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A TAXONOMIC REVISION OF *CHILOPSIS* (BIGNONIACEAE)

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ABSTRACT

The genus *Chilopsis* contains one species, *C. linearis*, with two subspecies: subsp. *linearis* of the Chihuahuan Desert characterized by erect, straight leaves, and subsp. *arcuata* of the Sonoran and Mojave deserts with longer, arcuate leaves and other distinguishing characteristics. Populations of subsp. *linearis* east of the Sierra Madre Oriental in eastern Mexico have woolly stems and are described as a new variety, *tomenticaulis*. Relationships between *Chilopsis* and *Catalpa* are discussed and data are presented supporting continued recognition of *Chilopsis* as a distinct genus.

Key words: Bignoniaceae, *Chilopsis*, *Catalpa*, Sonoran Desert, Chihuahuan Desert, Mojave Desert.

INTRODUCTION

The genus *Chilopsis* was proposed by D. Don (1823) based on a Mexican collection from Pavon deposited in the Lambert Herbarium. Don's genus contained one species, *C. saligna*; however, the species was previously published as "*Bignonia? linearis*" by Cavanilles (1795). The combination *Chilopsis linearis* (D. Don) Sweet was first made in Sweet's *Hortus Britannicus* in 1827. In 1848 Engelmann noted that Wislizenus's specimens from Chihuahua, Mexico, had narrow, glutinous leaves and branches, and, although not sure of the characteristics of *C. linearis*, he suggested that these may represent a new species *Chilopsis glutinosa* Engelm.

The first taxonomic treatment of *Chilopsis* by Fosberg (1936) accepted *Chilopsis* as monotypic, consisting of three varieties: an eastern *C. linearis* var. *linearis* with "woolly" branchlets and straight leaves with prominent venation; a western *C. linearis* var. *arcuata* Fosberg with glabrous branches and distinctly arcuate leaf-blades usually without prominent venation; and a more centrally located *C. linearis* var. *glutinosa* (Engelm.) Fosberg with branches and leaves glutinous and leaf-blades either erect or arcuate.

Fosberg's 1936 work was based largely on field studies and specimens at UC. His study was stimulated by the discovery of plants with strongly glutinous stems from south-central New Mexico. He correctly separated specimens with straight leaves from central Mexico and Texas from plants more to the west having arcuate leaves. But in recognizing his glutinous-stemmed taxon he was forced to include in that taxon material with both straight and curved leaves, which resulted in a series of rather ambiguously defined taxa.

Since its publication Fosberg's treatment has been variously followed in major floras. His taxa are referred to in Kearney and Peebles (1951), Correll and Johnston (1970), and Martin and Hutchins (1981), are questioned in Benson and Darrow (1954), but are accepted in Benson and Darrow (1981). Munz and Keck (1959) and Munz (1974) refer to his var. *arcuata* as a form while Abrams and Ferris (1960), Shreve and Wiggins (1964), Wiggins (1980), and Cronquist, Holmgren,

Holmgren, Reveal and Holmgren (1984) have all placed his varieties into synonymy.

This reevaluation of *Chilopsis* is an outgrowth of the preparation of the treatment of Bignoniaceae for the Chihuahuan Desert flora. In addition to field studies through the southwestern United States and Mexico, specimens were examined or borrowed from A, ARIZ, ASU, CSLA, ENCB, GH, JEPS, LL, MEXU, MO, NMC, NY, POM, RSA, SRSC, TEX, UC, UNM, UNLV, and US, photographs of authentic specimens were provided by MA.

In addition to a systematic revision of *Chilopsis*, this paper also addresses questions regarding the relationships to the genus *Catalpa*.

RESULTS AND DISCUSSION

Relationships of Chilopsis and Catalpa

Chilopsis is most closely related to the genus *Catalpa* Scop. Within the Bignoniaceae *Chilopsis* and *Catalpa* are placed in the largely pantropical tribe Tecomeae Endl., characterized by a tree-shrub growth habit, 2-loculed ovaries, and fruits that dehisce perpendicular to the septum. Within the Tecomeae they have been placed by Bentham and Hooker (1876), along with *Sparattosperma* Mart. in DC., in subtribe Trichosperminae, characterized by seeds having separate, long hairs extending from each end. The Brazilian *Sparattosperma*, however, has palmately compound leaves and differs in many other features, and Gentry (pers. comm.) rejects the notion of relationship with *Sparattosperma* and considers that *Chilopsis* and *Catalpa* represent a distinct and separate lineage within the Tecomeae of unknown affinities (Gentry 1980).

Catalpa is sometimes allied with *Paulownia* Sieb. & Zucc. (e.g., Airy Shaw 1966), but Armstrong (1985) has shown that *Paulownia* has ovary characteristics typical of Scrophulariaceae, while *Catalpa* clearly shows character states of Bignoniaceae.

Chilopsis and *Catalpa* share many characteristics. They are both small to large trees. They are nearly identical in fruit, seed, embryo, style, and anther characteristics. They have similar thickened, obovoid calyces that open irregularly into upper and lower lips. Their corollas are similar in texture, coloration, and lobing though those of *Catalpa* are often larger with more ampliate throats and vary from white to yellowish in background coloration. They also share a unique pollen type in the family (Fig. 4d) consisting of tetrads with sculpturing limited to coarsely reticulate areoles (Gentry and Tomb 1979), and both have 20 pairs of chromosomes (Goldblatt and Gentry 1979) though that number occurs throughout the family. In addition sterile hybrids have been formed between *Chilopsis linearis* and *Catalpa* cf. *bignonioides* (Rusanov 1964).

Most North American botanists know *Catalpa* from our two native southeastern species: *C. bignonioides* Walt. and *C. speciosa* Warder. *Catalpa*, however, consists of about 11 species placed in two sections (Paclt 1952): section *Catalpa* with six species showing an Asian-eastern North America disjunction (Li 1952) with two species native to southeastern North America and four to temperate China; and section *Macrocatappa* Grisebach with five species native to the West Indies. Species of *Catalpa* share many basic flower, fruit, seed, and growth habit characteristics. Flowers are borne in terminal racemes or panicles, and are distinguished from

most other Bignoniaceae in having only two fertile stamens and three staminodia. The five-lobed corollas have ampliate throats with a pair of basal ridges and are variously spotted or striped with contrasting color patterns. Leaves are usually opposite to verticillate, petiolate, and dorsiventral in structure with bundle sheath extensions continuing to the minor veins. Leaf blades bear clusters of distinctive capitate glands sunken in pockets in the axils of midrib and secondary (and sometimes tertiary) veins on the lower surface that serve as extrafloral nectaries attracting ants, which protect the leaves from various sucking insects (Elias and Newcombe 1979). Species of section *Catalpa* are winter deciduous, distinguished by having large, rather soft, ovate to broadly ovate, entire to variously coarsely lobed, long-petiolate leaves, and, as in *Chilopsis*, the seed body bears hairs only at the ends of the seeds. Species of the West Indian section *Macrocatappa*, in contrast, are semideciduous, have smaller, coriaceous to chartaceous, elliptic-lanceolate to ovate, entire to denticulate, short-petiolate leaves, and the bicomose seeds are also hairy on their dorsal surfaces. They also have fewer nectariferous glands on their leaves, and tend to have more delicate pedicels, etc.

Chilopsis linearis differs fundamentally from *Catalpa* in having flowers with four stamens and one staminode (Fig. 3f)—a plesiomorphy occurring in all but two genera in the Bignoniaceae. Other differences appear associated with the adaptation of *Chilopsis* to semiarid habitats in southwestern United States and Mexico where it occurs as a phreatophyte mostly along dry streambeds. *Chilopsis linearis* is a small tree. Its leaves are linear to linear-lanceolate, attenuate, isolateral (with stomata and palisade cells on both surfaces—Fig. 4e–f) and they lack the concentrations of nectariferous glands in depressions in the vein axils on the abaxial surface (as leaves are isolateral, they lack a homologous abaxial leaf surface). They have reduced racemose to racemose-paniculate inflorescences and their corollas have narrower throats, etc. (Fig. 3a–d, 4a–c).

The relationship of *Chilopsis* with *Catalpa* is not evident. Is *Chilopsis* just a xeromorphic derivative of *Catalpa* section *Catalpa*, or is it a sister group of the genus *Catalpa*? To test the relationships of *Chilopsis* with *Catalpa*, character states were recorded for *Chilopsis* and *Catalpa* using data from Paclt's (1952) synopsis of *Catalpa* and other descriptions. As no reliable outgroup is known (Gentry, pers. comm.) it was not possible to polarize the data using outgroup comparison so three separate data sets were developed considering the character states of section *Catalpa*, section *Macrocatappa*, or *Chilopsis* as plesiomorphic. The data were analyzed with the WAGNER option of PHYSYS on the California State University central Cyber computer. The data sets included 11 to 10 OTU's and 13 to 11 characters—the reduced sets eliminated closely related taxa and those character states whose polarity was more difficult to establish. Without evidence as to the correct ancestral group we end up with an uprooted tree of three convex groups sensu Duncan (1980; Meacham 1980) as shown in Figure 1a. However, it may be possible to establish a root within this tree. Only one character used in this data set can be polarized with some degree of confidence on the basis of external evidence—that of four stamens vs. two stamens. As noted above, only two genera in the Bignoniaceae exhibit the two stamen-three staminodia character state—*Catalpa* in the Tecomeae and the unrelated genus *Pseudocatappa* in the Bignoneae (A. Gentry, pers. comm.). I believe this strongly implies that the two-stamened characteristic is apomorphic and the four-stamened character state found

Fig. 1. a. Unrooted cladogram showing three lineages uniting at one point representing the three convex lines of *Chilopsis*, *Catalpa* section *Catalpa*, and section *Macrocatappa*. Species in sections of *Catalpa* are not shown.—b. Same diagram shown rooted between *Chilopsis* and *Catalpa* on the basis of the plesiomorphic four stamens one staminode character state found throughout Bignoniaceae and in *Chilopsis* that supports recognition of *Chilopsis* as a generically distinct sister group of *Catalpa*.

in *Chilopsis* is plesiomorphic. This single character can be used to root the tree between *Chilopsis* (four stamens) and *Catalpa* (two stamens) which makes *Chilopsis* a sister group to the lineage of *Catalpa* and *Macrocatappa* (Fig. 1b). While it could be argued that it is rather risky to root a tree on the basis of a single character it is, in my opinion, the most concordant option available. To root the tree with either section *Catalpa* or section *Macrocatappa* would make *Chilopsis* part of the sister group with the alternate section, which would either demand that the two-stamen characteristic evolved independently in the two sections of *Catalpa* or that the four-stamened character of *Chilopsis* would represent a reversal from a two-stamened character state (as in *Catalpa*) to a four-stamened state and would thus be homoplastic.

It should be noted that while *Catalpa* is characterized by having two stamens and three staminodia, occasional plants of our native southeastern *Catalpas* have four fertile stamens and a single staminode (Fernald 1950; Gleason 1952)—apparently representing an atavism. However, in these flowers, one anther sac of the proximal anther pair is usually not completely developed. This raises a question whether or not the four stamens of *Chilopsis* could represent a fixed atavistic character state? This question is basically unresolvable with the data at hand.

The resulting generic treatment allows for retention of the current classification recognizing *Chilopsis* as a distinct genus forming a sister group to *Catalpa* with its two sections *Catalpa* and *Macrocatappa*.

Classification of Taxa within Chilopsis

Field studies and analysis of the herbarium material show that three well-defined taxa exist over the range of the species. Plants from the Sonoran and Mojavean deserts in Baja California, Sonora, California, Arizona, and extreme northwestern portion of the Chihuahuan Desert in the western half of New Mexico (Fig. 6) have arcuate, long leaves, light-colored corollas, glabrous to sparsely pilose, glandular or somewhat glutinous stems, and a tendency to have widely spreading to

decurved branches (Fig. 2c–d, 3b). This taxon, named *C. linearis* var. *arcuata* by Fosberg, is easily recognized by its curved leaf blades alone. In contrast the type taxon from the Chihuahuan Desert region in central Mexico, trans-Pecos Texas, and the eastern half of New Mexico (Fig. 6) is characterized by straight, moderately short, erect-ascending leaves, more strongly colored corollas, and a tendency to have erect-ascending branches (Fig. 2a–b, 3a). Through most of this range their stems are strongly to weakly hirtellous to nearly glabrous and variously glandular to glutinous. This constitutes *C. linearis* var. *linearis* of Fosberg in part. Populations east of the Sierra Madre Oriental in Tamaulipas and Nuevo Leon (Fig. 6), however, represent a third, heretofore undescribed taxon that has slightly larger flowers and distinctly woolly stems—taxon “*tomenticaulis*.” The rationale for establishing this classification is explained in detail in the systematic section of this paper.

To reflect this pattern, taxa *arcuata* and *linearis* are here recognized at the rank of subspecies while “*tomenticaulis*,” which differs from taxon *linearis* mainly in stem vestiture, is considered a variety of *linearis*. The subspecific rank in this classification is used to allow taxon *tomenticaulis* to be relegated to a subordinate (varietal) rank thus providing for a hierarchical classification.

TAXONOMY

CHILOPSIS D. Don, Edinb. Phil. Journ. 9(18):261, 1823. Type: *Chilopsis saligna* D. Don, loc. cit.

From the Greek *Cheilos*, labium, and *opsis*, resemblance, and thus pronounced *Kilopsis* (fide Shinnars 1961). With one species. A much amplified species description is here presented in lieu of a separate discussion of the characteristics of *Chilopsis*.

CHILOPSIS LINEARIS (Cav.) Sweet

Deciduous, rounded, erect to widely branched shrubs to small or moderate-sized trees (1.5–)2–8(–9) m tall; main branches ascending; lateral branches erect-ascending or spreading-drooping; young stems having sessile glands with heads 0.05–0.07(–0.11) mm wide with 16(–60) vertical cells, these often breaking down (rupturing) along their periphery on internodes but tending to persist at nodes where they may function as extra-floral nectaries, sometimes sparsely hirtellous-pilose, rarely densely villous with straight to crinkled, uniseriate, rarely forked or branched white hairs (0.05–)0.1–0.4(–1.5) mm long, often glabrate; all stems terminating in inflorescences; internodes 0–30(–45) mm long, yellowish, glutinous when covered with exudate from ruptured glands; second-year and older stems more maroon to reddish brown, often drying grayish, marked with light gray punctate to horizontal lenticels; larger branches with gray-black, vertically fissured, roughened, corky bark. Leaves alternate, usually partially opposite to whorled, simple, linear-lanceolate to linear, (4.5–)6–15(–26.5) cm long, (1.5–)2–6(–13) mm wide, long attenuate at tips, narrowly cuneate, tapering to narrowly winged, yellowish, (1–)2–10(–15) mm long petiolelike bases, entire or nearly so, thickish, isolateral in structure, erect-ascending and straight or more arcuate and drooping with one edge uppermost with lamina often positioned by distinct twisting above base, glabrous or very sparsely puberulent-hirtellous with scattered hairs to 0.1–

0.2(–0.4) mm long along bases, midveins and margins, initially with sessile, large-headed glands, on both surfaces, these usually breaking down leaving distinct glandular punctae, sometimes causing leaves to become glutinous, with midvein and sometimes secondary veins yellowish, raised beneath, yellowish and somewhat impressed above, minor veins raised or not in dried leaves, with or without bundle sheath extensions; foliar nectaries lacking. Flowers borne in terminal, indeterminate racemes or racemose panicles (3–)5–10(–20)[–30] cm long, inflorescence and adjacent stems usually more strongly vestitured than subtending stems, sparsely hirtellous-pilose to densely villous-tomentose with hairs (0.1–)0.2–0.5(–1.2) mm long, often with sessile or stipitate glands; peduncles 1–5(–9) mm long; pedicels 1–5(–7) mm long, the pair 2.5–8(–14) mm long in flower, to 23 mm long and becoming thick and woody in fruit; lower peduncles sometimes with 2(–3) flowers; bracts-bracteoles lanceolate, more linear-subulate when small, (2–)3–8(–11)[–24] mm long, (0.3–)0.5–1(–3.5) mm wide, acute-acuminate at tip, broad at base, or when larger, abruptly narrowing above base, 1–3(–5)-veined, pilose to villous outside, yellowish green, caducous; calyces obovoid in bud, 8.5–14 mm long with 5 subulate terminal teeth 0.4–1.5 mm long, splitting longitudinally as corolla expands to within (0.5–)2–3(–7) mm of base, usually bilabiate with abaxial and adaxial lips, occasionally splitting only down the abaxial side, membranous to thickened and spongy in texture, variously hirtellous-pilose to villous with hairs 0.2–1.2 mm long, variously glandular, cream-white to yellowish green, often suffused with purple or sometimes purple or maroon maculate, with 14–20 vertical veins visible outside, glabrous or glandular inside; corollas sweetly aromatic, bilabiate, funnelform-campanulate, irregular, tending to bend in lower tube and become horizontal to declined, (25–)32–50(–60) mm long, basal tubes cylindrical, 5–10 mm long, thickened, curved, grooved inside between the four thickened adnate filament bases; throats ampliate, somewhat vertically compressed, 15–25 mm long, 7–9 mm high, to 9–14(–20) mm wide at orifice (pressed), ventricose with a pair of distinct ridges on throat floor extending to mouth; lobes 5, upper 2 lobes reflexed-erect, partially united, free lobes (5–)8–16 mm long and wide, lower 3 lobes spreading, forming a landing platform, lower medial lobe spreading or declined, oblong-obovate to obovate, (8–)12–20 mm long, (6–)9–14(–16) mm wide, lower lateral lobes orbicular-reniform to obovate, 13–18 mm long, 11–17 mm wide, all lobe margins crisped, sometimes erose-fimbriate, throat white, tinged with pink, lavender, purple or rather strongly red-maroon outside, lobes whitish or suffused with lavender-purplish to dark maroon-red on inner lower lobe surfaces, throat floor with yellow to dark yellow on the paired raised ridges, usually with 9–15 parallel, slender maroon to purple lines on floor with 3–5 lines between the yellow ridges, and 3–5 lines external to ridges on throat sides with lines extending and frequently expanding onto strongly colored lower corolla lobe surfaces; corollas glabrous outside, with subsessile glands inside basal, thickened tube and with scattered, wavy multicellular, uniseriate hairs 1–2.5(–4) mm long on inner throat floor and extending on lower lobes; stamens 4, didynamous, posterior (upper lateral) pair shorter; filaments adnate to corolla tube for 2–5(–7) mm; posterior free filaments (6–)9–18 mm long; anterior free filaments (10–)13–22 mm long, whitish, stipitate glandular at base, glabrous above; anther sacs separate, oblong, cream-white, subparallel in bud, divergent 90–120 degrees

before anthesis; anther sacs broadly oblong-ovate after dehiscence, with distal anther sac slightly larger than proximal anther sac, anther sacs 2.1–3 mm long (dry) and diverging about 180 degrees after opening as the outer anther sac swings upward; pollen shed in tetrads 58–70 μm in diameter with coarsely reticulate sculpturing restricted to distinct areoles; uppermost (posterior) stamen reduced to a filamentous staminodia 4–10(–20) mm long often capped with an aborted anther 0.2–0.3 mm long; ovary narrowly cylindrical-conical, 2-loculed, covered with subsessile glands, with swollen nectary at base; styles (13–)17–23(–26) mm long, extending beyond anthers but included in throat; style lobes oblong, 1–2 mm long, rounded to acute at tip, thigmotrophic. Fruits of terete, loculicidal, dark brown, pendent, glabrous capsules (9–)14–30(–36) cm long, 3.5–6(–8.5) mm in diameter; septa flattened, 2–4 mm wide; seeds produced in 2 rows in each locule; seed bodies oblong, (6–)8–12 mm long, 2.5–3.2(–4) mm wide, concavo-convex, obtuse with a coma of straight to somewhat wavy, separate, unicellular, white hairs (5–)9–15 mm long, (7–)14–35 μm in diameter at each end; cotyledons each bilobed (Fig. 2–5).

The species is here divided into three subordinate taxa, two subspecies, one with two varieties as indicated in the following key.

- A. Leaves straight or nearly so, erect-ascending, 5–9(–11) cm long; young stems (below inflorescence) usually hirtellous-pilose or glabrous and sparsely glandular, rarely densely villous with erect to crisped-curved hairs 0.05–1.5 mm long; mature fruits (4.5–)5–7(–8.5) mm in diameter; plants usually erect with erect-ascending upper stems. . . . *C. linearis* subsp. *linearis*
 - B. Young stems moderately to sparsely hirtellous-pilose with hairs (0.05–)0.1–0.4 mm long to glabrous, with sessile glands or variously glutinous. . . . *C. linearis* subsp. *linearis* var. *linearis*
 - BB. Young stems densely villous tomentose with crisped-curved, white hairs (0.3–)0.5–0.8(–1.3) mm long. . . . *C. linearis* subsp. *linearis* var. *tomenticaulis*
- AA. Leaves falcate-arcuate, curving away from stem, often distally pendent, (8–)10–18(–21) cm long; young stems glabrous or very sparsely pilose with widely scattered, erect hairs 0.05–0.2 mm long; mature fruits 3.5–5 mm in diameter; plants more rounded with spreading to drooping branches. . . . *C. linearis* subsp. *arcuata*

CHILOPSIS LINEARIS (Cav.) Sweet subsp. LINEARIS

Erect-ascending, small to moderate-sized trees 2–6(–9) m tall with mostly erect-ascending young stems and branches; leaves erect-ascending, straight or nearly so, (4–)5–10(–15) cm long, (2.8–)4–8(–12) mm wide, broader leaves usually with bundle sheath extensions over minor veins, sparsely pilose-hirtellous along margins, midribs, and petioles or glabrous, with sessile glands on both surfaces or these breaking down and forming glandular punctae and rendering blades somewhat glutinous; young stems glabrous, hirtellous to densely villous-tomentose, with sessile glands, sometimes becoming glutinous; inflorescences hirsute to densely villous-tomentose; pedicels-peduncles together (2–)5–14 mm long; calyces (8.5–)10–15 mm long, moderately membranous to thick and spongy; corollas (30–)40–55(–60) mm long, light lavender-pink to commonly vividly red-maroon outside throat and on upper surface of lower lobes; mature fruits 13–32 cm long, (4.5–)5–7(–8.5) mm wide.

Chilopsis linearis subsp. *linearis* is easily distinguished from subsp. *arcuata* by its straight, erect-ascending leaves (Fig. 2b, 3a). Several other quantitative trends

Fig. 2. Growth habit and leaf differences in taxa of *Chilopsis linearis*.—a–b. *C. l.* var. *linearis*.—a. Erect growth habit of shrub ca. 2 m tall showing many small basal stems and erect-ascending upper stems.—b. Leafy stems with erect-ascending leaves. Both from *Henrickson 19699* near Sheffield, Texas.—c–d. *C. l.* subsp. *arcuata*.—c. Characteristic rounded growth habit in tree ca. 2.5 m tall with spreading to drooping stems.—d. Leaves in lateral, spreading stems showing their characteristic arcuate shape. Both from *Henrickson 20226* near Baker, California.—e–f. Stems showing periderm development.—e. Young stem ca. 5 cm in diameter showing smooth maroon-brown bark and white horizontal lenticels (from *Henrickson 20226*).—f. Mature trunk showing grayish anastomosing bark on trunk ca. 30 cm in diameter (from *Henrickson 19699*).

are also apparent in subsp. *linearis*: (1) young stems tend to be more erect as are major branches giving at least young plants more erect growth habits (Fig. 2a); (2) leaves tend to be shorter, mostly 4–11 cm in length, and may be very narrow (2.8–4 mm wide) or broader (5–11 mm wide) within a population; (3) inflorescences tend to have longer, less noticeably glandular peduncles and pedicels; (4) corollas tend to be larger and are accompanied with longer styles, filaments, staminodia, etc., and though variable in color even within a population they tend to be more strongly colored often having rather vivid maroon-red outer corolla tubes and more extensive coloration on the inner corolla lobe surfaces (Fig. 4b); and (5) fruit are usually noticeably thicker than those of subsp. *arcuata*.

There is recognizable geographical-based variation within subsp. *linearis* involving development of young stem vestiture and a number of secondary character trends that support recognition of two varieties within subsp. *linearis*.

CHILOPSIS LINEARIS (Cav.) Sweet subsp. *LINEARIS* var. *LINEARIS*, Hort. Brit. ed. 1: 283, 1827; DC. Prod. 9:227, 1845.—*Bignonia linearis* Cav., Icon. Pl. 3:35, t. 269, 1794.—*Chilopsis linearis* (Cav.) DC. Prodrum 9:227, 1845.—*Chilopsis linearis* var. *originaria* Fosberg, Madroño 3:365, 1936.—TYPE: Grown from seed from an unknown Mexican source at Madrid in the Horti Pharmaceutico in 1792–93. Holotype: MA; photo, TEX!

Chilopsis saligna D. Don, Edinb. Phil. Journ. 9(18):262, 1823.—TYPE: Mexico: *Pavon s.n.* (in Lambert Herbarium at BM! [examined for the author by Dr. Lee W. Lenz, Dec. 1985]).

Chilopsis glutinosa Engelman., Bot. Wislitz. Exped. 94, 1848.—*Chilopsis linearis* var. *glutinosa* (Engelm.) Fosberg, Madroño 3:365, 1936.—TYPE: Mexico: Coahuila; Cienega between Parras and Saltillo, 18 May 1847, *A. Wislizenus* 289. Lectotype (here designated): MO!

Leaves (4–)5.5–9(–12.5) cm long, (2.8–)4–7(–10)[–14] mm wide, mostly glabrous, occasionally with scattered hairs 0.05–0.3(–0.4) mm long along margins, bases and midveins, in broader leaves with minor venation raised due to bundle sheath extensions. Young stems moderately hirtellous-pilose with erect, spreading or upcurved hairs (0.05–)0.1–0.3(–0.4) mm long, or these absent or few, with scattered, sessile glands throughout or these breaking down and persisting as glutinous dots, but tending to persist intact near nodes and on buds, petioles and lower leaf blades surfaces; glands sometimes rendering young stems and leaves somewhat glutinous; inflorescence more hirsute-pilose to villous; corollas light lavender, pink to often rather vividly maroon on outside throat and lobes, (30–)36–52(–58) mm long, throat 8–15[–20] mm wide (pressed); posterior filaments 13–17(–22) mm long, anterior filaments 10–15(–18) mm long; staminodia 5–10[–20] mm long; styles 21–26 mm long; mature fruit (7–)14–25(–32) cm long, (4.5–)5–6.5(–8) mm thick.

Chilopsis linearis subsp. *linearis* var. *linearis* can be distinguished from subsp. *arcuata* by its straight, erect-ascending, noncurved leaves and from var. *tomenticaulis* by its glabrous to moderately hirtellous-pilose young stems with scattered hairs only 0.05–0.4 mm long.

Fosberg (1936) recognized two varieties within this taxon: *C. linearis* var. “*originaria*” was distinguished in his key as having “sterile branches somewhat woolly, veins in leaves prominent”; and *C. linearis* var. *glutinosa* was distinguished by having “sterile branchlets and leaves glabrous, glutinous, the veins in leaves not usually prominent.” This he contrasted with nonglutinous stems and young leaves of his variety *arcuata*. I have been confused by Fosberg’s use of the term woolly to describe stem vestiture in this taxon as young stems tend to be only hirtellous to pilose or they may lack nonglandular hairs altogether (Fig. 5a–b), though inflorescences do tend to be densely villous to woolly as do the young stems of var. *tomenticaulis*. I have also been confused by his term glutinous (sticky) as I have found specimens throughout the range of *Chilopsis* (except in var. *tomenticaulis* where the woolly vestiture obscures this characteristic on stems) to have some degree of stickiness expressed at least in young stems, e.g., all stick to the newsprint when removed from the press.

With regards to vestiture, stems and leaves of all taxa of *Chilopsis* have two types of trichomes. There are series of scattered, subsessile glands with conspicuous, flattened heads (0.3–)0.4–0.6(–1.0) mm in diameter that usually consist of a single series of 16 vertically-oriented cells (Fig. 4g). Occasional glands, however,

Fig. 3. *Chilopsis linearis*.—a. *C. l.* var. *linearis*. Young stem with terminal inflorescence. Note erect leaves.—b. *C. l.* var. *arcuata*. Young stems with terminal inflorescence. Note longer, arching leaves.—c–f. Flowers drawn from photographs showing various views.—c. Lateral view showing bract, two bractlets on pedicel, 2-lipped calyx and ampliate corolla.—d. Face view showing orientation of five lobes.—e. Lower view showing position and extent of invaginations forming distinct ridges on the floor of throat, sectional view at left shows prominent development of ridges.—f. Upper transparent view of flower showing shape of lobes and orientation of didynamous stamens in throat. Style shown at right.—g. Capsule and seeds. Capsule is similar in color and texture to those of *Catalpa* and dehisces along lines perpendicular to the septum. Seeds occur in two rows in each locule. Seeds have coma of long separate hairs at each end. Hairs have thickenings when seen in water mounts.—h. Seedling showing strongly lobed cotyledons and linear first leaves. (Vertical bar in a holds for a–b, g–h; vertical bar in c holds for c–f. Drawing by Bobbi Angell.)

are larger and have 30–60 vertical cells (Fig. 4h). These glands contain a viscid substance and they may eventually rupture along their outer margins exuding these contents onto stem internodes and leaf surfaces causing the structures to become variously glutinous (Fig. 5e–f). The exudate, however, gradually dries and becomes less viscid over time. If the glands are still intact, they can easily be seen on stems and leaf surfaces. After the glands rupture on leaf surfaces the glutinous contents remain in the slightly recessed pockets that contained the glands and appear as series of glandular punctae. The glands along nodes, on basal portions of leaves, and on axillary buds tend not to break down and thus persist on specimens. Whether these serve as extra-floral nectaries as in *Catalpa* (Elias and Newcombe 1979) is unknown. These glands occur on plants throughout the range of the species.

Stems and leaves also contain series of erect or upcurved, whitish, uniseriate, multicellular hairs. These are usually only scattered on leaves confined to lower margins and along the midvein and petioles. Their development on stems is highly variable. In var. *linearis* plants from much of Texas and along the eastern border of the Chihuahuan Desert (generally from near Muzquiz to Cuatro Ciénegas and the Sierra Santa Fe del Pino in Coahuila) tend to have a hirtellous vestiture on young stems with moderately dense, erect or upcurved, uniseriate trichomes 0.05–0.3(–0.4) mm long mixed with glandular trichomes (Fig. 5a). Only rare plants ever develop a stem vestiture that could be termed woolly. Plants around El Paso and the Chisos Mountains and in the central Chihuahuan Desert in Chihuahua, Durango, and adjacent Coahuila, San Luis Potosí, in contrast, tend to have more scattered, shorter or no uniseriate trichomes on young stems (Fig. 5b) and in this characteristic they blend towards the more western subsp. *arcuata* that has only widely scattered uniseriate trichomes on young stems. These plants also tend to have slightly longer leaves. Engelmann, when describing Wislizenus's collections from northern México (Engelmann 1848) noted that the plants "from New Mexico and Chihuahua, with longer, narrower glutinous leaves, perfectly glabrous, glutinous branchlets, and darker and smaller flowers may be *Ch. linearis*, DC., or a new species, *Ch. glutinosa*." While admitting that Engelmann's *glutinosa* was rather dubiously published, Fosberg (1936) accepted the taxon at the varietal level mainly as he had collected specimens north of El Paso, Texas, with very glutinous stems and leaves. In so circumscribing this taxon on the basis of glutinous stems, Fosberg was forced to accept into his var. *glutinosa* some glutinous-stemmed specimens with arcuate leaves that would otherwise fit well into his var. *arcuata*. This caused him to deemphasize the leaf character in his keys.

Interestingly, none of the four *Chilopsis* specimens collected by Wislizenus during his journey and seen by Engelmann had entirely glabrous stems, i.e., completely lacking uniseriate hairs—all were sparsely hirtellous with very short hairs. Also the glutinous condition dissipates in herbarium specimens as the exudate dries and at the present time none of Wislizenus's now 136-year-old specimens show any indication of a glutinous nature though they undoubtedly did the year after their collection when observed by Engelmann.

Generally, stem vestiture exhibits too much variation to be useful in classification here. Development of nonglandular hairs shows intrapopulational variation, and the glutinous character is variably expressed during the season.

Fosberg (1936) also noted that his varieties could be divided on the basis of

Fig. 4. Flowers and leaves of *Chilopsis linearis*.—a–b. *C. l.* var. *linearis*.—a. Lateral view of flower showing tube, orientation of lobes.—b. Face view of flower showing development of color on lower lip, note style at tip of throat orifice (cultivated at RSA).—c. *C. l.* subsp. *arcuata*. View of three flowers and buds (Henrickson 20226).—d. Pollen consists of tetrads with coarsely reticulate areoles. (Grain

the prominence of leaf venation. I have found a strong tendency for all material in this variety to have prominent minor leaf venation caused by the development of bundle sheath extensions over tertiary and quaternary veinlets (Fig. 4e). In dried leaves this may be evidenced by mere darkened lines following minor venation or by variations in blade thickness over and between minor venation. The character is often not expressed in young and very narrow leaves.

There are several very good characteristics that can be used to separate subsp. *linearis* from subsp. *arcuata* (see above) with the leaf shape (whether straight or arcuate) being the most easily recognized. However, even the leaf shape characteristic is not consistent. Occasional specimens will have mostly erect leaves with a few, scattered, somewhat arcuate leaves. I interpret the western populations of var. *linearis*—those with reduced young stem vestiture and slightly longer leaves—as exhibiting some degree of intergradation with subsp. *arcuata*.

Variety *linearis* occurs mostly in the Chihuahuan Desert ranging from south-central New Mexico where it co-occurs and intergrades with subsp. *arcuata*, trans-Pecos Texas south through east-central Chihuahua, Coahuila with scattered localities through Durango, in northern Zacatecas, and northern San Luis Potosí (Fig. 6). It is cultivated well outside its range in Texas, Oklahoma, Kansas, Louisiana, Missouri, and California as well as in Europe and the Soviet Union and in many places in west Texas (Randall, Hall, and Lynn counties), Oklahoma (Payne and Jefferson counties) and in Kansas (Comanche and Barber counties) it appears to have naturalized. It grows in sandy and gravelly washes along streams and canyons from areas of *Larrea* scrub to oak and juniper woodlands, and grasslands occurring with such species as *Prosopis glandulosa* Torr., *Brickellia laciniata* Gray, *Fallugia paradoxa* (D. Don) Endl., *Celtis pallida* Torr., *Acacia berlandieri* Benth., *A. greggii* Gray, *Forestiera angustifolia* Torr., *Juglans microcarpa* Berl., *Pistacia texana* Swingle, *Baccharis salicifolia* (Ruiz & Pavon) Pers., etc. from 550 to 1650 m elevation. It flowers primarily in the spring from May to July but some flowering may continue until September.

CHILOPSIS LINEARIS (Cav.) Sweet subsp. LINEARIS var. **tomenticaulis** Henrickson, var. nov.

A var. *linearis* caulibus juvenilibus valde tomentosis pilis undulato-crispatis (0.3–)0.5–1.0(–1.5) mm longis, foliorum marginibus et costis proximalibus puberulento-hirtellis pilis 0.1–0.4 mm longis differt (Fig. 5c).

Leaves (5.5–)8–13(–15) cm long, (2–)3–10(–12) mm wide, glabrous except for scattered to moderately dense curled hairs 0.1–0.4 mm long along lower midvein and margins, lateral minor veins not raised but bundle sheaths often visible in dried leaves. Young stems densely canescent to villous-tomentose with appressed

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ca. 65 μ m in diameter, from Henrickson 20226).—e–f. Cross section of mature leaves showing isolateral structure with two layers of palisade cells below each epidermis.—e. *C. l.* var. *linearis* showing well-developed bundle sheath extensions over all veins, note capitate glands on upper right.—f. *C. l.* subsp. *arcuata* lacks bundle sheath extensions on all but major veins.—g–i. Leaf glandular trichomes from *C. l.* var. *tomenticaulis* (Henrickson 19137).—g. Sessile glands on leaves contain a single basal cell and typically have only 16 head cells.—h. Occasional glands have up to 45(–60) cells in the head.—i. Lateral view showing sunken gland with single basal cell. (Gland heads in g–h are ca. 65 μ m in diameter; in i head is ca. 55 μ m in diameter. Horizontal bar in e holds for f.)

to wavy-crisped, simple, occasionally branched hairs (0.3–)0.5–0.7(–1.5) mm long, these obscuring underlying glands; inflorescences densely tomentose-villous; calyces (8.5–)10–14 mm long, usually thick and spongy, with conspicuous glands in distal half, moderately pilose with scattered hairs; corollas light lavender-pinkish with strong purple-maroon lines in throat that extend onto lower lobes, (37–)45–62 mm long, throat 12–25 mm wide (pressed); posterior filaments 18–22 mm long; anterior filaments 12–18 mm long; staminodia 7–12 mm long; styles 25–27 mm long; mature fruit 13–31 cm long, 5–8.5 mm thick. TYPE: Mexico: Tamaulipas: Sierra de San Carlos, vicinity of San Miguel, La Tamaulipeca, tree 20 ft, valley floor, 25 Jul 1930, *H. H. Bartlett 10576*. (Holotype: US!, isotype MICH.)

The primary character that distinguishes var. *tomenticaulis* from var. *linearis* is the densely canescent to villous-tomentose young stems that are covered with whitish-gray, ascending-appressed hairs 0.3–0.5 mm long or more commonly wavy to crisped, ascending hairs 0.5–1.0(–1.5) mm long (Fig. 5c). The hairs occasionally are branched or forked. A number of additional trends are apparent including usually very strongly villous-tomentose inflorescences, thick, often spongy, only sparsely pilose calyces, and generally large, strongly colored corollas. The new taxon shares many characteristics with var. *linearis* including tendencies to have more strongly colored, large corollas, longer filaments, styles, etc., erect-ascending, mostly straight leaves, paniculate-racemose inflorescences, and thickened fruits. But unlike var. *linearis* leaves are relatively thin and do not have raised secondary to quaternary veins, though bundle sheath extensions may be present at least on broader leaves.

The tomentose stem characteristic is conspicuous and usually present in all plants of a population though occasional plants within a population, e.g., *Henrickson 19071* (TEX), or all plants of a gathering (*Palmer 390*) have glabrous stems and calyces indicating perhaps a simple genetic basis of the character. As in var. *linearis* occasional plants show a scattering of falcate leaves. The stem vestiture character is not completely restricted to these plants as occasional isolated collections of subsp. *linearis* such as *Pope s.n.* (NY) from Texas (exact locality not given) have hairy stems as in subsp. *tomenticaulis*. It appears that this woolly stem characteristic merely became fixed in the populations east of the Sierra Madre Occidental perhaps when the populations were greatly restricted in extent during the holocene.

The taxon is confined to extreme eastern Coahuila, Nuevo Leon, and adjacent Tamaulipas east of the Sierra Madre Oriental (Fig. 6) mostly in sandy to gravelly arroyos and streamsides from tropical scrub to chaparral-oak and pine woodlands where it occurs in association with species of *Populus* L., *Baccharis* L., *Salix* L., *Platanus* L., *Rhus* L., *Fraxinus* L., *Yucca* L., *Berberis* L., *Acacia* Mill., etc., from about 300 to 1800 m elevation. Flowering occurs from May to July, often continuing into September.

Representative collections.—MEXICO. COAHUILA: Near Nuevo Leon-Coahuila boundary, road from Monterrey to Saltillo, 5 Sep 1937, *White and Chatters 201* (GH).—NUEVO LEON: Linaris, Los Anacuas canyon, 670 m, 12 May 1980, *Hinton 17781* (TEX); W of bridge to Colonia del Valle, Monterrey, 19 Jun 1960, *Smith M255* (TEX); 12 mi W of Linaris where Hwy. 31 enters mts., 1200 ft, 26 Jul 1956, *Fearing and Thompson 22* (TEX); Hwy. 58, 10.8 mi E Iturbide, 650 m, 11 Aug 1984, *Daniel and Baker 3642* (ASU); 8 mi E of Galeana, 5440 ft, 29 Aug 1940, *Shreve and Tinkham 9760* (ARIZ, GH);

Fig. 5. Scanning electron micrographs of *Chilopsis linearis* taxa.—a–d. Young stem vestiture.—a. *C. l.* var. *linearis* showing characteristic moderately dense, somewhat upcurved hirtellous vestiture. Note sessile glands. *Marsh 89* from Chisos Mountains, Brewster Co., Texas.—b. *C. l.* var. *linearis* showing absence of uniseriate hairs and density of sessile glandular trichomes. *Hinton 16598* from Sierra de Paila, near Saltillo, Coahuila.—c. *C. l.* var. *tomenticaulis* showing characteristic dense villous-tomentose vestiture of crinkled, sometimes branched hairs. *Bartlett 10450* from Tamaulipas, Mexico.—d. *C. l.* subsp. *arcuata* showing characteristic scattered pilose vestiture and sessile glands.—e–f. Glands on leaf surface before (e) and after (f) rupturing and spilling their contents onto epidermis. These contents often render stems and leaves somewhat glutinous. Note stomata.—e. *C. l.* var. *linearis*, *Hinton 16598*.—f. *C. l.* subsp. *arcuata*, *Henrickson 20226*. (Horizontal bar in a = 100 μ m and holds for a–d; bar in e = 100 μ m and holds for e–f.)

7 mi W of Iturbide, 3.2 mi E from jct. of road to Galeana, 1700 m, 4 Sep 1984, *Henrickson 19726* (TEX); Colonel Hilsenbeck's Ranch, 1600 ft, 11 Aug 1901, *Braswell 103* (TEX); Monterrey, patio del Colegio, 540 m, Aug 1911, *Arsene 6246* (AA, MO, NY); Rancho Resendez, Lampazos, 21 Jun 1937, *Edwards 283* (ARIZ, TEX, UC).—TAMAULIPAS: ca. 52 air km WNW of Jaumave, 10 km NW of Miquihuana, 1800 m, 9 Oct 1982, *Henrickson and Hess 19233* (TEX); Entre La Perdida y Bustamente, 1970 m, 15 Aug 1972, *González-Medrano 4692* (MEXU, TEX); Road between Miquihuana and Dr. Arroyo, 6000 ft, 15 Jun 1898, *Nelson 4510* (MO, US); Sierra de San Carlos, vic. of San José, tree 1 ft diam, fls. purple, 2000 ft, 21 Jul 1930, *Bartlett 10540* (US); Victoria, 320 m, 1 May to 13 Jun 1907, *Palmer 390* (vegetatively glabrous) (NY, UC).

CHILOPSIS LINEARIS (D. Don) Sweet subsp. **arcuata** (Fosberg) Henrickson, comb. et stat. nov. — *Chilopsis linearis* var. *arcuata* Fosberg, Madroño 3:336, 1936. — TYPE: California, San Bernardino County, Mission Creek E of San Bernardino Mts. 1000 m, 12 Aug 1932, F. R. Fosberg 8600. Holotype: UC!, isotype MO!

Usually rounded, small to moderate-sized trees 1.5–5(–7) m tall with mostly ascending to spreading-drooping young stems and branches; leaves falcate-arcuate, oriented with one edge towards stem and typically drooping terminally, (7.5–) 10–18(–26.5) cm long, (1.5–)2–8(–13) mm wide, with winged petioles to 2–10 (–16) mm long, moderately thin, minor venation not raised and without bundle sheath extensions, usually glabrous or sparsely puberulent-hirtellous along margins, initially with sessile glands on both surfaces but these breaking down and surfaces becoming glandular punctate; young stems glabrous to very sparsely hirtellous-pilose with scattered hairs 0.05–0.5(–0.7) mm long, rarely more strongly hirtellous, with sessile glands or these breaking down to leaving open glands, usually persisting near nodes and on buds and petioles; stems and young leaves sometimes glutinous; inflorescences more hirtellous-pilose than stems, often villous-tomentose with curved to crinkled hairs 0.1–0.4(–1.2) mm long, rarely glabrous; pedicels-peduncles together 1–7(–11) mm long in flower; calyces (8–)9–14 mm long, membranous to thick-membranous, pilose to villous, rarely glabrous; corollas light pink to lavender with yellow on ridges and purple lines on floor of throat extending onto lower corolla lobes, (25–)32–45(–50) mm long, tubes (7–) 9–11(–12) mm wide at throat (pressed), posterior free filaments 10–16(–19) mm long, anterior free filaments 6–11(–13) mm long, staminodia 4–6.5(–8) mm long, styles (13–)16–24 mm long; mature fruit (8–)15–30(–36) cm long, (3.5–)4–5 mm wide.

Chilopsis linearis subsp. *arcuata* can be distinguished entirely by leaf orientation and shape. Leaves are usually twisted at the base with leaf-blades oriented with one edge towards the stem with the blades arching outward or downward (Fig. 2d, 3b). As young stems also tend to be more spreading in this taxon, all blades of a stem commonly droop in the same direction (Fig. 3b). Leaves also tend to be much longer than in subsp. *linearis*, tapering to often elongated, winged, petiolelike bases. As in subsp. *linearis* leaf-blades are isolateral in structure (Fig. 4f), they initially are covered with sessile glands on both surfaces but with age the glands break down leaving distinct glandular punctae. Young leaves tend to have scattered, upcurved marginal hairs but these seldom persist. Mature leaves also tend to be thinner than in subsp. *linearis* with bundle sheath extensions forming only along mid and secondary veins (Fig. 4f).

Developing leaves on young shoots will commonly be erect and straight; they become increasingly falcate with age. Occasional specimens with only developing leaves or with very short leaves will have only erect leaves as in subsp. *linearis*.

As noted in the discussion under subsp. *linearis*, inflorescences in subsp. *arcuata* tend to have shorter peduncles-pedicels, the pair seldom exceeding 8 mm in total length, usually with only one flower per peduncle, and corollas tend to be shorter as are filaments, staminodia, styles, etc., though they are structurally identical. Corollas also tend to be less vividly colored with the throat and lobes often being white, light pink, or lavender marked with the characteristic yellow and purple-maroon lines along and between the ridges on the corolla floor. Considerable

Fig. 6. Native distribution of taxa of *Chilopsis linearis* taxa in southwestern United States and Mexico. Naturalized plants of *Chilopsis l. var. linearis* from northern west Texas, Oklahoma to southern Kansas, and cultivated collections are not shown.

intra- and interpopulation variation is also observed in corolla color with some plants having nearly white corollas and others having somewhat lavender or strongly-colored corollas with vivid purple-maroon markings on the lower lobes. Orientation of the mid lower corolla lobe is also variable within a population, declining in some individuals, spreading in others.

Young stems in most specimens appear glabrous but are usually initially covered with scattered, sessile glands that usually break down along internodes but persist near nodes, lower petioles, and on axillary buds. Young stems may also be weakly pilose with a scattering of spreading to slightly curved hairs 0.1–0.5(–0.7) mm

long (Fig. 5d) and in occasional plants young stems are moderately hirtellous-pilose as in subsp. *linearis*.

Inflorescence axes, pedicels-peduncles, bracts-bracteoles, and calyces are always somewhat densely pilose to pilose-villous or occasionally strongly villous with scattered to dense, curved or crinkled, simple, occasionally branched hairs 0.2–0.7(–1.2) mm long. This feature is often accompanied by an understory of sessile or stipitate glands that are particularly common on the pedicels and calyx bases. Occasionally plants have nearly glabrous inflorescences and calyces.

Chilopsis linearis subsp. *arcuata* ranges from southern California, through Arizona to southern Nevada, southwestern Utah, southeastern New Mexico (where it co-occurs and intergrades with subsp. *linearis*), south to northern Sonora, and into Baja California (Fig. 6). It is considered a facultative phreatophyte typically occurring in sandy washes in the Sonoran and Mojave deserts in association with such species as *Onleya tesota* Gray, *Acacia greggii*, *Cercidium microphyllum* (Torr.) Rose & Jtn., *C. floridum* Benth., *Psoralea spinosa* (Gray) Barneby, *Hymenoclea salsola* T. & G., *Prunus fasciculata* (Torr.) Gray, *Rhus trilobata* T. & G., *Fallugia paradoxa*, *Chrysothamnus* Nutt. spp., and *Brickellia* Ell. spp. from near sea level to 5000 ft. It also ranges into Joshua tree, juniper, and oak woodlands, and in Graham County in eastern Arizona it has been recorded from oak-ponderosa pine woodlands up to about 6200 ft elevation [*vide Moore et al.* 6471 (ASU)]. Plants become deciduous in November, leaves are produced in late March (to May at higher elevations), and the new shoots flower from late April through May–June (into July at higher elevations) with some flowering continuing into September if conditions permit.

The three taxa appear to represent distinct vicariants—subsp. *arcuata* in the west, var. *linearis* in central Mexico, with var. *tomenticaulis* isolated east of the Sierra Madre Occidental. It would be reasonable to consider that the taxa have been separated and of a more southern distribution at some point during the quaternary, and with reduction in xeric habitats their distributions would be commensurately reduced. This isolation and reduced population size would allow for differentiation and character fixation. In the present post-pluvial period their ranges are apparently expanding northward (the species is winter-deciduous and thus somewhat frost tolerant) and the distribution pattern shown in Figure 6 can be considered to show subsp. *arcuata* moving northward into Nevada and western New Mexico meeting with var. *linearis* in eastern New Mexico while var. *tomenticaulis*, a more recent derivative from var. *linearis* differing only in stem vestiture, is restricted to the east side of the Sierra Madre Oriental—fitting well into a vicariance pattern.

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