barnes, Fattig 2857 (DUKE); Benson, Lunell 11 August 1907 (NY); Dickey, Bergman 706 (RM); McHenry, Brown 53-49 (ISC); Richland, Metsoff 105 (NY); Rolette, Turfe 197 (RM).

Oklahoma: Adair, Wallis 7485 (OKLA, SMU, TEX); Bryan, Cory 58856 (ISC, OKLA, SMU); Carter, Penny 20 (TEX); Cherokee, Wallis 2334 (OKLA); Choctaw, Wemple & Jackson 595 (ISC); Delaware, Wallis 3273 (OKLA); Garvin, Duffer 529 (OKLA); Kay, Byler 423 (OKLA); Mayes, Wallis 2981 (OKLA); McCurtain, Little & Olmsted 53 (OKLA); Murray, Duffer 418.
(OKLA); Muskogee, Wallis 4380 (OKLA); Oklahoma, Waterfall
2084 (OKLA); Osage, Webster 4271 (OKLA, SMU); Ottawa, Wallis
4637 (SMU); Payne, Briscoe 17 July 1937 (OKLA); Pittsburg,
Shinners 18863 (SMU); Pottawatomie, McLean 183 (TEX);
Sequoia, Wallis 7469 (SMU, TEX).

South Dakota: County unknown, Vasey 16 August 1906 (US);
Hanson, Weber 17 August 1927 (FLAS); Turner, Johnson 48 (ISC, NY).

Tennessee: Davidson, Gattinger year 1877 (US); Rutherford, DeSelm 1847 (TENN).

Texas: Bastrop, Lundell & Lundell 9055 (US); Caldwell,
McBryde 12 June 1931 (OKLA, TEX); Dallas, Reverchon 3751 (NY, SMU, US);
Fannin, Van Vleet 1577 (SMU, TEX); Grayson, Gentry
50-227 (FLAS, TEX); Galveston, Turner 2191 (SMU); Hardin,
Wemple & Jackson 693 (ISC); Harris, Reverchon 3752 (SMU);
Hopkins, Shinners 20431 (SMU); Jasper, Cory 56593 (SMU);
James, Reese (SMU, TEX); Lee, Hall 195 (NY, US); Liberty,
Wemple & Jackson 694 (ISC); Palo Pinto, Tracy 6 June 1902
(TEX); Bed River, Tharp 47391 (ISC, TEX); Smith, Shinners
11425 (SMU); Tarrant, Ruth 194 (TEX).

Wisconsin: Dane, Seymour & Jones 1040 (DUKE); Juneau,
Meares 231 (NY, US); LaCrosse, Pammel year 1887 (ISC);
Outagamie, Leuders 13 July 1889 (US); Sauk, Grotjan 172
(TENN).

Petalostemon carneum -- specimens examined

Florida: County unknown, Britton 304 (NY); Chapman year
1871 (NY); Chapman year 1901 (US); Chapman 719 (US); Cooper
year 1859 (NY); Curtiss year 1875 (NY); Keeler 7 October 1905
(NY); Lighthipe 242 (NY); McFarlin 17 July 1927 (FLAS); Palmer
year 1874 (NY, US); Palmer 106 (MO, NY); Safford 14 July 1917
(US); Simpson year 1889 (US); Bradford, Murrill & Watson 112
(FLAS). Brevard, Fredholm 5917 (MO, US); Kral 5280 (FLAS);
Rhoads (FLAS). Broward. Hood 28 April 1910 (FLAS); Small &
Carter 1205 (NY); Small et al 3375 (NY). Charlotte. Bennett
11 July 1959 (FLAS); Gaiser et al 18 August 1945 (FLAS); Kral
17877 (Louisiana Polytechnic Institute). Citrus. Isely &
Wemple 9271 (ISC); Kral 7759 (GA); Kral 7815 (FSU, NY). Clay.
Knight 2 July 1936 (FLAS); Murrill 308 (US); Murrill 309 (MO, US).
Colliner. Brass 15914 (US); Kral 18102 (Louisiana Poly­
technic Institute). Dade. Britton 276 (NY); Garber April –
June 1877 (FSU, NY, US); Kral 18074 (Louisiana Polytechnic
Institute); McAllister 243a (DUKE); Meredith March 1917 (TENN);
Moldenke 205 (MO, NY); Moldenke 310 (DUKE, US); Pollard &
Collins 255 (NY, US); Small 3844 (NY); Small 3873 (NY); Small &
Carter 739 (NY); Small & Carter 744 (NY); Small & Mosier
6344 (NY); Small & Nash 177 (NY); Small & Wilson 1816 (NY);
Small et al 3253 (NY); Small et al 5969 (NY). Dixie. Arnold
16 August 1937 (FLAS); Isely & Wemple 9230 (ISC); Kral 5384
Petalostemon carollinense ssp. carollinense -- specimens examined

Florida: County unknown. Hood 30 September 1913, Orange City (FLAS); O'Neill 25 October 1925, Ft. Leo (MO); Singletory 7 October 1936, Loughman to Lake Wilson (DUKE); Smith 26 November 1871, Pilatka (NY). Alachua. Arnold 12 October 1931 (FLAS); Fattig 6 (US); Isely & Wemple 9246 (ISC); Murrill 12 October 1937 (MO); Murrill 440 (US); O'Neill 24 October 1924 (FLAS); Weber & West 30 September 1927 (FLAS); West & Arnold 21 September 1937 (FLAS). Citrus. Brass 20819 (US); Isely & Wemple 9267 (ISC). Clay. Watson & Murrill 29 October 1939 (FLAS). Columbia. Isely & Wemple 9368 (ISC); Perdue 1823
Petalostemon caroliniense ssp. trifoliatum — specimens examined

Alabama: County unknown. Buckley September 1821 (MO); Gates year 1831 (NY); Graves 1109, Spring Hill (MO, US); Mohr 1 October 1886, Spring Hill (US). Beldwin. Isely & Wemple
Petalostemon compactum — specimens examined


Colorado: Adams. Kelso 363 (RM). Denver. Eastwood 34 (US); Letterman 19 (ISC); Letterman 108 (NY); Letterman 241 (US); Tracy 900 (NY); Ward 20 August 1881 (US). Jefferson. Kuntze 19 September 1874 (NY). Larimer. Crandall 26 August 1898; Swezy 930 (ISC, NY, RM, US); Weld. Ewan 12284 (MO); Greene 20 July 1872 (NY); Johnston 817A (RM); Osterhout 29 July 1899 (NY, RM); Osterhout 1059 (RM); Osterhout 2311 (NY, US); Custer 19149 (RM); Osterhout 7475 (RM).


Nebraska: County unknown. Hapeman 4 August 1891 (RM).


New Mexico: County unknown. Cookerell 12, Rio de los

Oklahoma: Cimarron. Rogers 4762 (US); Rogers 6145 (TEX, US).

South Dakota: Fall River. Hayward 539 (NY).


Petalostemon decumbens — specimens examined

Colorado: County unknown. Young 26 May 1916.

Oklahoma: Bryan. Taylor 726 (OKLA); Wemple & Jackson 579 (ISC); Choctaw. Wemple & Jackson 571, 586, 587, 590, 594 (ISC); Wemple 421, 422, 424, 428 (ISC); Ripley & Barneby 7427 (NY); Smith & Randle 66 (SMU); Waterfall 7570 (OKLA, TEX); Waterfall 1608 (OKLA); McMurtry. Houghton 3639 (NY); Reed 7 June 1950 (TEX, ISCU, SMU); Waterfall 12427 (US, OKLA, SMU); Wemple & Jackson 599, 604, 605 (ISC); Waterfall 16983 (OKLA).


Petalostemon feayi — specimens examined

Florida: County unknown. Curtiss 568 (GA, MO, NY); Hood 14 August 1910 (FLAS); Pammel 24 February 1928 (ISC); Tracy 6879 (MO, NY, US). Brevard. no collector listed 3 August 1929 (TENN). De Soto. Small & DeWinkeler 9771 (FLAS, DUKE).

Franklin. Ford 3150 (US); Godfrey 52374 (DUKE); Godfrey 60267 (FSU); Godfrey et al 53463 (DUKE, FSU, NY); Jackson 423 (DUKE, FSU); Kral 2404 (FLAS); Kurz 1 November 1941 (FLAS); Sargent 23 June 1950 (GA). Hernando. Cooley & Ray 7013 (FSU); Hardin 296 (GA); Small et al (US). Highlands. Brass 15564 (FSU, US); Ford & Bennett 6 August 1960 (FLAS); Isely & Wemple 9316 (ISC); Isely & Wemple 9319 (ISC); Isely & Wemple 9330 (ISC); McFarlin 9376 (CLAS); Sargent (OKLA); Small & West 5 September 1934 (FLAS); Thorne 15245 (US); Webster 4209 (US). Hillsborough. Blanton 6691 (MO, US); Britton & Milson 2 (NY); Fredholm 6391 (ISC, MO, US); Garber May 1876 (FLAS); Lakela 23281 (FLAS). Indian River. Lemaire 169 (FSU). Lake. Hitchcock 1104 (MO, NY); Murrill 17 July 1939 (FLAS); Nash 1523 (MO, NY, US); Nash 1524 (NY, US); Nash 1557 (DUKE); O'Neill 2 August 1920 (FSU, US); Turner 4673 (TEX); Wilbur & Webster 2658 (US). Manatee. Tracy 6337 (US). Marion. West & Arnold 16 September 1941 (FLAS); Kral 7676 (FSU, GA, NY); Murrill 680
(US); West 12 May 1933 (FLAS). Martin. Beck 24 October 1950
(FLAS); Small et al 10699 (TENN). Orange. Isely & Wemple 9315
(ISC); Lewton 10 August 1894 (NY); Weislahn 128a (US);
Moldenke 5360 (NY). Pasco. Burger & West 16 September 1927
(FLAS). Folk. Bottimer 575 (GA); Correll 6328 (DUKE); Curtiss
5880 (FSU, GA, ISC, MO, NY, US); Godfrey & Kral 53841 (FSU);
Kral (Louisiana Polytechnic Institute); Lekela 24582 (FLAS);
McFarlin 907 (FLAS); Weber & Kelbert 7 August 1928 (FLAS);
Wilbur & Webster 2631 (US). Putnam. Hume 8 August 1947 (GA);
Volusia. Curtiss 6699 (GA, ISC, MO, NY, US); Hood 8 September
1913 (FLAS); Van Cleef 10 July 1937 (FLAS). Wakulla. Ford
4691 (FLAS); Godfrey 58918 (FSU).


Petalostemon flavescens — specimens examined

Emery. Maguire 18421 (NY); Maguire 18481 (NY); Maguire et al
25 June 1933 (RM); Ripley & Barneby 8669 (NY). Garfield.
San Juan. Barneby 13082 (NY); Holmgren & Goddard 9990 (NY);
Holmgren & Hansen 3431 (NY, SMU).

Petalostemon foliosum — specimens examined

Illinois: County unknown. Beeb year 1880, Fountaindale
(ISC).

Tennessee: County unknown. Gattinger no date or number,
"Middle Tennessee" (TENN). Davidson. Gattinger no date or
number "Barrens around Nashville" (US); Gattinger year 1887
(NY); Gattinger July 1878 (NY, TENN, US); Gattinger 28 July
1878 (US); Gattinger July 1879 (NY); Gattinger 1 July 1881
(US); Gattinger July 1886 (US); Gattinger 570 (GA, US).
Franklin. Gattinger no date or number (NY). Knox. Lanher 20
September 1938 (TENN). Butherford. Gattinger July 1886 (NY);
Gattinger August 1886 (US); Sharp & Shanks 25455 (TENN);
DeSelma 1879 (TENN); Isely & Wemple 9420 (ISC).

Petalostemon gattingeri — specimens examined

Alabama: County unknown. Mohr 5 June 1892 (NY); Mohr
10 June 1892 (US). Franklin. James 20 May 1944 (US, NY);
Sargent 6521 (SMU); Wemple 470 (ISU).
Georgia: Catoosa. Churchill 25 May 1011 (TENN); Duncan
12455 (US, FLAS, TENN, GA, SMU, DUKE, ISC). Walker. Duncan
12532 (SMU, GA); Duncan & Hardin 15925 (GA).

Tennessee: County unknown. Gattinger June 1879 (NY);
Petalostemon gracile — specimens examined


Petalostemon griseum — specimens examined

Petalostemon microphyllum — specimens examined

Oklahoma: Marshall. Goodman 6152 (NY, OKLA, SMU); Goodman 6705 (OKLA); Wemple & Jackson 553 (ISC).
Texas: County unknown. Hall year 1872 (US); Thurow year 1894 (US); Vallum 3 June 1855 (US). Arkansas. Jones 889 (SMU); Tharp year 1932 (TEX); Tharp 2 July 1939 (NY, TEX); Turner 3971 (TEX). Austin. Wemple & Jackson 725 (ISC). Bastrop. Tharp 19 June 1939 (OKLA, TEX). Brazos. Parks 21 June 1947 (SMU). Caldwell. MacBride 12 June 1931 (TEX); Ochendon 31 May 1964 (ISC). Callahan. Wemple 249 (ISC). Dallas. LeRoy no date or location (NY); Orr 52 (SMU); Reverohon June (NY); Reverohon July 1876 (NY); Reverohon 233 (US); Reverohon June 1881 (US); Reverohon 233 (NY); Reverohon 1949 (NY, SMU, US). Freestone. Lenell 12964 (US); Wemple & Jackson 631, 635 (ISC).

Petalostemon multiflorum — representative specimens examined

MEXICO
Coahuila: Marsh 30, Muzzquiz (OKLA, TEX); Wynd & Mueller 223, Muzzquiz (NY, US).

UNITED STATES
Kansas: Bourbon, Bartley 1207 (NY, US); Chase, Stevens no number or date (US); Chautauqua, McGregor 15040 (SMU); Cowley, White June 1898 (NY); Geary, Gayle 573 (NY); Green-
wood, Hall August 1870 (NY); Miami, Oyster August 1882 (ISC); Pottawatomie, Crevecoeur 1 (US); Pratt, Smyth 104 (NY, US); Riley, Norton 96 (NY, RM, US); Sedgwick, Bartley 1126 (NY).

Missouri: Jackson, Bush 826 (NY, US).

Oklahoma: Atoka, Howard 28 (TEX); Bryan, Blain 70 (US); Canadian, Waterfall 1527 (NY); Carter, Wemple 401 (ISC); Choctaw, Waterfall 12431 (OKLA); Comanche, Kaeser 28 (NY); Cotton, Wemple 396 (ISC); Jefferson, Wemple 399 (ISC); Kay, Davy 96 (OKLA); Kiowa, Barnes 19 July 1947 (OKLA, TEX); Lincoln, VanVleet 15 July 1905 (US); Marshall, Wemple 404 (ISC); McClain, Demeree 13183 (NY); Murray, Demeree 13193 (GA, NY, OKLA, SMU, TEX, US); Osage, Sizemore 269 (OKLA); Payne, Renfro 147 (TEX); Pontotoc, McCoy 1743 (OKLA); Seminole, Hopkins & Demeree 47 (OKLA); Tillman, Wemple 395 (ISC).

Texas: Austin, Wurglow 30 (US); Bastrop, Tharp 10 June 1939 (TEX); Bee, Wemple & Jackson 762 (ISC); Bell, York & York 5462 (SMU, TEX); Bexar, Groth 144 (ISC, NY, US); Bosque, Whitehouse 21 July 1929 (TEX); Brazos, Reverchon 1948 (SMU, US); Brown, Henderson 62-850 (ISC); Burnet, Schaupp 3 August 1892 (US); Caldwell, Tharp & Tyson 52-537 (ISC, TEX); Calhoun, Tharp 22 May 1930 (OKLA, TEX); Callahan, Warmock 46359 (TEX); Clay, Shinniers 15230 (SMU); Comal, Lewton 746 (FSU); Cooke, Correll & Correll 12959 (FSU, SMU); Coryell, Muller 8734 (SMU); Crockett, Tharp 6405 (OKLA, TEX); Dallas, Reverchon 1947A (NY, SMU, US); Denton, Dobbins 1 (SMU); De Witt, Riedel 3 June 1942 (TEX); Duval, Jroft 175 (NY); Ellis, Cory 53338 (SMU); Erath, Cory 58070 (OKLA, SMU); Fayette, Tharp 2345 (OKLA, TEX, US); Galveston, Turner 3067 (OKLA, TEX); Gillespie, Jemmy 752 (US); Goliad, Wemple & Jackson 773 (ISC); Grayson, Hennen 223 (ISC, SMU); Grimes, Turner & Tharp 3076 (OKLA, TEX); Harris, Traverse 146 (SMU); Hays, Stanfield summer 1897 (NY); Hood, Wemple 242 (ISC); Jackson, Drumel 8799 (NY, US); Johnson, Lamb 17 July 1937 (SMU); Jones, Adams 3 (SMU); Karnes, Johnson 992 (TEX); Kendall, Parks 43102 (TEX); Kerr, Heller year 1903 (NY, US); Matagorda, Palmer 9732 (US); McCulloch, Gould 5689 (SMU, TEX); McLennan, Smith 930 (TEX); Montague, Whitehouse 10503 (SMU); Navarro, Bryant 13 (SMU); Nueces, Heller 1814 (ISC, NY, RM, SMU, US); Rockwall, Cory 53312 (RM, SMU, US); Runnels, Gould 7074 (SMU, TEX); San Patricio, Wemple & Jackson 753 (ISC); Schleicher, Reed 255 (FSU); Sutton, Reed 258 (FSU); Tarrant, Ruth 28 (ISC, NY, RM, SMU, TENN, US); Taylor, 7443 (ISC, NY, TEX); Travis, Johnson & Barkley 6055 (SMU, TEX); Val Verde, Palmer 13585 (US); Walker, Dixon 378 (NY); Walker, Hall 138 (NY, US); Washington, Brackett 128 (TEX); Williamson, York & York 55189 (SMU, TEX); Wise, Shinniers 24084 (ISC, OKLA, SMU).
Petalostemon obovatum — specimens examined


Petalostemon occidentale — representative specimens examined

CANADA

Alberta: Moodie 60, vicinity of Calgary (NY); Moodie 1147, vicinity of Rosedale (NY); Mcss 287, N of Pincher (US); Rusby 29 July 1915, near Medicine Hat (NY).

Manitoba: Bolvin & Dore 7740, Brandon (NY).

Saskatchewan: Bird 1274, W of Val Marie Reservoir (OKLA); Ledingham 1184, SW of Boharm (ISC, NY); Macoun July 1880, Moose Jaw (NY).

MEXICO

Chihuahua: Goldman 420, Casas Grandes (US); Mexia 2621, between Calera and Basuchil (NY, US); Pringle 1216, near Guerrero (NY, US); Shreve 7971, N of Rubio (US).

UNITED STATES

Arizona: Apache, Peebles 12460 (US); Cochise, Gooding 2350 (RM); Coconino, MacDougal 260 (ISC, NY, RM, US); Graham, Fosberg 55387 (NY); Navajo, Pultz 1672 (NY); Santa Cruz, Peebles 5229 (US); Yavapai, Peebles et al 4254 (US).

Colorado: Boulder, Tweedy 5267 (NY, RM); Denver, Eastwood 35 (US); Douglas, Livingston 294 (DUKE); El Paso, Livingston 496 (DUKE, TEX); Fremont, Shear 3443 (NY, US); Huerfano, Vreeland 632 (NY); Larimer, Crandall 2 July 1892
Las Animas, Rollins 1870 (NY, RM, US); Lincoln, Ownbey 1344 (NY, RM); Pueblo, Ripley and Barneby 7644 (NY); Weld, Osterhout 2366 (NY, RM); Yuma, Ilit's and Ilit's 19271 (ISC).

Iowa: Harrison, Morrill 905 (ISC); Monona, Morrill 912 (ISC); Plymouth, Thorne 14670 (FLAS, NY, SMU); Woodbury, Pammel 13 (FLAS, ISC, NY, US).

Kansas: Barber, McGregor 14443 (SMU, US); Clark, Welsh 671 (ISC); Comanche, White 9 September 1898 (US); Ellis, Bondy 225 (FLAS, RM); Grant, Thompson 40 (US); Gray, Wemple 309 (ISC); Hamilton, Rose 17042 (NY, US); Harper, Rydberg & Imler 619 (NY); Kearney, Wemple 313 (ISC); Kiowa, Ward 19 September 1897 (NY); Meade, Hott 3520 (DUKE, FLAS, OKLA, SMU, TX, US); Norton, Smyth 333 (NY); Osborne, Shear 138 (RM, US); Phillips, Harshbarger 4 August 1892 (US); Pratt, Hulbert 3195 (OKLA); Sherman, Harshbarger 1 August 1892 (US); Stevens, Wemple 326 (ISC); Trego, Hott & Hott 4164 (NY); Wallace, Redfield 16 July 1872 (NY).

Minnesota: Big Stone, Pammel 2 September 1920 (ISC).

Montana: Carbon, Wilcox 402 (NY); Cascade, Blankinship 680 (RM, US); Custer, Crider & Atkins 30 (RM); Dawson, Aron June and July 1892 (NY); Park, Schober 1 August 1901 (ISC, US); Powder River, Barneby 13231 (NY); Sheridan, Larsen 216 (NY, US); Sweetgrass, Hitchcock & Muhlick 13311 (NY, RM); Wheatland, Wooten 21 July 1921 (US); Yellowstone, Hunt 20 July 1902 (ISC).

Nebraska: Brown, Rutter June 1893 (US); Chase, Tolstead 41102 (ISC); Dawes, Welsh 729 (ISC); Deuel, Rydberg 25 June 1891 (NY, RM, US); Dundy, Isely 8175 (ISC); Garfield, Ilit's 18563 (ISC); Hooker, Rydberg 1480 (NY); Kearney, Hapeman 21 July 1928 (NY); Kimball, Klin 28646 (US); Knox, Clements 2899 (ISC); Scotts Bluff, Rydberg 8 July 1891 (US); Sheridan, Buchanan 2-20 August 1905 (ISC); Sioux, Tolstead 13 July 1940 (ISC); Valley, Davidson et al 46911 (TEX).

New Mexico: Bernalillo, Kunzke 23203 (NY); Catron, Eggleston 20336 (RM, US); Chaves, Earle & Earle 30 August 1900 (NY); Curry, Shimmers 20875 (SMU); Dona Ana, Wooten 122 (NY, RM, US); Grant, Metcalf 121 (NY, RM, US); Guadalupe, Rose 17657 (NY, US); Lincoln, Wooten 250 (NY, RM, US); McKinley, Ripley & Barneby 7060 (NY); Otero, Waterfall 12463 (OKLA); Quay, Fisher 178 (US); Rio Arriba, Eggleston 20565 (NY); San Juan, Wooten 8 August 1904 (US); San Miguel, Standley 4955 (NY, US); Sierra, Metcalf 1151 (NY, US); Socorro, Wooten 5 August 1900 (US); Valencia, Rusby 16 July 1880 (US).

North Dakota: Benson, Welsh 777 (ISC); Billings, Seymour 2 September 1884 (DUKE); Bottineau, unknown 19 August 1891 (NY); Burleigh, Lunell 23 August 1913 (US); Grant, Bell 1177 (RM); Morton, Sarvis 146 (US); Pembina, Bergman 2269 (RM); Slope, Moyer 716 (NY); Stark, Stevens 1554 (US); Ward,
Waldron 1834 (RM).

Oklahoma: Beckham, Welsh 692 (ISC); Blaine, Waterfall 8122 (OKLA); Bryan, Blain 77 (US); Caddo, Demaree 13067 (NY, SMU); Cimarron, Rogers 4673 (US); Cleveland, Demaree 13185 (DUKE, NY, SMU, TEX, US); Comanche, Stevens 1359 (OKLA); Creek, Fry 79 (OKLA); Custer, Waterfall 1508 (OKLA); Ellis, Welsh 686 (ISC); Greer, Stevens 998 (NY, OKLA, US); Harmon, Waterfall 8338 (OKLA, SMU); Harper, Welsh 680 (ISC); Kingfisher, Blankenship 1 June 1896 (RM, US); Lincoln, Van Vleet 15 July 1905 (ISC); Major, Waterfall 8143 (OKLA); McClain, Demaree 13185 (DUKE, SMU, TENN, TEX); Noble, Harding 372 (OKLA); Oklahoma, Waterfall 2225 (OKLA); Payne, Ikenberry 38 (TEX); Roger Mills, Welsh 689 (ISC); Texas, Butler 120 (OKLA).

South Dakota: Brule, Isely 6034 (ISC, US); Clark, Williams August 1891 (US); Custer, Hayward 2559 (RM); Deuel, Isely 8125 (ISC); Fall River, Welsh 744 (ISC); Grant, Pammel 31 July 1918 (ISC); Harding, Visher 232 (RM); Lawrence, Carr 92 (NY, RM); Meade, Forwood 71 (US); Mellette, Tolstead 4-201 (ISC); Potter, Griffiths 257 (US); Todd, Tolstead 4-435 (ISC).

Texas: Bailey, Ferris & Duncan 3434 (NY); Brewster, Warnock 323 (SMU, TEX, US); Bristow, Whitehouse 10004 (SMU); Collingsworth, Wemple 381 (ISC); Childress, Childress High School Bio. Class 27 June 1931 (TEX); Culberson, Moore & Steyermark 3604 (NY, US); Dallam, Wemple 339 (ISC); Garza, Reed 3564 (US); Gray, Wemple 371 (ISC); Hall, Reverchon 3750 (SMU, US); Hartley, Palmer 14125 (US); Hemphill, Tharp & Miller 51-1-171 (TEX); Hutchinson, Cory 50293 (SMU); Jeff Davis, Cory 53102 (SMU, US); Lipscomb, Wallis 5100 (OKLA, SMU); Lubbock, Reed 4183 (RM, SMU); Mitchell, Pohl 4953 (ISC, SMU); Nolan, Palmer 13719 (US); Ochiltree, Wallis 4838 (OKLA, SMU); Oldham, Reverchon 3005 (SMU, TEX); Potter, Wemple 359 (ISC); Presidio, Hinkley 660 (NY, TEX); Randall, Cory 50437 (NY, SMU, US); Beeves, Henderson 62-639 (FSU); Roberts, Wallis 4942 (OKLA, SMU); Stonewall, Tharp & Gimbrede 51-998 (TEX); Swisher, Wemple 254 (ISC); Terry, Tharp 10 July 1941 (TEX); Wichita, Whitehouse 9889 (GA, SMU).

Utah: Emery, Harrison 9805 (ISC, US); Garfield, Maguire 7400A (NY); Grand, Purpus 6495 (US); San Juan, Holmgren 3789 (NY, US); Wayne, Maguire 19299 (NY).

Wyoming: Albany, Nelson 7378 (ISC, NY, RM, US); Big Horn, Moore & Moore 4 July 1896 (RM); Campbell, Porter and Porter 7576 (RM); Converse, Porter 3162 (RM, US); Crook, Ownbey 471 (RM); Goshen, Brenekle & Petrak 50085 (NY); Laramie, Williams 2537 (US); Natrona, Goodding 204 (ISC, NY, RM, TENN, US); Niobrara, Isely 6526 (ISC); Weston, Degener & Feller 16014 (NY).
Petalostemon ornatum — specimens examined

Idaho: Canyon. Christ & Christ 16734 (NY); Tucker 577 (NY). Elmore. Christ 11142 (NY); Christ & Christ 17896 (NY); Nelson & Macbride 1136 (NY, RM, US). Owyhee. Beath 18 May 1938 (RM); Christ 9562 (NY); Hitchcock & Muhlick 21984 (NY); Maguire and Holmgren 26229 (NY, US); Ripley & Barneby 6146 (NY).


Idaho: Canyon. Christ & Christ 16734 (NY); Tucker 577 (NY). Elmore. Christ 11142 (NY); Christ & Christ 17896 (NY); Nelson & Macbride 1136 (NY, RM, US). Owyhee. Beath 18 May 1938 (RM); Christ 9562 (NY); Hitchcock & Muhlick 21984 (NY); Maguire and Holmgren 26229 (NY, US); Ripley & Barneby 6146 (NY).


Washington: County unknown. Brandegge & Tweedy 714, near Columbia and Snake Rivers (NY). Benton. Hitchcock & Muhlick 22593 (RM); Rose 48155 (ISC, NY); St. John & Mullen 8645 (NO).


Petalostemon phleoides — specimens examined


Petalostemon purpureum — representative specimens examined

CANADA

Alberta: Andersson 4, Calgary (NY); Breitung 17754, Waterton Lakes National Park (NY, SMU); Degener 18316, Cordson (NY); Moodie 18 July 1913, Elbow River Valley (US); Moodie 1149, Rosedale (NY); Moss 61, W of Pincher Creek (US); Pammel 6 August 1909 (ISC); Ruth 29 August 1915 (NY); Turner 17, Ft. Saskatchewan (NY).
Manitoba: Bird 118, E. of Deloraine (OKLA); Degcner 959, McGregor (NY); Dore & Breitung 12655, NE of Melita (NY); Dudley, Birtle (OKLA); Fowler 7 July 1887, Brandon (US); Love & Love 5661, Langruth (US); Love & Love 6219, Indian Reserve 2A (US); Morris July 1894, Rosser (US).

Ontario: Denike 585, Ingolf (NY).

Saskatchewan: Bird 1326, W of Val Marie (OKLA); Bird 1404, W of Eastland (OKLA); Herriot 31 July 1906, Bare Hills (US); Johnson 30 July 1904, Assinibois (US); Johnson 936, Moose Jaw (NY); Ledingham 1185, SW of Bohor (NY); Ledingham 1355, N of Moose Jaw (ISC, TEX); Ledingham & Yip 11 August 1956, SE of Hirsch (ISC); Ledingham et al 2283, W of Caron (ISC); Macoun 17 July 1880, Moose Jaw (NY, US); Macoun & Herriot 70770, Grand Trunk Pacific RR (NY).

UNITED STATES

Alabama: Colbert, Isely 3742 (ISC); Greene, Sargent 16 June 1950 (GA); Hale, Mohr 25 May 1893 (US); Marenco, Harper 3385 (NY, US); Sumter, Shinnners 12634 (SMU).

Arizona: Yavapai, Peebles et al 4253 (US).

Arkansas: Baxter, Palmer 5950 (US); Benton, Demaree 6856 (SMU, TENN); Boone, Demaree 3218 (SMU); Clark, Demaree 17800 (ISC, SMU); Fulton, Demaree 26887 (ISC, SMU, TEX); Hempstead, Palmer 8036 (US); Howard, Iltis et al 5141 (US); Marion, Deamere 29102 (ISC, SMU, TEX); Newton, Demaree 22236 (NY, SMU); Pulaski, Hasse 5 September 1886 (NY); Randolph, Demaree 29210 (DUKE, ISC, OKLA, SMU, TEX); Stone, Demaree 23484 (NO, NY, SMU); Washington, Turner summer 1939-1940 (TEX).

Colorado: Denver, Eastwood 36 (US); Boulder, Welsh & Charette 1378 (ISC); Chaffee, Waterfall 11514 (OKLA); El Paso, Livingstone 389 (DUKE); Huerfano, MoAllister 31 August 1923 (TEX); Jefferson, Isely 8639 (ISC); Larimer, Crandall 24 July 1895 (NY); Las Animas, Rogers 4589 (US); Logan, Osterhout 12 August 1897 (NY); Weld, Osterhout 371 (RM); Yuma, Osterhout 4073 (RM).

Idaho: Allen no location or date (NY).

Illinois: Adams, Wehmeyer 22 (GA, NY); Champaign, Storm 11 July 1948 (SMU); Coles, Pepoon & Barrett 522 (US); Cook, Farcett 1 September 1903 (ISC); DuPage, Ward 31 August 1893 (US); Henderson, Patterson July 1874 (NY); Kane, Eldredge 23 July 1888 (ISC); Kendall, Umbach 22 July 1897 (US); Lake, Gates 17252 (US); Madison, Sargent 27 June 1932 (TENN); Mason, Gleason 9216 (NY); Peoria, Chase 8332 (GA, ISC); Platt, Seymour 9 August 1886 (US); St. Clair, Eggert 5 July 1875 (ISC, NY); Stark, Chase 9 July 1896 (RM); Winnebago, Foll & Fell F 53-1046 (NY).

Indiana: Benton, Kriebel 5541 (SMU); Boone, Hale July 1838 (US); Cass, Friesner 9413 (OKLA, TEX); Jasper, Welsh 15606 (SMU); Knox, Tryon 3228 (DUKE); Lake, Dean 2413 (NY); Newton, Friesner 22382 (SMU); Tippecanoee, Miller & Milstead
Iowa: Allamakee, Schultz 80 (OKLA); Appanoose, Fitzpatrick & Fitzpatrick 11 July 1896 (NY); Boone, Isely (OKLA, US); Clayton, Shimek 29 July 1919 (NY); Dickinson, Thorne 12995 (US); Emmett, Cratty July 1895 (ISC, US); Fayette, Fink 223 (US); Fremont, Morrill 999 (FSU); Greene, Isely 5760 (ISC, OKLA); Jasper, Russell 74552 (TENN); Johnson, Shimek 3 July 1911 (FSU); Lucas, Bruggen 2701 (SMU); Lyon, Isely 5977 (ISC, SMU); Muscatine, Shimek 17 August 1920 (NY); Oceola, Shimek 14 September 1921 (FSU); Palo Alto, Hayden 4098 (GA, NY, SMU, US); Story, Pammel & Ball 12 (FLAS, ISC, NY, US); Union, Pay 3161 (US); Warren, Bruggen 1252 (FLAS); Webster, Isely 5888 (ISC, SMU); Winneshiek, Shimek 3 August 1919 (SMU); Worth, Wallis 21 August 1950 (OKLA).

Kansas: Anderson, Hulbert 3797 (OKLA); Barber, McGregor 14447 (SMU, US); Clark, White 14 September 1898 (US); Cowley, White 21989 (NY); Douglas, Horr E89 (DUKE, FLAS, GA, ISC, NO, OKLA, SMU, TEX, US); Ellis, Bondy 226 (FLAS); Ford, McGregor 15767 (SMU); Geary, Wemple 296 (ISC); Greenwood, Ripley & Barneveld 7252 (NY); Labette, McGregor 16987 (SMU); Marion, Horr 3478 (TEX, US); Osborne, Shear 135 (US); Pottawatomie, Marsh 1745 (SMU); Pratt, Wemple 306 (ISC); Reno, Smyk 35 (US); Riley, Norton 93 (NY, US); Russell, Jackson 95 (SMU); Sedgwick, Andrews 82 (ISC); Woodson, Lathrop 1418 (US).

Kentucky: County unknown, Pease 565, New York (KY); Nelson, Wharton 5575 (KY, NY).

Louisiana: Caddo, Dorman June 1930 (NY); LaSalle, Shinners (ISC, SMU, TEX); Natchitoches, Ware 24 June 1956 (SMU, TEX).

Minnesota: Anoka, Jukkola 114 (TENN); Becker, Grant 13 August 1929 (NY, US); Benton, Moore & Huff 18791 (OKLA); Brown, Isely 8160 (ISC); Chippewa, Moyer 8 August 1897 (NY); Crow Wing, Sandberg 867 (ISC); Hamneepin, Pammel 29 August 1903 (ISC); Kittson, Johnson 478 (ISC, NY); Lyon, Isely 8135 (ISC); Nicollet, Ballard July 1892 (NY); Norman, Bormann 111 (DUKE); Otter Tail, Sheldon August 1892 (TENN); Permington, Moyle 1316 (NY); Ramsey, Gmelin July 1875 (ISC); Redwood, Isely 8149 (ISC); Rice, Pammel 22 July 1922 (ISC); St. Louis, Lakela 2666 (SMU); Stearns, Omelin August 1875 (ISC); Stevens, Pammel 4 August 1922 (ISC); Todd, Hotchkiss & Jones 4133 (US); Winona, Hasse 24 July 1892 (NY).

Mississippi: Anoka, Jukkola 114 (TENN); Becker, Grant 13 August 1929 (NY, US); Benton, Moore & Huff 18791 (OKLA); Brown, Isely 8160 (ISC); Chippewa, Moyer 8 August 1897 (NY); Crow Wing, Sandberg 867 (ISC); Hamneepin, Pammel 29 August 1903 (ISC); Kittson, Johnson 478 (ISC, NY); Lyon, Isely 8135 (ISC); Nicollet, Ballard July 1892 (NY); Norman, Bormann 111 (DUKE); Otter Tail, Sheldon August 1892 (TENN); Permington, Moyle 1316 (NY); Ramsey, Gmelin July 1875 (ISC); Redwood, Isely 8149 (ISC); Rice, Pammel 22 July 1922 (ISC); St. Louis, Lakela 2666 (SMU); Stearns, Omelin August 1875 (ISC); Stevens, Pammel 4 August 1922 (ISC); Todd, Hotchkiss & Jones 4133 (US); Winona, Hasse 24 July 1892 (NY).

Mississippi: Lee, McDougall 1701 (US).
Lansing 5-12 June 1911 (US).

Montana: Carbon, Hitchcock 16582 (NY); Cascade, Blankenship 679 (US); Dawson, Ward 15 July 1883 (US); Lewis & Clark, Muth 11 August 1892 (NY); Park, Scheyber 25 July 1901 (ISC); Ponderosa, Brenkie & Shinner 41096 (NY); Stillwater, Hitchcock 16559 (NY); Sweetgrass, Hitchcock & Muhlik 13297 (NY); Teton, Hermann 12343 (US); Toole, Cratty 27 August 1915 (ISC); Wheatland, Wooten 21 July 1921 (US); Yellowstone, Hood 1183 (FLAS).

Nebraska: Banner, Hydberg 59 (NY); Cherry, Isely 6520 (ISC); Custer, Webber 6 July 1889 (US); Dawes, Welsh 734 (ISC); Dawson, Mohl 22 July (ISC); Deuel, Hydberg 59 (NY); Gage, Washburn 2 July 1899 (US); Holt, Delisle 447 (ISC); Hooker, Wemple & Wemple 798 (ISC); Kearney, Hapeman 4 July 1934 (SMU); Kieth, Welsh 710 (ISC); Lancaster, collector unknown 426 (TEX); Lincoln, Pammel 11 August 1923 (ISC); McPherson, Wemple & Wemple 795 (ISC); Red Willow, Wemple & Wemple 787 (ISC); Sheridan, Buchanan 2-20 August 1905 (ISC); Thomas, Blumer Sept-Oct 1902 (ISC); Valley, Davidson et al 10 July 1949 (TEX).

New Mexico: Colfax, Mahler 866 (NY); Mora, Arsen & Benedict 17102 (US); Sandoval, Ripley & Barneby 8347 (NY); San Miguel, Standley 5116 (NY, US); Santa Fe, Brendan 23030 (SMU).

North Dakota: Barnes, Fattig 2858 (DUKE); Benson, Welsh 778 (ISC); Billings, Bollen 7 July 1891 (NY); Burleigh, Seymour 29 August 1894 (DUKE); Cass, Waldron & Manns 16 August 1801 (US); Grant, Bell 1907 (BM); Kidder, Mears 22 July 1889 (US); Lamoure, E. L. B. Summer 1927 (DUKE); McHenry, Brown 53-50 (ISC); Morton, Rollins and Munoz 2815 (US); Nelson, Seymour et al 16019 (NY, SMU); Ramsey, Pope 20 August 1907 (US); Richland, Stevens 25 July 1949 (US); Stark, Holmgate 23 July 1908 (US); Williams, Welsh 772 (ISC).

Oklahoma: Blaine, Stevens 817 (NY, OKLA); Bryan, Cory 58855 (OKLA, SMU); Caddo, Demaree 13072 (NY, SMU, US); Carter, Tharp 7111 (TEX, US); Cherokee, Wallis 2329 (OKLA); Choctaw, Wemple 420 (ISC); Cleveland, Demaree 13184 (GA, ISC, OKLA, SMU, US); Comanche, Demaree 13000 (GA, SMU, US); Creek, Bush 72 (NY, US); Custer, Waterfall 2234 (OKLA); Delaware, Wallis 1757 (OKLA); Garvin, Duffer 513 (OKLA); Haskell, Bebb 5469 (OKLA); Johnston, Tharp 19 June 1929 (TEX); Kingfisher, Byers 48 (OKLA); Lincoln, Eaton 31 (OKLA); Logan, Davy 247 (TEX); Love, Cory 59016 (OKLA, SMU); Marshall, Cory 58957 (SMU); Mayes, Wallis 2984 (OKLA); McClain, Demaree 13095 (GA, NY, OKLA, SMU, TEX, US); McCurtain, Waterfall 12429 (OKLA, SMU, US); Murray, Barkley & Barkley 21 OK 002 (SMU, TEX); Muskogee, Waterfall 9558 (OKLA, SMU); Noble, Divine 32 (TEX); Oklahoma, Waterfall 2836 (NY); Osage, Webster 4254 (SMU); Ottawa, Wallis 4636 (OKLA); Payne, Merrifield 43 (ISC); Pittsburg, Rogers 20 June 1957 (OKLA); Pontotoc, McCoy 733 (OKLA); Pottawatomie, Pope 65 (OKLA);
Roger Mills, Waterfall 7732 (OKLA, TEX); Sequoyah, Wallis 4632 (OKLA, SMU).

South Dakota: Brookings, Pammel 3 August 1918 (ISC); Brule, Isely 6038 (ISC, US); Charles Mix, Aikman 19 July 1955 (ISC, US); Custer, Rydberg 610 (NY); Day, collector unknown year 1894 (OKLA); Deuel, Isely 8124 (ISC); Fall River, Rydberg 611 (NY, US); Grant, Pammel 31 July 1918 (ISC); Haakon, Gilly et al 823 (RM); Hamlin, Isely 8120 (ISC); Hanson, Weber 17 August 1927 (FLAS); Harding, Visher 232 (RM); Kingsbury, Isely 8116 (ISC); Meade, Forwood 70, 70a (US); Mellette, Tolstead 4-443 (ISC); Minnehaha, Thorburn 23 August 1892 (US); Perkins, Visher 642 (RM); Todd, Tolstead 4-367 (ISC); Turner, Johnson 49 (ISC, NY).

Texas: Bell, Wolff 833 (US); Culberson, Warnock 6321 (TEX); Erath, Gough year 1924 (US); Grayson, Johnson 17 (TEX); Lamar, Turner & Tharp 3123 (TEX); Montague, Whitehouse 10080 (SMU); Palo Pinto, Tracy 8042 (US); Red River, Tharp 47398 (TEX); Wheeler, Tharp 17 June 1929 (TEX, US); Wichita, Tharp 586 (NY, TEX).

Wisconsin: Burnett, Fassett 16749 (DUKE); Dane, Grether 8185 (NY); Juneau, Mearns 230 (US); Le Crosse, Fassett 4405 (DUKE); Pierson, Fassett 4407 (DUKE); Waukesha, Wadmond 2793 (ISC); Sauk, Steele 77 (US); Trempealeau, Hermann 20 June 1937 (NY); Walworth, Fassett 17030 (DUKE); Winnebago, Clemens 30 July 1909 (ISC).

Wyoming: Albany, Nelson 7418 (ISC, NY, US); Campbell, Porter & Porter 7577 (RM); Converse, Long & Ownbey 1060 (RM); Crook, Porter & Porter 8389 (RM); Laramie, Nelson 3641 (NY, US); Natrona, Jozwik 243 (RM); Sheridan, Rollins 560 (NY).

Petalostemon sabinale — specimens examined


Petalostemon searlsiae — specimens examined

Arizona: County unknown. Jones 5095g, Pagumpa (US); Jones 11 June 1890, Willow Spring (US). Coconino. Collom 1074 (US); Maguire 12238 (NY); Maguire 12275 (NY); McDougal 15 June 1891 (US); Peebles 13055 (US); Ward 9 June 1901 (NY, US). Mohave. Lemmon and wife June 1884 (US). Yavapai. Toumey 7155 (ISC, NY).

California: Inyo. Roos & Roos 6167 (NY). San Bernardino. Alexander & Kellogg 1401 (NY, US); Brandegee 26 May 1902 (US); Wolf 9659 (NY); Wolf 9666 (NY, OKLA, TEX).

Nevada: County unknown. Gooding 961, Kershaw, Meadoro Valley Wash (RM). Churchill. Maguire & Holmgren 25409 (NY, US). Clark. Alexander & Kellogg 1643 (US); Bleak 18 May 1928 (ISC); Clokey 7155 (ISC, NY); Clokey 7158 (NY, RM); Clokey 8004
(DUKE, GA, ISC, NO, NY, OKLA, RM, TENN, TEX, US); Clokey & Anderson 7157 (NY, TEX); Clokey & Bean 7156 (ISC, NY, OKLA); Maguire 18012 (NY); Purpus 6059 (US); Tidestrom 9654 (US); Train 1991 (NY). Elko, Holmgren 19 (NY); Stramler 5 June 1939 (NY); Train 3816 (NY, TEX). Lincoln, Gentry 35 (US); Gooding May 1902 (RM); Mason 12446 (RM); Ripley & Barneby 4400 (NY). Nye, Maguire & Holmgren 25308 (NY).

Utah: County unknown. Bishop 196 (US); Thompson year 1872 (US). Boz. Elder, Pearse 242 (NY). Garfield. Harrison 1961 (ISC); McArthur & Beck 162 (ISC). Iron. Ogden 11 June 1961 (ISC). Juab. Jones 4 June 1891 (NY, RM, US). Kane. Maguire 12286 (NY); Maguire 12306 (NY); Maguire 18881 (NY); Ripley & Barneby 4843 (NY); Tidestrom 2408 (US). Washington. Jones 7 May 1923 (US); Jones 51391 (US); Jones 51831 (US); Jones 5196k (US); Jones 5224j (US); Jones 5229 (US); Palmer 131 (NY, US); Pennell & Schaefer 21665 (NY); Woodbury year 1927 (US).

Petalostemon tenue — specimens examined


Petalostemon tenuifolium — specimens examined

Colorado: Baca. Inglis 55 (SMU). Las Animas. Rogers (US); Rogers 6022 (ISC).

Kansas: Clark. Welsh 672 (ISC). Gove. Hulbert 3541


Oklahoma: Cimarron. Goodman & Kelting 5381 (NY, TEX); Higency 125 (OKLA); Rogers 4702 (US); Waterfall 10793 (OKLA); Welsh 696 (ISC); Wemple 329, 330, 335 (ISC). Payne. Higency 84 (OKLA). Texas. Waterfall 7412 (OKLA); Waterfall 7964 (OKLA).


Oldham. Bailey 132 (US); Reverchon 3006 (NY, US). Potter. Reverchon 3008 (NY, US); Wemple 354 (ISC). Randall. Correll & Correll 13048 (SMU); Cory 50436 (NY, SMU, TEX); Palmer 12503 (NY, US); Reverchon 3748 (NY); Tharp 7112 (TEX); Wemple 361 (US); Young 9 September 1917 (TEX). Roberts. Wallis 4940 (OKLA, SMU); Wemple 375376 (ISC). Sherman. Isely 6996 (ICH); Jespersen & Jespersen 2699 (NO, NY, RM, SMU, US).

Swisher. Wemple 253 (ISC); Whiteside 9955 (SMU).

**Petalostemon villosus** — specimens examined

**CANADA**

Saskatchewan: Ledingham et al 2280, W of Caron (SMU, TEX); Ledingham et al 2284, W of Caron (ISC).

**UNITED STATES**


Iowa: Blackhawk. Grant 11197 (ISC).

Kansas: County unknown. Carleton 23 October 1892,
Arkalon. Dickinson. Werthner July – August 1878 (US). Finney. Letterman 20 (ISC); Richards 3051 (SMU); Smyth 166 (US).


Michigan: Washtenaw. Clark. no date or number (NY).


Goodhue. Fammel 2 August 1923 (ISC). Hennepin. Aiton August 1891 (NY, RM, TENN); Aiton September 1891 (DUKE, RM); Burgheaus August 1891 (ISC); Oertlund August 1878 (NY); Sandberg July 1891 (NY); Sandberg August 1891 (RM); Sandberg 4920 (NY); Sheldon September 1891 (NY, TENN, US); Sheldon September 1892 (US); Sheldon September 1894 (NY). Morrison. Hotchkiss & Jones 4118 (US). Polk. Bormann 99 (DUKE); Johnson 521 (ISC, NY). Winona. White July 1891 (RM).


Ward 6 August 1883 (US).


Goodman & Kelting 5337 (NY, TEX). Blaine. Wallis 3404 (OKLA);
Smith 21 (TEX); Welsh 676 (ISC). Kay. Davy 86 (OKLA); Hast-
ings 99 (OKLA); Johnson 153 (OKLA); White 3 August 1899 (NY).
(OKLA). Oklahoma. Waterfall 2095 (NY, OKLA); Waterfall 2182
(OKLA). Woods. Stevens 1672 (OKLA); Stevens 1716 (NY, OKLA,
SMU, US); White 4 July 1900 (RM). Woodward. Gruver 1228 (TEX);
Hymowitz 202 (OKLA); Jackson 2085 (OKLA); Waterfall 3109
(OKLA).

South Dakota: County unknown. Skinner 185 (RM); Wallace
7 September 1896. Corn Creek (NY). Bennett. Over 16090 (US);
Harding. Visher 238 (RM). Pennington. Over 1908 (US); Williams
29 August 1891 (NY). Todd. Tolstead 4 - 504 (ISC). Tripp.
Wallace 30 June 1896 (NY).

Texas: Bailey. Cory 37481 (PSU); Ferris & Duncan 3476
(NY); MoVaugh 7288 (NY, SMU); Reed 1 (FSU); Tharp 14 June
1929 (TEX). Callahan. Henderson 62 - 756 (FSU); Isely 8351
(ISC); Wemple 251 (ISC). Collingsworth. Taylor 1 August 1
96 (US); Howell 99 (US); Howell 4215 (OKLA). Hockley. Reed
Harris 38 (US). Lipscomb. Howell 74 (US); Wallis 5130 (SMU).
Wheeler. Isely & Isely 8878 (ISC); Tharp 4396 (TEX, US).
Hartley & Peterson 2029 (US); Pammel year 1887 (ISC). Pepin.
Fassett 4415 (DUKE); Hale year 1861 (NY); Luders August 1887
(DUKE).