THE PENSTEMONS OF MEXICO. II. *PENSTEMON HARTWEGII*,
PENSTEMON GENTIANOIDES, AND THEIR ALLIES

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For size and brilliance of flowers, no other Penstemons equal those of the entire-leaved group of Mexican species that includes *P. hartwegii* Benth., *P. gentianoides* (HBK) Poir., and their allies. The purple-flowered *P. gentianoides*, a striking plant of near-timberline altitudes in the volcanic ranges of southern Mexico, was first described from plants collected on the Nevado de Toluca by Humboldt and Bonpland. The species was presumed to be in cultivation in Europe, but the earliest identifiable drawings attributed to it, e.g., in *Edwards Botanical Register*, NS 11: t. 3, 1838, *Paxton's Magazine of Botany*, 4: 265, 1838, and *Curtis' Botanical Magazine*, 65: t. 3661, 1839, are all clearly of *P. hartwegii*. This crimson-flowered species was not properly distinguished until 1840 on the basis of Hartweg's collections from near Real del Monte, Hidalgo. The material cultivated in Britain was said to have come from Belgium as plants or seed as early as 1836; from whom or whence it had arrived from Mexico is not stated. A specimen in the U. S. National Herbarium labeled "*Penstemon gentianoides* Lindl., Hort. Basil, Sept. 1839," is *P. hartwegii*. Another drawing almost surely of *P. hartwegii* in the *Floricultural Cabinet*, 7: 263, 1839, is called *P. gentianoides* var. *coccineus* Hort.; it was said to have been made from plants grown from seed received directly from Mexico. The earliest figure seen that is consistent with *P. gentianoides* itself is that in the *Flora des Serres*, Ser. I, 7: t. 730, 1851-52. It is probable that this species was not in cultivation much earlier, but that *P. hartwegii*, which was grown under that name before its description as a separate species, garnered this and other synonyms in the horticultural literature as a result of the confusion. I do not know if these species are still cultivated in Europe, but hybrid derivatives of *P. hartwegii* are grown there abundantly (Lenz, personal communication). Neither of these species is known to be cultivated in the United States or in Mexico, but hybrid derivatives are in the trade here as in Europe.

A third species belonging to this complex, *P. fasciculatus* Gray, was described in 1886, and a fourth, *P. isophyllus* Rob., was distinguished in 1904. The description of these species at that time reflected a renewed interest in the botanical exploration of Mexico, and several major collecting expeditions by such noted botanists as Pringle, Palmer, Rose, and E. W. Nelson near the turn of the century revealed many new taxa. Of these two species, only *P. isophyllus* is known to be cultivated in the United States, and this to a limited extent, primarily on the basis of a

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seed collection by L. W. Lenz made in Puebla in 1950 and first grown at the Rancho Santa Ana Botanic Garden, Claremont, California.

Until 1959, when *P. apateticus* Straw was described in the first paper of this series (Straw, 1959), no further species in this relatively distinct group had been distinguished. It is now necessary to add six more taxa to the group. The description of these entities reflects not so much a renewed interest in the botany of Mexico as it does the gradual accumulation of specimens from relatively remote areas that has been continuing sporadically throughout the present century.

The taxa considered in this paper constitute a subsection in a section to be described here. Two or possibly three additional subsections remain to be distinguished in later works. A majority of the Mexican species fall into the section.

Penstemon sectio *FASCICULUS* Keck ex Straw
sectio nova

Penstemon section *Fasciculus* (in text ascribed to Keck by Bennett),
nomen nudum in Bull. Am. Penstemon Soc., 12: 49, 1953.

Herbae perennes suffruticosae saepe robustae; foliis caulium oppositis vel rare ternis, filiformis ellipticis vel lanceolatis, semper fere cum foliolis fasciculatis in axilis foliorum; floribus magnis aut tubulo-campulatis subregularibus aut abrupte inflatis ventricosis bilabiatis; loculis antherarum omnino dehiscentibus, extensis, peltato-explanatis vel naviculatis, integris, glabris; staminibus sterilibus glabris vel luteo-barbatis.

Perennial suffrutescent herbs, mainly robust; leaves cauline, opposite or rarely ternate, filiform, elliptic, or lanceolate, mostly with conspicuous axillary fascicles of similar smaller leaves; flowers large, either tubular-campulate and subregular or abruptly inflated, ventricose, and conspicuously bilabiate; anthers dehiscent throughout, extended, peltate-explanate or naviculate, entire and glabrous; staminode glabrous or yellow-bearded.

The section is based on *Penstemon gentianoides* (HBK) Poir.

Penstemon sectio *Fasciculus* subsectio *FASCICULI*, subsectio nova
Folii integri

The subsection is also based on *Penstemon gentianoides* (HBK) Poir.

The leaves in the subsection are entire or, very rarely, some of the lowest leaves are remotely serrate. In general, the members of this group have the largest flowers of the section. Two series may be distinguished, one with crimson flowers that are gradually ampliate to a subregular

limb, and a second with purple flowers that are abruptly ventricose and bilabiate. In living flowers the inner faces of the lips are the same intense colors as the outer surfaces of the entire corollas, but the throats, beginning abruptly at the flexures of the lower lips or at the lateral sinuses, are typically white, usually with guidelines of deep color. In the red-flowered series the flowers have a somewhat fleshy, glaucescent appearance that is lost on drying. The flowers on herbarium sheets are frequently as much as thirty per cent shorter than in life and appear to have exerted anthers. This is due to the very rapid drying and shrinking of the corollas but not the filaments if pressing is delayed too long. Such artifacts are common throughout the genus.

These species are found at middle and upper altitudes, from the pineoak zone to timberline, of the Sierra Madre, from Nuevo Leon and Chihuahua southward to Chiapas and Guatemala. One species, *P. apateticus*, is found over a wide geographical range, but the others occupy relatively restricted areas.

The following key should serve to separate the taxa included:

- A. Corolla ventricose, expanding abruptly above a short tube to a width more than one-third the length, obviously bilabiate, of blue and purple colors; leaves lanceolate.
- B. Sepals acuminate to cuspidate; lowest inflorescence branches mostly over 2 cm. long; longest leaves 7-15 cm. long; staminode glabrous or sparingly bearded.
 - C. Sepals mainly cuspidate; total peduncle-pedicel length usually less than flower length; peduncles shorter than pedicels; leaves narrowly lanceolate, long acuminate, with conspicuous axillary fascicles.
 - 1. *P. gentianoides*
 - CC. Sepals short-acuminate; total peduncle-pedicel length (of lowest inflorescence branches) greater than flower length; peduncles longer than pedicels; leaves lanceolate, acute, without conspicuous axillary fascicles.
 - 2. *P. occiduus*
- BB. Sepals acute; inflorescence branches mostly under 2 cm. long; longest leaves under 6.5 cm. long, lanceolate, acute; staminode with conspicuous yellow beard.
 - 3. *P. leonensis*
- AA. Corolla tubular, expanding rather gradually to the orifice, nearly regular, width less than one-third the length, of reddish and crimson colors.
- D. Stem below and into the inflorescence densely puberulent in two longitudinal lines in each internode axillary to the decussate leaves (bilineate) (occasionally completely puberulent in 4.)

- E. Primary leaves filiform or acicular, 15-40 mm. long, rarely longer, with very conspicuous axillary fascicles of similar shorter leaves; stems mostly under 5 dm. tall, branching abundantly from a woody base. 4. *P. fascicularis*
- EE. Leaves lanceolate, usually 10 mm. or more broad; stems typically over 5 dm., reaching 10-15 dm. tall, woody below.
- F. Flowers 40-45 mm. long; leaves mostly 35-75 mm. long, the longest usually 4-5 times longer than wide, lanceolate and acute. 5. *P. hartwegii*
- FF. Flowers about 30 mm. long; leaves to 80-90 mm. long, the longest 6-7 times longer than broad, mostly attenuate. 6. *P. skutchii*
- DD. Stems below the inflorescence wholly puberulent, glabrate or glabrous, not bilineately puberulent; leaves not acicular.
- G. Staminode with short yellow beard; corolla 25-30 mm. long, sepals linear, acute, 4-5 mm. long, 1 mm. broad. 7. *P. filisepalis*
- GG. Staminode glabrous; sepals lanceolate to ovate, acute to acuminate or caudate.
- H. Longest leaves 60-90 mm. long, 15-30 mm. broad, lanceolate; flowers large (over 40 mm. long). 8. *P. mchinoranus*
- HH. Longest leaves either less than 10 mm. broad, linear or narrowly lanceolate, and up to 130 mm. long, or if more than 10 mm. broad, rarely over 50 mm. long, broadly lanceolate, elliptic, or obovate.
- I. Corolla typically 25-30 mm. long; stems fine, scarcely woody, little branched. 9. *P. apateticus*
- J. Leaves narrowly elliptic, 30-50 mm. long, 15-20 mm. broad (Durango). 9a. *ssp. durangensis*
- JJ. Leaves linear to linear-lanceolate, under 10 mm. broad, up to 130 mm. long.
- K. Leaves linear; stems glabrate or scarcely puberulent (southern mountains). 9b. *ssp. apateticus*

KK. Leaves narrowly lanceolate; stems densely fine-puberulent (Chihuahua). 9c. *ssp. townsendianus*

II. Corolla 35-45 mm. long; stems heavier, usually several branched from a persistent woody base.

L. Leaves lanceolate to elliptic, mostly more than four times longer than broad; many pairs at mid-stem about the same length. 10. *P. isophyllus*

LL. Leaves broadly elliptic to obovate, the longest mostly less than three times longer than broad, fewer pairs, not of sub-equal lengths, sometimes minutely toothed. 11. *P. plagapineus*

DESCRIPTION OF TAXA

1. *Penstemon gentianoides* (HBK) Poiret, Dict. Sci. Nat. 38: 385, 1825. *Chelone gentianoides* Humboldt, Bonpland et Kunth, Nov. Gen. et Sp. Pl. 2: 363, t. 172, 1817.

Penstemon gentianoides (HBK) G. Don, Gen. Hist. Dichlam. Pl. 4: 636, 1838.

Penstemon verticillatum Martens et Galleoti, Bul. Acad. Brux. 12, pt. 2: 18, 1845 (from description).

Erect, perennial, suffrutescent herb with many stems from the woody base, or in older plants sometimes branching profusely well above the base, becoming 15 dm. or more tall in favorable conditions, or in less favorable sites, as at timberline, reaching only 5 dm. or less in height. The stems glabrate to completely puberulent or puberulent only in two lines which in each internode are axillary to the leaf pair below (bilineately puberulent). The stems densely leafy, with many-leaved, very conspicuous axillary fascicles, the upper primary leaves lanceolate, sometimes broadly so, middle and lower primary leaves and most fascicular leaves narrowly lanceolate or linear-elliptic and long-acuminate, the longest leaves commonly 7-15 cm. long, 1-3 cm. broad, entire, glabrous or puberulent on basal margins and midrib, rarely puberulent on the surfaces. Inflorescence a compact thyrse, the stem in the inflorescence completely or bilineately puberulent, the bracts lanceolate, conspicuous, at least the lower ones longer than the flower clusters, becoming smaller upward; the aspect of the inflorescence leafy-verticillate. Peduncles and pedicels puberulent to somewhat glandular-pubescent, the peduncles short, conspicuously bibracteolate, 3-6 or more-flowered, the longest pedicels longer than the peduncles and often similarly bibracteolate. Sepals elliptic to ovoid or rhomboid, acuminate to long—or short—cuspidate, 9-11 mm. long, 4-5 mm. broad, glabrous or basally and mar-

ginally glandular-pubescent. Corolla tube about the length of the calyx, abruptly expanding into a broadly inflated throat, the limb strongly bilabiate, the lobes rounded and somewhat spreading, the lower lip sparingly white-villose at the flexure, the total length usually over 3 cm. The stamens didynamous, the filaments glabrous, white, the anthers included, explanate or nearly so, with a strong median ridge in each cell, glabrous, purple or dark colored. The sterile filament dilated distally, glabrous or with a few short yellow hairs, included. Ovary glabrous, ovoid, acuminate into a filiform style that reaches the position of the anthers and bends downward at maturity, the stigma truncate; the capsule ovoid, acuminate, splitting at maturity by four lines, septal and carpelar; seed black, angulate, small (under 2 mm. long).

The flower color is typically a bright to dark purple without and on the inner faces of the lips (5-10P 2-4/6-10, in the Munsell system, but often more variable); lighter below and abruptly white within, usually with strong purple guide lines. It is visited and apparently primarily pollinated by large bees of the genus *Bombus*, which are able completely to enter the corolla seeking the nectar that is copiously secreted on the outer bases of the upper pair of stamens. It is also visited, however, by other bees and at least occasionally by hummingbirds, any of which presumably could make an effective pollen transfer.

The species is found at upper altitudes, to or slightly above timberline and in the high pine forests, typically in open or disturbed sites, on the major volcanic peaks of the eastern parts of the transverse volcanic ranges and southward into Chiapas and Guatemala. The type is Humboldt's number 4368, from the Nevado de Toluca, Mex., in the Museum National d'Histoire Naturelle, Paris (P). (Photographs of the Berlin isotype seen.) Specimens seen include the following: (Abbreviations of herbarium names follow the Index Herbariorum; see also the acknowledgements at the end of this paper.) See also figure 1.

MEXICO

MICHOACAN: Zitacuaro-Cerro Pelon, *Hinton 13236* (GH, MICH, US); Anganguero, *Hartweg 359* (NY);

ESTADO DE MEXICO and DISTRITO FEDERAL: Las Cruces, Dist. of Temascaltepec, *Hinton 1032* (F, GH, PH), *Hinton 3990* (GH, NY, US), *Hinton 3282* (MICH, PH, UC, US), *Pringle 6448* (CAS, F, GH, MO, ND, NY, MEXU, PH, UC, US, VT), *Pringle 11655* (F, GH, MICH, MO, US), *Harshberger 31* (US), *Straw & Gregory 1111* (MEXU, MICH, RSA); Nevado de Toluca, *Seler 4416* (CAS, GH, US), *Rose & Painter 7961* (US), *Schery 91* (MICH, MO, US), *Nelson 19* (US), *Balls 4985* (US), *Balls 4085* (US), *Straw & Gregory 1172* (GH, MICH, MEXU, RSA); Contreras Canyon, *Munz 15002* (POM), *Seler 5254* (CAS, US), *Lyonnet 1615* (US); Popocatepetl, *Rose & Hay 6006* (US),

Kenoyer A236 (F, MICH, MO), *Balls* 4174 (UC, US), *Straw & Gregory* 999 & 1018 (MEXU, MICH, RSA); *Gilly & Dodds* 8 & 26 (MICH), *Moore* 37 (GH); *Iztaccihuatl*, *Purpus* 29 (MO, POM, UC, US), *Purpus* 1706 (F, GH, MO, NY, UC, US); *Cima*, *Orcutt* 3794 (US); *Peña de Charras*, *Russell & Souviron* 138 (PH, US); *Crucero - Agua Blanca*, Dist. of Temascaltepec, *Hinton* 8250 (GH, US); *Desierto Viejo*, Valle de México, *Borgeau* 876 (GH, US); *Ajusco*, near *Pedregal*, *Matuda* 19181 (US); *Llano Grande*, *Matuda* 19079 (F);

PUEBLA: Side of Popocatepetl, *Miranda & Barkley* 17M158 (PH, TEX); Mt. Orizaba, *Seaton* 210 (F, GH, NY, US), *Rose & Hay* 5725 (GH, US), *Balls* 4387 (US); Open slope above Huejotzingo, *Sharp* 45962 (TENN);

TLAXCALA: Mt. Malinche, 11,000 ft., *Balls* 4891 (US);

OAXACA: Cerro (or Sierra) San Felipe, *Nelson* 1042 (GH, US), *Conzatti* 4075 (MEXU, NY, US), *C. L. Smith* 541 (MEXU, MICH, MO, NY, US), *Andrieux* 171 (GH); northwest side of Mt. Zempoaltepec, *Nelson* 642 (US); Villa Alta, Cerro Yalina, *Conzatti* 963 (GH); Zempoaltepetl, *Camp* 2625 (NY); near Teotitlan del Valle, *Carlson* 1413 (F);

CHIAPAS: Volcan Tacana, *MacDougal* s.n. (NY, UC), *Matuda* 2350 (F, GH, MICH, PH); San Felipe, near San Cristóbal de las Casas, *Carlson* 2395 (F, MICH).

GUATEMALA

ZACATEPEQUEZ: Volcan de Agua, *J. D. Smith* 2151 (GH, NY, US), *Kellerman* 7578 (F, NY), *Kellerman* 7418 (NY), *Johnston* 882 (F), *Standley* 65235 (F);

CHIMALTENANGO: Volcan Acatenango, *J. D. Smith* 3617 (US), *Standley* 61904 (F, NY);

QUEZALTENANGO: Volcan Santa Maria, *Skutch* 828 (GH, PH), *Steyermark* 34177 (F, US); Volcan Zunil, *Steyermark* 34850 (F, PH); Volcan Santo Tomas, *Steyermark* 34812 (F);

SAN MARCOS: between Sibina and the peak of Volcan Tacana, *Steyermark* 36150 (F); Volcan Tajumulco, *Sharp* 46115 (PH), *Steyermark* 37068 (F), *Schmidt* s.n. (F).

2. *Penstemon occiduus*, species nova

Herbae perennes erecti; caulibus teretibus in partibus inferioribus dense puberulentibus; foliis lanceolatis acutis integris; sepalis anguste ovatis, breve acuminatis, glabris; corollis abrupte inflatis super tubos aequae cum sepalis longis, ventricosae bilabiatis, partibus interioribus labiorum inferiorum paulim villosis; loculis antherarum confluentibus naviculatis divaricatis; apicibus filamentum sterile dilatis paulum breve barbatis.

This species is at this time known only from the type collection.

The type is a perennial herb, erect, about 6 dm. tall, with a terete stem densely puberulent in the lower parts and sparingly pubescent or glabrate in the inflorescence. The leaves are lanceolate, acute, and entire, and are minutely puberulent on the upper surface and on the midvein below; the longest leaves are those in mid-stem, reaching 8 cm. in length and 11 mm. in width. The bracts are narrowly lanceolate, about as long as the peduncle-pedicel length. The total length of the peduncle and longest pedicel of the lowest inflorescence branches is about 35 mm., about 1.2 times the length of the flowers, a characteristic that appears to differentiate this species from its closest relatives. The peduncles bear 1-3 flowers each. The sepals are lanceolate or narrowly ovate, short acuminate, and glabrous. The corolla has a short tube about the length of the sepals, above which it expands abruptly into a ventricose throat. The limb is bilabiate, the lobes rounded or obtuse, the lower lip somewhat villose within, the entire corolla glandular pubescent without. The flowers on the type are about 30 mm. long and 14 mm. wide, pressed. The anther locules are dehiscent throughout their lengths, confluent, divaricate, naviculate with strong central ridges, entire and glabrous, and included.

This species differs from *P. gentianoides* in its acute rather than acuminate leaves, which are finely puberulent on the upper surfaces (some specimens of *P. gentianoides* are similarly puberulent), and from *P. leonensis* in its somewhat larger flowers. The difference in the ratios of peduncle-pedicel lengths to flower lengths between *P. occiduus* and *P. gentianoides* is just significant at the .05 level, on a two-sided "t" test for the difference between a sample and a single specimen. The difference between *P. gentianoides* and *P. leonensis* in this ratio is not significant ($p = \text{about } 0.1$). The peduncles are nearly twice the lengths of the pedicels in *P. occiduus*, resembling *P. leonensis* in this, but significantly different from *P. gentianoides*, in which the peduncles are mostly shorter than the pedicels. The type is shown in figure 2; see also figure 4.

Penstemon occiduus is found in an area far distant from either of the other species to which it is most closely related. The name, *occiduus*, alludes to its western location.

The type is: E. W. Nelson's number 4804, in the United States National Herbarium (US), number 332854, collected in the Sierra Madre Occidental at an elevation of 7500-8500 feet, sixty miles south of Guadalupe y Calvo, Chihuahua, in August 1898. According to the label this is in southwestern Chihuahua, but if the distance is correct it is probably in northwestern Durango (figure 1).

3. *Penstemon leonensis*, species nova

Herba perennis erectis, basibus caulium suffruticosis, caulibus puberulentibus soli in lineis duobus axillaribus foliorum; foliis lanceolatis

integris superne subamplexicaulibus glabris; sepalis ovatis acutis pubescentibus; corollis brevis late ventricosis, in labiis inferioribus leviter albovillosis; antheris glabris peltato-explanatis, septis loculorum prominentibus; apicis staminodorum dilatis flavo-villosis.

Erect perennial herbs, the stems somewhat woody at the base, five or more dm. tall, and puberulent in two lines in each internode axillary to the decussate subtending leaves. The leaves are lanceolate, entire, subamplexicaulous at least above, glabrous, to 5 cm. long and 2 cm. wide. The bracts are leafy, the lowest longer than the flower clusters, becoming shorter upward. The total peduncle-pedicel length is less than the flower length, with the peduncles mostly 2-3 times the length of the pedicels; the pedicels and peduncles are pubescent, with some of the hairs glandular. The sepals are ovate and acute, 7-8 mm. long, and pubescent. The corolla is short and broad, abruptly inflated above the short tube, to 25 mm. in length and 12 mm. in width (pressed), sparingly glandular without; the limb is bilabiate, the lobes rounded and erect, the lower lip somewhat villose within. The anther locules are dehiscent throughout, confluent, naviculate or at last peltate-explanate, with prominent median ridges, entire, glabrous, and included. The staminode is dilated apically and yellow villose-bearded. See figure 3.

As seen on Cerro Potosi, *P. leonensis* is a species of high, open pine forests and scrub, at about 3000 meters elevation. Flower colors are deep to strong purple and reddish purple (Munsell designation 7.5-10 P 3/9 - 5/10) over most of the corolla, but lighter below, with the lips similar or somewhat lighter. The throat within is whitish with deep purple guide lines. The flower color is similar to or somewhat darker than that of *P. campanulatus* (Cav.) Willd., which grows over many hectares at lower elevations on the same mountain. The two species are ecologically distinct, and the morphology of *P. leonensis* clearly relates it to *P. gentianoides* rather than to *P. campanulatus*. Although both may be within the range of the same pollinating bees, there is no evidence at this time suggesting hybridization. As the weather was inclement during our brief visit no pollinators were seen, but the species is almost certainly visited by bees of the *Bombus* type, as are other species of similar corolla shapes and colors.

The species resembles *P. gentianoides* but is not nearly so tall or so robust. It differs from *P. gentianoides* in its smaller flowers and in the significantly different peduncle to pedicel length ratios ($p < 0.001$ on a "t" test for the difference between means; the variance ratio, "F", is also significantly different at $p < 0.01$). It is a smaller plant, with much less conspicuous axillary fascicles than *P. gentianoides*, and consistently (apparently) has bilineate pubescence, which the latter species has only occasionally. The species differs from *P. occiduus* in the peduncle-pedicel to flower length ratios, mentioned above, and in its

smaller flowers (see figure 4). It is also widely separated from the two species geographically. The name, *leonensis*, refers to its primary distribution in the state of Nuevo Leon.

F. W. Pennell in 1939 had segregated several sheets of this species, labeling them "P. codonophorus Pennell n.sp." As the name remains unpublished it is rejected under recommendation 23B(i) of the International Code of Botanical Nomenclature of 1956.

The type of the species is a collection of C. H. and M. T. Mueller (= Muller), number 1245, in the United States National Herbarium (US), number 1746959, collected in the Sierra Madre Oriental, on the ascent of Sierra [Cerro] Potosi by the north hogback, about 20 miles northeast [sic!] of Galeana, Nuevo Leon, at 10,000 to 11,000 feet elevation, July 25, 1934. Isotypes are in F, GH, MICH, PH, TEX. Other records known are (see figure 1):

NUEVO LEON: Monterrey, *Runyon 1791* (US); peak of Cerro Potosi, *C. H. Muller 2266* (F, GH, MICH, MO, PH), *Schneider 1053* (F, NY), *Straw & Forman 1372* (GH, MEXU, MICH, RSA, US); Cerro del Viejo, 15 miles west of Dulces Nombres, *Meyer & Rogers 2987* (MO, PH); Peña Nevada, *Gillett 1236* (MSC, RSA).

Distinctions among the three species discussed above are made easily on several metric and qualitative characteristics summarized in Table 1, some of which are shown diagrammatically in figure 4. No single character can be used to distinguish all three, but each represents a different combination of several useful characteristics. In addition, the three are geographically distinct (figure 1).

4. *Penstemon fasciculatus*. A. Gray, Proc. Amer. Acad. Arts & Sci. 21: 403, 1886.

Low, subshrubby plants usually not over 5 dm. tall, with many erect stems arising from a perennial woody rootstalk spreading over as much as one-half a square meter, presenting a clumped appearance with dark leaves and stems and many bright crimson flowers. The primary leaves are crowded, short, filiform, subulate, and usually 1.5-3 cm. long, but sometimes rather longer (to 5 cm. in rare specimens), and bear in their axils dense fascicles of shorter, similar leaves. The stems may be glabrate or entirely or bilineately very densely gray puberulent with short hairs about 0.2 mm. long; the bilineate form is the most frequent in colonies seen by us. The leaves are usually glabrous in the glabrous—or bilineately—puberulent-stemmed forms, but puberulent in those with wholly puberulent stems. The inflorescence is thyrsoid, with longer internodes than the lower stem, puberulent or glabrate, with bracts similar to the leaves but much shorter. The peduncles are rather conspicuously bibracteate, bearing 1-2 (-3) flowers on shorter pedicels, the whole

generally glabrate. The sepals are obovate or broadly elliptic and apiculate, 4-5 mm. long, 2-3 mm. broad, sparingly glandular or glabrous. The corollas are tubular, subregular, gradually inflated from the base to short rounded lobes that are erect or somewhat spreading, 30-35 mm. long, 6-10 mm. broad (pressed), and somewhat glandular without. Flower color is near strong red (2.5R 4/12 in the Munsell system), lighter within the throat, with red guidelines in most flowers. The filaments and anthers are light colored or white, the anthers peltately explanate, each locule nearly orbicular, and in many flowers just barely included. The staminode is filiform, somewhat dilated distally, and glabrous. The capsules are typical of the genus, ovoid-attenuate, 7-8 mm. long, dehiscent into 4 sections, with a persistent central column. The seeds are black, angular, about 2 mm. long.

The species is moderately common on the limestone rocks in an apparently rather limited area from Creel to the southwestern corner of Chihuahua. It is a conspicuously handsome species, visited frequently by hummingbirds, but not seen by us to be visited by insects. The flower type is clearly of the *PP. hartwegii-apateticus* group, and is very different from the more northern *P. pinifolius* Greene, which it resembles vegetatively.

The type is Palmer's number 264, in the Gray Herbarium (GH), collected in southwestern Chihuahua, "at the Frailes, halfway between Batopilas and the Cumbre" at an elevation of over 7000 feet, in October, 1885. Isotypes are in PH, US. Other examples seen are (see figure 5):

CHIHUAHUA: Mojarachic, *Knoblock* 5797 (MSC); 6 miles south of Creel, *Straw & Forman* 1875 (GH, MEXU, MICH, RSA, US); 33 miles south of Creel, *Straw & Forman* 1907 (RSA); 43 miles south of Creel toward Batopilas, *Straw & Forman* 1904 (GH, MEXU, MICH, RSA, US); Tecolote, municipality of Guadalupe y Calvo, *Gentry, Correll, & Arguellos* 17964 (US).

5. *Penstemon hartwegii* Benth., Pl. Hartw. 48, 1840.

Penstemon gentianoides Lindl., Bot. Reg. 24: t. 3, 1838; Bot. Mag. 65: t. 3661, 1838, *non* (HBK) Poir., Dict. Sci. Nat. 38: 385, 1825.

Penstemon gentianoides var. *coccineus* Hort., Floricult. Cab. 7: 263, 1839.

Penstemon puniceus Lilja, Tidning für Trädgårds. No. 5, 1842, *et* Linnaea 17: 111, 1843, *non* A. Gray in Torr., Bot. Mex. Bound.: 113, 1859 (= *P. supurbus* A. Nels.)

Penstemon coccineus Hoffmgg., Linnaea 16: 281, 1842, *non* Engelm., Wisz. Tour N. Mex.: 107, 1848 (= *P. barbatus* [Cav.] Roth).

Erect, perennial, suffrutescent herbs, sparingly to abundantly branched above the woody base, to 15 dm. tall, although usually under 10 dm., the stems densely puberulent in two lines axillary to the decussate leaves; leaves lanceolate, the lowest on the stem narrowly lanceolate, becoming broader toward the inflorescence, the longest leaves in mid-stem, 35-75 mm. long, 10-15 mm. broad, sometimes larger, acute, rarely acuminate, the margins entire, often narrowly revolute, glabrous, lower margins and midribs sometimes puberulent; bracts like the leaves, becoming smaller upward. The inflorescence bilineately or completely puberulent to somewhat glandular, pedicels and sepal bases glandular-pubescent; in the lower inflorescence branches the peduncles are 1-3 times longer than the pedicels, the total peduncle-pedicel lengths 50-100 mm.; the peduncles ascending or somewhat spreading, usually conspicuously bibracteolate, 1-3 (-4) flowered. The sepals broadly elliptic, acute or short-acuminate, 7-10 mm. long, 4-5 mm. broad. The corolla tubular, gradually expanding from the base to the bilabiate, subregular limb, the lobes rounded, spreading; total length is 40-50 mm. The colors outside and on the lips within are near deep purplish red (10RP 3/10 in the Munsell system), abruptly white within the throat, with strong guidelines. The filaments are white, the anthers included, peltately explanate, the sacs rotund and glabrous. The staminode is glabrous or moderately bearded. The ovary and capsule are ovoid, acuminate, glabrous; the seed are angular, black, 1-2 mm. long.

This species is one of the largest-flowered of the genus, with a broadly open tubular corolla that is visited regularly both by hummingbirds and bees, especially of the genus *Bombus*. Its reddish-purple color and broader shape are not typical, although its general aspect and pendulous attitude are more consonant with typical bird-pollinated species.

Penstemon hartwegii appears to be limited in its natural distribution entirely or nearly entirely to a relatively small area along the upper edges of the central plateau in the state of Hidalgo, where it occupies openings and banks in the pine-oak woodland between approximately 2100 and 2800 meters elevation. This species has been cultivated for many years, however, and is one of the parents (apparently with *P. cobaea* Nutt.) of the common cultivated hybrids. Considering this, several collections from South and Central America present some difficulties of interpretation. A collection from Colombia (Boyaca: Labranzgrande; *Amortegui* 322, US), by its flower shape, pubescence, and leaf serrations, is clearly one of these hybrids, and the sheet is marked in what would appear to be the collector's hand, "(cult.?)". Two other sheets (Cundinamarca: Paramo de Chipaque, *Camilo* 4183, US, and Region of Bogota, *Ariste-Joseph s.n.*, US) are not clearly distinct from the present species in any characteristic found so far, and are interpreted as escapes from cultivation. A similar interpretation applies to a few other collections from Bolivia, Chile, and Honduras.

The type is Hartweg's number 362, collected at or near the mining community of Real del Monte, Hidalgo, in 1839, in the Bentham Herbarium at Kew (K) (type photographs seen). Other examples seen are (see figure 5):

HIDALGO: various localities between Zimapan and Jacala: *Moore* 3377 (GH, UC), *M. T. Edwards* 821 (DS, F, MO, TEX), *Hitchcock & Stanford* 6995 (DS, GH, UC, US), *Fisher* 37023 (GH, MO?, NY?, US), *Lyonnet & Elcoro* 1158 (US), *Lundell* 12164 (MICH), *Waterfall* 14142 (OKLA, NY), *Sharp* 45639 (PH, TENN), *Langman* 2831 (PH), *Clark* 7031 (NY), *Kenoyer* 638 and A238 (F), *Straw & Gregory* 1137 (GH, MEXU, MICH, NY, RSA), *Straw & Forman* 2067 (MEXU, MICH, RSA, US); 26 miles north of Jacala, *Manning & Manning* 53626 (GH); Sierra de Pachuca, *Rose & Hay* 5603 (GH, US); Real del Monte, *Ehrenberg s.n.* (US), *Straw & Gregory* 1127 (GH, MEXU, MICH, NY, RSA, US);

STATE OF MEXICO: Ometusco, *Rose & Hough* 4498 (US), a hybrid?

6 *Penstemon skutchii*, *species nova*

Herba perennis suffruticosa, basibus caulum ligneis, caulibus teretis tenuis puberulentis in lineas duas in axillis foliorum; foliis lanceolatis integris glabris; sepalis ellipticis vel ovatis vel rhomboidiis breve acuminatis erosis; corollis tubulosis, sensim inflatis ad lobis rotundis patentibus; antheris peltato-explanatis; apicis staminodorum glabris vel levis pilosis.

This species is a suffrutescent perennial herb with slender stems from a woody base, reaching a height of nearly two meters but usually lower. The stem is terete, densely puberulent in two longitudinal lines in each internode axillary to the decussate leaves; the peduncles and pedicels are completely puberulent but scarcely or not at all glandular. The leaves are lanceolate, entire, glabrous or slightly puberulent on the midrib above, reaching 80 mm. in length, 20 mm. in breadth. The bracts are similar to the leaves, becoming smaller upward in the inflorescence. The sepals are elliptic, ovate or rhomboid, short-acuminate, with erose margins and glandular pubescence at least basally, 6-8 mm. long, 3-5 mm. broad. The tubular corolla is gradually inflated from the base to spreading, rounded lobes, 30 mm. long and about 10 mm. wide (pressed), bilabiate but nearly regular, and glandular pubescent without. The anthers are peltately explanate, with rounded glabrous lobes, and are included. The staminode is slightly dilated, glabrous or sparingly pilose.

The color of the flower was described by the collector of the type as reddish maroon, which with the form and size of the corolla indicate

strongly that this species belongs to the hummingbird-pollinated group including *PP. hartwegii*, *isophyllus*, and others. It is abundantly distinct from all of this group in such characteristics as the lengths of the corollas and leaves, in the ratio of leaf length to width, and from all but *PP. hartwegii* and *fasciculatus* in the bilineate pubescence. In its vegetative parts it is very similar to *P. gentianoides*, and there are no significant differences between them in the major metrical characteristics of these parts. The form of the corolla, however, distinguishes it clearly as having an adaptive mode very different from that of *P. gentianoides*, and several metric differences between the two in inflorescence characteristics have statistical significance at $p < 0.01$ in appropriate "t" tests; the total peduncle-pedicle length is greater in *P. skutchii*, as is also the ratio of corolla length to width, and the ratio of peduncle-pedicle length to corolla length. The inflorescence thus has a more open aspect, compared to the rather densely verticillate appearance of *P. gentianoides*. Furthermore, the anthers of *P. skutchii* do not have such prominent median ridges as are found in *P. gentianoides*. It is possible, naturally, that these two species hybridize in their native locations and thus confuse the distinctions between them. Dr. John Beaman, of Michigan State University, has informed me that he has collected two distinct species from the type region of this species, one of which appears to be *P. gentianoides*, and the other agrees with *P. skutchii* as I have discussed it with him, but I have not yet been able to examine his specimens. His observations, however, confirm the differences in the colors of the corollas of these two species, a characteristic that is very difficult to establish from herbarium specimens but is of great importance to the modes of pollination.

The type (figure 6) of the species is Skutch's number 1250, in the Herbarium of the Arnold Arboretum at Harvard University (A), collected in the Sierra Cuchumatanes, Department of Huehuetenango, Guatemala, on a rocky ridge at an elevation of 11,100 feet, September 15, 1934. Isotypes are found in F, PH, NY, US.

It is a pleasure to be able to name this species for its collector, Alexander F. Skutch, whose arduous and efficient studies over many years have added so greatly to our knowledge of the botany and ornithology of Central America.

Other examples seen are:

HUEHUETENANGO: Sierra de los Cuchumatanes, *Steyermark* 48361 (F, PH), *Steyermark* 50162 (F, PH), *Standley* 81694 and 81700 (F), *Johnston* 1774 (F).

7. *Penstemon filisepalis*, species nova

Herba perennis, caule erecto tereti glabrato; foliis linearibus vel anguste lanceolatis ad apicem caulis, acutis, integris glabris, cum foliolis

similis fasciculatis in axillis foliorum; sepalis linearibus 5 mm. longis 1 mm. latis integris acutis glanduloso-pubescentibus; corollis anguste tubulosis sensim inflatis ad ora, labiis inferioribus paulim albo-vilosis; antheris subexsertibus peltato-explanatibus; filamentis sterilis dense luteo-barbatis.

A perennial herb with erect, terete, glabrate stems. The leaves are linear to linear-lanceolate toward the inflorescence, up to 55 mm. long, 3-5 mm. broad, acute, entire, glabrous, with axillary fascicles of smaller, similar leaves. The inflorescence is strict, thyrsoid, sparingly glandular-pubescent on all parts. The bracts are similar to the leaves, becoming smaller upward, the lowest about as long as the peduncles and pedicels together. The peduncles are longer than the pedicels, the lowest ones almost twice as long, the total length of peduncle and pedicel 30-50 mm.; peduncles are bibracteate and 1-3 flowered. The sepals are linear, about 5 mm. long, 1 mm. broad, scarcely or not overlapping basally, acute and entire. The flowers are narrowly tubular, gradually inflated from the base, about 25 mm. long, 7 mm. broad (pressed), scarcely bilabiate, the lobes short, rounded, and the lower lip sparingly white-vilose within. The longer pair of anthers is subexserted; the anther sacs are confluent, peltate-explanate, oblong, small (about 2 mm. long, 1 mm. broad), glabrous and entire. The staminode is about as long as the stamens, filiform, slightly inflated distally, with a dense, short, yellow beard on the terminal 2-3 mm. The young capsules are ellipsoidal with the base of the style persistent. The flower color is quite apparently red. The type is shown in figure 7.

The species is now known from a single collection, but is a member of this subsection on the basis of the flower form, anthers, and leaves, being closest in the latter to *P. apateticus* ssp. *townsendianus*, and yet is so clearly distinct on the basis of its sepals, staminode beard, and glabrate stem that it must represent a separate species. No new examples were found during a week of collecting in the type area in the summer of 1960.

The type is a collection of E. W. Nelson, number 4847, made "at the base of Mt. Mohinora, Chihuahua, 8 miles from Guadalupe y Calvo", at an elevation of 7000-7500 feet, August 23-31, 1898. It is deposited in the United States National Herbarium (US), number 332894. See also figure 5.

The name refers to the linear sepals.

8. *Penstemon mohinoranus*, species nova

Herba perennis, caule erecto terete puberulento, ad inflorescentem glabrato et in inflorescentibus leviter glanduloso-pubescente; foliis anguste ellipticis vel lanceolatis, vel ad basim caulis minutis oblanceolatis, integris; bracteis minute linearibus; pedunculis quam pedicilibus longio-

ribus; sepalis lanceolatis longe acuminatis, marginibus inferioribus scariosis; corollis tubulosis sensim inflatis ad ora subregularis patentis, labii inferioribus leviter villosis; antheris inclusis vel subexsertibus peltato-explanatibus; filamentis sterilibus inclusis leviter dilatis glabris.

A perennial herb with erect, terete stems, usually little branched above the sub-ligneous base, completely puberulent below, becoming glabrate upward, and in the inflorescence lightly glandular-pubescent. The leaves are narrowly elliptic or lanceolate, to 90 mm. long, 30 mm. broad, but the lowest leaves on the stem are much smaller and oblanceolate; all are entire, with the margins and major veins minutely puberulent. The bracts are small, linear, usually inconspicuous. The peduncles are longer than the pedicels, with a combined peduncle-pedicel length of 50-90 mm.; the peduncles ascending, 1-4 flowered, bibracteate, sparingly glandular-pubescent. The sepals are lanceolate, long-acuminate, to 10 mm. long, 3 mm. broad basally, the lower margins scarious and glandular pubescent. The corolla is tubular, gradually inflated from the base to the patent, subregular orifice, 42-50 mm. long, 8-12 mm. broad (pressed), with the lower lip sparingly villous within. The anthers are included or subexserted, peltate-explanate, the lobes rounded, glabrous, and entire. The staminode is included, somewhat dilated distally, and glabrous. The type is shown in figure 8.

The species is a native of extreme southwestern Chihuahua, where it is known only from the vicinity of Cerro Mohinora, southwest of Guadalupe y Calvo. It is found in open pine woods or margins of clearings in granitic soils, at elevations of about 2300 meters. The flowers on the specimens seen by us are vivid red (5R 5/13 in the Munsell system), lighter within the throat and marked with some guidelines. It is visited by hummingbirds and possibly by some bees, as is *P. hartwegii*, which it most closely resembles in shape and size of flower. Its flowers, however, seem to have much less of the purple shades than those of *P. hartwegii*.

Penstemon mohinoranus is adequately distinct from its closest relatives. In 1959 (Bol. Soc. Bot. Mex. 24: 46) I assigned the type specimen to *P. apateticus* ssp. *durangensis*, but the availability of more material makes it clear that this is a distinct entity in spite of several similarities in shape. Both the corollas and the longest leaves are significantly longer in the present species (with probabilities less than 0.001 on appropriate "t" tests), the sepals are larger, narrower, and more attenuate, and the general size of the plants is greater. The other species in the same general region with which it might be confused is *P. plagapineus*, from which it also differs significantly ($p < 0.001$ on "t" tests) in corolla length, leaf length, and leaf length to width ratios. From *P. hartwegii* it is distinct in sepal shape and size and in leaf length, as well as in the pubescence of the stem, which is complete in this species but bilineate in *P. hartwegii*. That its closest relatives are probably *PP. apateticus* and *plagapineus* may be indicated by the presence of small oblanceolate or spatulate lower

cauline leaves in all three species in addition to the general features that it shares with all of the red-flowered species in this subsection.

The type is a collection of E. W. Nelson, without number, in the United States National Herbarium, number 332938, collected on "Mt. Mohinora, S. W. Chihuahua", September 1, 1898. The only other known collection is from the same locality, made in 1960: *Straw & Forman 1913* (MEXU, MICH, RSA, US). See figure 5.

The name derives from the type locality.

9. *Penstemon apateticus* Straw, Bol. Soc. Bot. Mex. 24: 42, 1959.

Perennial herbs with subwoody persistent bases, fine stems that are erect or ascending, glabrate or finely puberulent below, and glabrate to sparingly glandular in the inflorescences. Leaves vary with the subspecies, from linear (in ssp. *apateticus*), to narrowly lanceolate (in ssp. *townsendianus*) or narrowly elliptic to more broadly lanceolate (in ssp. *durangensis*), entire, glabrous or with fine pubescence on the margins, mid-ribs, and sometimes on the surfaces. The sepals are lanceolate, acuminate, entire, sparingly glandular, 5-8 mm. long. The corollas are narrowly tubular, gradually ampliate from the base, usually 25-30 mm. long (rarely longer), the exterior color bright red (2.5-5 R 5-6/12 in the Munsell system), similar on the lips within, becoming abruptly white or lighter within the throat, with or sometimes without red guidelines. The anthers are included, peltately explanate, glabrous, entire, usually light-colored. The staminode is filiform and glabrous. The seed are small, angular, and black, in capsules typical of the genus.

The geographical ranges of the subspecies are distinct, the typical subspecies being found in the southern transverse volcanic ranges of Mexico from Jalisco and Michoacan to Puebla and Oaxaca, subspecies *durangensis* limited to western Durango, and subspecies *townsendianus* to western Chihuahua.

Only subspecies *durangensis* has much chance to be confused with other species, especially *PP. mohinoranus* and *plagapineus*, and the critical differences are discussed under those names. Never the less, the possibility remains that, although the three appear to be distinct, more complete collections from the critical areas will show that their limits are less clear than I now believe, and another taxonomic conclusion will need to be reached.

A map of the distributions and lists of examples were presented in the paper in which the species was described (1.c.), and will not be repeated here.

10. *Penstemon isophyllus* Robinson, Proc. Boston Soc. Nat. Hist. 31: 267, 1904.

Erect or somewhat decumbent perennial herbs with several to many stems arising from the woody base to a meter or more in height, completely and densely puberulent throughout their lengths. The leaves are in many pairs, those in mid-stem sub-equal in length, 40-60 mm. long (rarely longer), 8-15 mm. broad, narrowly elliptic or lanceolate, the margins entire and revolute, the leaves on herbarium specimens often conduplicate, glabrous or puberulent on the lower margins. Axillary fascicles of smaller, similar leaves are commonly present but not usually conspicuous. The inflorescence is an open thyrse, the peduncles usually 2-3 times longer than the pedicels, the total combined lengths 30-60 mm., the peduncles 1-5 flowered, puberulent, and some of the hairs glandular. The sepals are broadly ovate or elliptic, acute or short-acuminate, the margins erose, 7-9 mm. long, 3-4 mm. broad. The corolla tubular, gradually ampliate toward the orifice, 35-45 mm. long, the limb bilabiate, subregular, the rounded lobes spreading; the color is deep purplish red (near 10RP 5/10 in the Munsell system) without and on the lips within, white in the throat with strong guidelines. Anthers are included, peltate-explanate, entire, and glabrous. The staminode is filiform, glabrous or rarely somewhat hairy. The seeds are black, angular, 1-2 mm. long, in ovoid, acuminate capsules typical of the genus.

This species is usually found in openings in the lower oak or pine-oak zone at altitudes between 1800 and 2800 meters, where it often forms clumps of stems about a meter high with very showy flowers. The typical pollinators appear to be hummingbirds, but bees visit the flowers and presumably also pollinate them. This species is quasi-sympatric with *P. apateticus* ssp. *apateticus* in Puebla and Oaxaca, but the latter species is more commonly found at higher altitudes in the pine and pine-oak zones, and the two species have not been seen together. There is slight evidence (in stem pubescence) of possible introgression between them.

Penstemon isophyllus is found in the states of Puebla and Oaxaca, geographically intermediate between *PP. hartwegii* and *skutchii*. The type is a collection of C. G. Pringle, number 8568, collected "on hills above Chalchicomula, Puebla, alt. 2750 m., 13 August 1901", in the Gray Herbarium of Harvard University (GH), with widespread isotypes seen in the following herbaria: F, MIN, MO, POM, UC, US, VT. Other specimens seen include the following (see also figure 5):

PUEBLA: Boca del Monte, *Purpus* 2470 (DS, F, GH, MO, UC, US); Mt. Orizaba, *Seaton* 172 (F, GH, NY, US); Los Chinos, San Manuel de la Sierra, Sierra Negra, *Balls* 5398 (US); Cerro Tepoxuihutl, *Nicolas s.n.* (PH); San Andres, above Serdan, Cabecero, *Sharp* 441035 (PH, TENN);

VERACRUZ: Los Molinos, Perote, *Balls* 5426 (NY, UC, US);

OAXACA: Cerro Verde, *Purpus* 3276 (F, GH, MO, NY, UC, US); San Pedro Alto, *Liebmann* 9410 (US); Rio San Jose, *Reko* 3319 (US);

Valley of Oaxaca, *Nelson 1547* (GH); between Cuauhtlilla and Omiltingo, *Seler 1412* (GH); La Mixteca, *Conzatti 114* (GH); Telixtlahuaca, *L. C. Smith 475* (GH); east of Yanhuítlan, *Sharp 45875* (PH, TENN); Tamazulapan, *Straw & Gregory 1037* (RSA); Nochixtlan, *Straw & Gregory 1041* (MEXU, MICH, RSA).

11. *Penstemon plagapineus*, species nova

Herba perennis erecta ad basim ramosa; foliis crassis. supremis late lanceolatis, mediis ellipticis, inferioribus oblanceolatis vel fere rotundatis vel infimis minute oblanceolatis vel spatulatis, integris vel aliis minute serratis; bracteis minute lanceolatis; pedunculis multiramosis; sepalis ovatis vel lanceolatis acuminatis, glanduloso-pubescentibus; corollis anguste tubulosis sensim inflatis ad ora, subregularibus; antheris inclusis peltato-explanatis; staminodiis filiformis glabris.

An erect perennial herb, suffrutescent and (in those seen) of many stems from the base. The stems are terete, minutely puberulent or glabrate below, becoming glabrate or glabrous above and in the inflorescence. The leaves change in form the length of the stem: the uppermost are lanceolate or broadly lanceolate, becoming by mid-stem elliptic, and downward, more broadly oblanceolate or nearly rotund in some; the lowest cauline leaves are very small and oblanceolate or spatulate, entire or in some specimens minutely serrate distally, glabrous or somewhat puberulent on the base. The longest leaves are 35-60 mm. long. 10-30 mm. broad, with the ratio of length to width usually 2-3 (in *P. apateticus* ssp. *durangensis* it is 4-5). The corolla is tubular, gradually inflated toward the orifice, bilabiate but subregular, the lips rounded and spreading, total length 35-45 mm., vivid red (near 5R 5/15 + in the Munsell system) in those seen, lighter in the throat and with or without guidelines. The anthers are included, peltate-explanate, glabrous, entire. The staminode is filiform, glabrous, and included. The capsule is ovoid-acuminate, the seed small, angled, and black.

This species, as now conceived, is distributed on the higher parts of the western slope of the Sierra Madre Occidental from Durango and Sinaloa south to Nayarit, where it occupies openings in the pine-fir-hardwood forest at elevations (apparently) on the order of 2600-2900 meters. It has been seen by me only in one locality, where it formed a densely branching clump similar to *P. isophyllus*, from which it is distinct in morphology and distribution. It is probably visited regularly by hummingbirds, although none were seen during the short time we observed it in rainy weather. It may be confused with *P. apateticus* ssp. *durangensis*, but is larger in general size, has larger flowers, and broader leaves, and is apparently more westerly in distribution. A photograph of a specimen from Nayarit is seen in figure 9.

The type is a collection of Pennell, number 18395, in the Herbarium of the University of California, Berkeley (UC), number 1,003,695, collected at "Metates, north of Cueva", Durango, at an altitude of 2800-2900 meters, August 29-30, 1934. Isotypes are found in MICH, PH.

The habitat as described by Pennell is "pineland", and the name, from the Latin, may be translated as "place of pines".

Other specimens seen are the following (see also figure 5):

DURANGO: Los Articulos, on the railroad east of Purisima, *Pennell 18599* (MICH); State of Durango, *García 373* (US); between Villa Union and El Salto, 21.7 miles north east of El Paraiso, Sin., *G. B. & Findley Ownbey 1983* (MICH, MIN, RSA); 7-8 miles west of Buenos Aires on the Durango-Mazatlan highway, *Straw & Forman 1790* (MEXU, MICH, RSA, US);

SINALOA: mountainside 2 miles northeast of Revolcaderos. *Waterfall 12727* (OKLA); Cerro de la Sandia, northeast of Panuco (Carrizo), *Pennell 20105* (US);

NAYARIT: between Santa Gertrudis and Santa Teresa, Terr. de Tepic, *Rose 2072* (PH, US).

CHROMOSOME COUNTS

Chromosomes have been counted for the several species tabulated below:

P. apateticus ssp. *townsendianus*

Straw & Forman No. 1646, Largo, Chih. $n = 8$

Straw & Forman No. 1682, Cuauhtemoc, Chih. $n = 8$, $2n = 16$

P. fasciculatus

Straw & Forman No. 1875, Creel, Chih. $n = 8$

P. gentianoides

Straw & Gregory No. 1111, Las Cruces, Mex. $n = 8$

Straw & Gregory No. 1172, Nevado de Toluca, Mex. $2n = 16$

P. hartwegii

Straw & Gregory No. 1153, San Vicente, Hgo. $2n = 16$

P. isophyllus

Straw & Gregory No. 1037, Tamazulapan, Oax. $2n = 16$

P. leonensis

Gillett No. 1236, Peña Nevada, N. L. $n = 8$

Except for the last, the haploid chromosome counts are based on buds collected in the field in Newcomer's (1953) solution, stained with propionic carmine, and made permanent with Hoyer's medium following the technique of Beeks (1955). Newcomer's-preserved buds have not deteriorated in quality over a period of four or more years, even though stored at room temperature. The haploid count on *P. leonensis* was made on buds fixed in 3:1 alcohol-acetic-acid, and kindly sent to me by Dr. George Gillett, of Michigan State University. Diploid counts were made on root tips from seed germinated on filter paper and treated by the acetic-lacmoid squash method of Darlington and LaCour (1960). Seeds preserved under dry conditions have remained viable for at least four years. Vouchers are deposited in the Herbarium of the Rancho Santa Ana Botanic Garden (RSA).

EVOLUTIONARY PATTERNS WITHIN THE SUBSECTION

As has been seen above, the subsection *Fasciculi* comprises two series or species groups, one with widely inflated purple-colored flowers, the other with narrower, gradually inflated, red corollas (figure 10). Members of both species groups, totalling three taxa in the first group and ten in the second, occupy relatively similar habitats in the pine and pine-oak belt of the major mountain chains of Mexico and Guatemala, entirely within those regions designated as pine-oak forest on the vegetation map of Mexico prepared by Leopold (1951). The distribution maps (figures 1 and 5 of this paper and figure 2 of Straw, 1959) show that within each species group the taxa are essentially allopatric, replacing units, mostly of relatively limited distributions. In the case of the red-flowered group, the most wide-spread species, *P. apateticus* and its sub-species, occupies a relatively central distribution on the plateau of central Mexico, whereas the several other species are found in smaller, more peripheral ranges on or over the edges of the plateau in more dissected terrain.

The clearest evolutionary pattern indicates that widespread taxa, that at some earlier time occupied a large part of the pine-oak zone (or its precursor) in the Sierra Madre of Mexico and Guatemala, were fragmented into a series of geographic subunits, each of which now occupies a rather restricted portion of the former range. The events that precipitated this breaking up were most likely climatic. Increased aridity following the Pleistocene, with the fragmentation and isolation of ecologically acceptable habitats, accompanied by the "normal" course of geographic speciation, would seem adequate to have produced the observed pattern. The original taxa must have numbered at least two, one representing the wide, purple-flowered, bee-pollinated adaptive mode, and the other the tubular, red-flowered, hummingbird-pollinated mode described earlier.

In this section, as in the genus as a whole (Pennell, 1935), the most primitive floral type would appear to be the bee-pollinated group. The primary adaptations of the genus, of the staminode and nectaries (Straw, 1956), support this conclusion. A second major evolutionary trend visible in this section, as in some others (e. g., *Peltanthera*, and the *Habroanthus-Elmigeria* complex), is a shift from the bee-adapted mode to the hummingbird-pollinated type, under the influence of the pollinator that was not apparently involved in the earlier evolution of the genus. Once a new floral type was fixed, it must have spread rapidly throughout much the same habitats to which the original stock was adapted. Each of the two types, both now fragmented, exhibits the same geographic distribution patterns.

It is not clear to what extent other factors have influenced the present status of the taxa considered here. It may seem anomalous that the subsection should be based in large part on the fact that its members have entire leaves (except for *P. plagapineus*, which sometimes has remotely serrate leaves). It has been seen that in such hybrids as are known, as, for instance, the commercial hybrid, *P. hartwegii* X *cobaea* (*P. gloxinoides* Hort., et. al.), that leaf serrations are apparently inherited at least as semi-dominant characteristics. Thus, their absence in all or most of the group might indicate a fundamental status. In those instances in which some of the leaves are somewhat serrate, as in several sheets of *P. plagapineus* and in a specimen of *P. hartwegii* from Ometusco, Mex., an explanation may lie in the possibility of introgression from another species (e.g., *P. kunthii* G. Don, representing another subsection of this section, and widely sympatric with these species).

The leaves of *P. fasciculatus* are least in consonance with the remainder of the subsection, and are most similar to those of *P. pinifolius* Greene. Bennett and Keck (1953, in an informal treatment) have placed these two together. Their flowers, however, are very different. The flowers of *P. fasciculatus* are in every way consistent with the other members of this group, whereas those of *P. pinifolius* are very deeply dissected into long, narrow lobes, and present an aspect most unlike any member of the subsection. If one considers the floral characteristics to be the more fundamental, as I do, it becomes impossible to include *P. pinifolius* in the subsection *Fasciculi*; its status, however, is not at all clear, and it may indeed represent another subsection in section *Fasciculus*. This "subsection" would at this time appear to be monotypic. *Pentstemon fasciculatus* is limited, so far as I can tell, to the limestones of southwestern Chihuahua, and its vegetative morphology may reflect in part the more arid physiological conditions which it must endure. Occasional specimens with much longer leaves than is usual may represent either introgression from or incomplete divergence of the gene pool from *P. apateticus* ssp. *townsendianus*, which seems to be its closest relative and neighbor.

TABLE 1

Summary of Differences Between *PP. gentianoides*,
leonensis, and *occiduus*

Character	Metric (quantitative)				Qualitative				
	Total peduncle + pedicel length	Flower length	Ratio peduncle + pedicel: flower lengths	Ratio peduncle: pedicel lengths	Sepal length	Leaf length	Sepal shape	Leaf shape	Staminode beard
Between: gentianoides- leonensis	+	+		+		+	+	+	+
leonensis- occiduus	+		+		+	+	+		+
occiduus- gentianoides		±	+					+	

+ = metric difference significant at $p < .05$ or qualitative difference judged significant by writer.

It may be suggested that the taxonomic status given each of the units here described is not the most representative of the biological facts. Whereas some of the units are quite distinct, the taxa within the two primary species-groups represent for the most part different combinations of a group of variable characteristics in a more or less chaotic substitution pattern, not unlike those described by Mayr (1942) for some birds of Asia and the East Indies. Figure 4 shows several average dimensions for the three species of the purple-flowered group, and table 1 summarizes these and other differences between the species. It can be seen that only a combination of characteristics will separate the three units. Similarly, figure 11 shows, on a base map, average leaf lengths, widths, and shapes, and average corolla lengths, for the several taxa of the red-flowered group. The apparent randomness of the combinations supports the notion that they are all segregates from what was once a common gene pool. Each taxon is, on the whole, adequately distinguishable from the others, yet all are closely related and distinctions must be made on combinations of characters rather than single ones. Three units have been called subspecies (of *P. apateticus*), the others species. It is left for the informal term, species group, to represent what Mayr might have called on the one hand a superspecies, or on the other, a species with many subspecies. Either level is able to indicate equally well the same facts of evolution

Some aspects of the groups, especially the red-flowered one, suggest the *syngameon* as used by Grant (1957). There does appear to be some introgression between certain members of the group, but for the most part the taxa are clearly allopatric. No breeding results are yet available on these species, but since all are apparently of the same haploid chromosome number ($n = 8$), and results from other groups (e.g., Nisbet & Jackson, 1960) indicate few genetic barriers in the genus as a whole, it is quite possible that they might be able to exchange genes freely in the garden or if they were to come into sympatric contact. The dominant source of confusion is, however, believed to be a relatively low level of divergence rather than any great amount of hybridization among the taxa.

Since the biological statuses of all the taxa are not completely clear, the primary justification for naming most of them species is precedence. The units here called species seem to me to be as distinct from one another as are the species in other, better known, groups. To take any other course would cause even greater inequalities in the meaning of specific rank within the genus than would exist naturally as a result of several different taxonomists' having worked in it.

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RESUMEN

En el género *Penstemon* de México son descritas una sección, *Fasciculus*, y una subsección, *Fasciculi*, nuevas. La subsección contiene once especies, de las cuales seis son nuevas: *PP. occiduus*, *leonensis*, *skutchii*, *filisepalis*, *mohinoranus* y *plagapineus*. Se discute la evolución en este grupo.

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FIG. 2. Photograph of the type of *Penstemon occidus* Straw

FIG. 3. Photograph of an isotype of *Penstemon leonensis* Straw

FIG. 4. Diagrammatic comparison of corolla lengths, sepal lengths, total peduncle-pedicle lengths, ratios of peduncle to pedicle lengths and lengths of the longest leaves in *a*, *Penstemon gentianoides*, *b*, *P. leonensis*, and *c*, *P. occiduus*, all to the same scale. Measurements indicate means $\pm$ their standard errors, based on 22-29 specimens for *a*, 14 specimens for *b*, and one for *c*.

FIG. 5. Map of the distribution of the red-flowered species in *Penstemon* subsection *Fasciculi*, not including *P. apateticus*.

FIG. 6. Photograph of the type of *Penstemon skutchii* Straw

FIG. 7. Photograph of the type of *Penstemon filisepalis* Straw

FIG. 8. Photograph of the type of *Penstemon mohinoranus* Straw

FIG. 9. Photograph of a specimen of *Penstemon plagapius* Straw

FIG. 10. Types of flowers seen in the red-flowered species group (1, after *P. mohinoranus*) and the purple-flowered species group (2, after *P. gentianoides*) of *Penstemon* subsection *Fasciculi*.

FIG. 11. Distribution of corolla lengths and of leaf lengths, widths, and shapes, shown to the same approximate scale, to demonstrate part of the chaotic variation pattern among the taxa of the red-flowered species group of subsection *Fasciculi*. Abbreviations are: towns., *P. apateticus* ssp. *townsendianus*; fasc., *P. fasciculatus*; mohin., *P. mohinoranus*; fili., *P. filisepalis*; dgo., *P. apateticus* ssp. *durangensis*; plag., *P. plagapineus*; apat., *P. apateticus* ssp. *apateticus*; hartw., *P. hartwegii*; iso., *P. isophyllus*; skutch., *P. skutchii*.