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XEROSPIRAEA, A GENERIC SEGREGATE OF *SPIRAEA*
(ROSACEAE) FROM MEXICO

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ABSTRACT

The xeromorphic Mexican spiraeas (*S. hartwegiana* and *S. northcraftii*) are shown by cladistic and phenetic analysis to be more closely allied to *Petrophytum*, *Kelseya*, and *Luetkea* than to the more mesophytic *Spiraea*. Within *Spiraea* the Mexican spiraeas appear more closely related to the Old World subgenus *Metaspiraea*. The xeromorphic Mexican spiraeas, as well as *Petrophytum*, *Kelseya* and *Luetkea*, are considered to be New World derivatives of Old World *Spiraea* subgenus *Metaspiraea* that have become part of the Madro-Tertiary Geoflora, with each genus achieving some level of xeromorphic adaptation. The Mexican spiraeas are thus considered generically distinct and are placed in a new genus *Xerospiraea* containing one species *X. hartwegiana*. The more northern *Spiraea northcraftii* is placed in synonymy under *X. hartwegiana*.

Key words: Rosaceae, *Spiraea*, *Xerospiraea*.

INTRODUCTION

Recent field expeditions throughout Mexico have provided sufficient flowering and fruiting specimens of *Spiraea northcraftii* I. M. Johnston of montane portions of the Chihuahuan Desert and *Spiraea hartwegiana* Rydb. [= *S. parvifolia* Benth., 1840, *non* Raf., 1838] of central Mexico to allow critical evaluation of their relationships with one another and with the genus as a whole. At the time of the initial description of *S. parvifolia* by Bentham (1840), *Spiraea* L. contained a wide assortment of morphological types, many of which have since been relegated to some nine segregate genera. Accordingly, the generic limits of *Spiraea* have been greatly narrowed. This study will show that the above Mexican taxa represent an additional discordant element within *Spiraea* that is as distinct as other currently recognized related genera.

Historical Change in the Generic Concept of Spiraea

In the first edition of *Species Plantarum*, Linnaeus (1753) recognized 11 species in his *Spiraea*, which was based mainly on the presence of 20 or more stamens, inserted on a hypanthium (Class XII, Icosandria), and five carpels (Pentagynia). The genus, as defined in the fifth edition of *Genera Plantarum* (Linnaeus 1754), had five sepals; five oblong, orbicular petals; and oblong, acuminate, compressed bivalved fruits. Linnaeus's initial 11 species, however, were otherwise quite diverse, including taxa with both shrubby and herbaceous habits, with simple, compound, exstipulate or stipulate leaves, a variety of inflorescence types, and perfect or polygamous flowers with ovaries free or variously united. Only five of the initial 11 Linnean species presently remain in *Spiraea*, the others have been placed in segregate genera including *Aruncus* Schaeff., 1760; *Filipendula* Miller,

1754; *Gillenia* Moench, 1802; *Sobaria* (Ser.) A. Br. in Ascher., 1864; and *Physocarpus* Maxim., 1879.

In the nineteenth and early twentieth centuries, additional elements were placed in *Spiraea* that are now recognized as distinct genera, including *Chamaebatiaria* (Porter) Maxim., 1879; *Holodiscus* (K. Koch) Maxim., 1879; *Sibiraea* Maxim., 1879; *Spiraeanthus* Maxim., 1879; and *Stephanandra* Seib. & Zucc., 1843. As Watson (1890a) noted, in the nineteenth century *Spiraea* was accepted as a very variable genus divided into a number of well-marked sections. The above genera now have been placed into four of the five recognized tribes of the subfamily Spiraeoideae: Sobarieae (*Chamaebatiaria*, *Gillenia*, *Spiraeanthus*, *Sobaria*), Holodisceae (*Holodiscus*), Neillieae (*Physocarpus*, *Stephanandra*), and Ulmarieae (*Filipendula*) (see Rydberg 1908 for characteristics of the tribes). The other genera (*Aruncus*, *Sibiraea* and *Spiraea*) along with *Kelseya* Wats., *Luetkea* Bong. and *Petrophytum* (Nutt.) Rydb. are members of tribe Spiraeae distinguished by their alternate, exstipulate leaves, usually five distinct carpels located alternate with the sepals, dehiscent follicular fruits, nonwinged, fusiform-shaped seeds with thin seed coats, and lack of or very scanty endosperm.

Western North American Species and Genera

In the early nineteenth century a number of distinct plants pertinent to this discussion were described from western North America. In 1834 W. J. Hooker erected a monotypic genus *Eriogynia* Hook. in the Saxifragaceae to distinguish *Saxifraga pectinata* Pursh. This genus contained a distinct, trailing, coriaceous-, biternate-leaved, mat-forming perennial herb of northwestern North America whose fruits dehisce along both the dorsal and ventral traces. Torrey and Gray (1838), recognizing its relationship with Rosaceae, transferred the species to *Spiraea*. In the same work Nuttall (Torrey and Gray 1838) described as *Spiraea caespitosa* Nutt., a mat-forming species from the Rocky Mountains, and placed it in section *Petrophytum* Nutt. In 1840 Bentham named a shrubby species with a racemose inflorescence from the Mexican collections of Theodor Hartweg, *S. parvifolia*, that he related to the Eurasian *S. hypericifolia* L.

Maximowicz (1879) considerably narrowed the generic limits of *Spiraea*, recognizing all the above-listed genera including *Eriogynia* as distinct from *Spiraea* with the exception of *Petrophytum*. He recognized *Spiraea* much as it is recognized today, but with three sections: (1) sect. *Petrophytum* Nutt. with flowers in terminal, simple, cylindrical to subcapitate racemes; (2) sect. *Chamaedryon* Ser. with flowers in simple corymbs or umbels, terminating short lateral branches (with two series); and (3) sect. *Spiraria* Ser. with flowers in branched corymbs or pyramidal-cylindrical panicles terminating branches of the current year (with two series). Foche (1888) followed Maximowicz (1879) recognizing one additional section, *Calospira* K. Koch, with flowers produced in broad corymbose, ovoid panicles terminating basal long-shoot branches.

The entire picture became more complex when Watson (1890a), in describing a species from the Rocky Mountains with a similar habit to *Spiraea* (*Petrophytum*) *caespitosa*, but with a single terminal flower on each stem, recognized the similarity of its coriaceous fruits that dehisce along both the ventral and dorsal traces with those of *Eriogynia* and named the new taxon *Eriogynia uniflora*. This he placed in section *Kelseya* of *Petrophytum*. Later, Watson (1890b) also transferred *Spiraea*

caespitosa into *Eriogynia* placing it in section *Petrophytum*. At that time *Eriogynia* contained three species in three sections—the above two species and *E. pectinata* (Pursh) Hook. Bentham's *S. parvifolia*, which Maximowicz (1879) had also placed in section *Petrophytum* of *Spiraea*, however, was not transferred into *Eriogynia* as Watson (1890a, b) considered *S. parvifolia* more closely related to *Holodiscus* than to *Spiraea*. In 1900 Rydberg recognized the three sections of Watson's redefined *Eriogynia* as distinct genera: *Petrophytum* (Nutt.) Rydb., *Kelseya* (Wats.) Rydb., and *Luetkea* Bong., which, as noted by Kuntze (1891), had priority over *Eriogynia*. Schneider (1905), independently, also recognized these three genera and likewise retained *S. parvifolia* in *Spiraea* but in a separate subgenus *Homiospiraea* Schneid. These three segregate genera have been recognized in all North American floras in which they occur with the exception of those by McVaugh (1942) and Harrington (1954).

Finally, at the infrageneric level, Nakai (1916) divided the remaining *Spiraea* into two subgenera: (1) *Protospiraea* (=subgenus *Spiraea*) with paniculate inflorescences terminating new, leafy long shoots that arise from older stems or from the plant base, occurring in both New and Old Worlds and having two sections, and (2) subgenus *Metaspiraea* with smaller corymbose to umbellate inflorescences terminating short leafy shoots, which develop from buds all along the preceding year's stems (e.g., as in the cultivated Bridal Wreath) that is exclusively Old World and contains three sections.

There remains, then, in *Spiraea* one last element that this study will show shares several characteristics with *Luetkea*, *Kelseya*, and *Petrophytum* and is as distinct as these genera are from *Spiraea* s.s. This element, consisting of the Mexican species *S. hartwegiana* (= *S. parvifolia*) and *S. northcraftii*, is proposed in this paper as a distinct genus *Xerospiraea* Henrickson.

As noted above, *Petrophytum* with one to five species and the monotypic *Kelseya* and *Luetkea* have been grouped together in the same genus by Watson (1890b) and recognized as closely related but distinct genera by Rydberg (1900, 1908). These genera differ from *Spiraea* by their reduced growth habits and, as emphasized particularly by Rydberg (1908), in the mode of fruit dehiscence. In these genera mature fruit dehisce along the entire ventral trace and about a third to half way along the dorsal trace. In contrast, *Spiraea* initially dehisces along the ventral trace only. McVaugh (1942) felt the differences in fruit dehiscence to be one of degree and thus concluded there was no strong line where *Petrophytum* could be separated from *Spiraea*. However, the differences in fruit dehiscence are basically real. In *Spiraea*, mature fruit normally dehisce only along the ventral trace, but, as they weather, they often continue to split across the dorsal trace. In *Petrophytum*, *Kelseya*, and the proposed new genus, the fruit walls are relatively thick and, as they dry, split along both the ventral and dorsal traces initially. In *Luetkea* the fruit walls are much thinner but still dehisce the same way. To erect genera based merely on this fruit dehiscence character, would, in my opinion, be untenable but other characteristics including the distinct habit differences of these three evergreen genera set them apart from the deciduous *Spiraea*.

In this paper phenetic and cladistic analyses are used as tools to show the similarity and relationships of the proposed new genus *Xerospiraea* to other members of the Spiraeaceae. This contribution is considered primarily a taxonomic paper and thus these analyses are only summarized.

MATERIALS AND METHODS

Data were accumulated on the above-noted taxa from literature and from an intensive search for characters from herbarium material. Additional characteristics were obtained from clearings and paraffin-sectioned leaves and flowers. Data sets were run on the PHYSYS program on the California State University central Cyber computer.

DATA ANALYSIS

Data in Table 1 present character states for characters of six genera of the tribe Spiraeeae. The two subgenera of *Spiraea* are treated separately as is the proposed new genus *Xerospiraea*. The dioecious, rhizomatous, compound-leaved *Aruncus* that was included in the phenetic analyses is excluded from the table for lack of space. The principal genera and subgenera are illustrated in Figure 2–4. The unifying characteristics of this portion of the tribe Spiraeeae are indicated in the legend of Table 1 and distinguishing characters of each genus or subgenus are also indicated in the table. These data formed the basis of various data sets using 18 to 22 characters for eight taxa with variable data being scored as 0, 1 or 0, 1, 2. Phenograms prepared from these data and various modified and/or reduced data sets based on Euclidean distance and UPGMA clustering on the PHYSYS program on the California State University central Cyber computer varied in particulars but generally conformed to the tree shown in Figure 1a, which can be compared to one derived by hand from a simple similarity matrix totaling all positive and negative matches (Fig. 1b). In all cases the greatest similarity was shown between *Sibiraea* and the subgenera of *Spiraea*. *Aruncus* showed greatest similarity with these taxa but at a lower level. A second group consists of four North American taxa but no similarity between the taxa exceeded 75 percent. Of these *Kelseya* and *Petrophytum* usually exhibited greatest phenetic similarity, with *Luetkea* usually showing slightly less similarity and the proposed new genus *Xerospiraea* the least similarity. In other data sets *Luetkea* and *Xerospiraea* both joined into *Kelseya* and *Petrophytum* at about the same degree of similarity. The *Spiraea* group and the *Kelseya-Luetkea-Petrophytum-Xerospirea* groups always joined below the 50 percent similarity level. All data sets showed the same basic similarities but levels of similarities, of course, were dependent on the number of characters used that were unique to one species. All phenetic analyses show that *Xerospiraea* is more similar to *Petrophytum*, *Kelseya*, and *Luetkea* than to *Spiraea* and its associates.

The same basic character set used in phenetic analyses, but excluding the genus *Aruncus*, was polarized for use in a series of cladistic analyses. Choosing the proper outgroup was a problem, but it was felt that characters found within other shrubby Spireoideae such as *Holodiscus* and *Physocarpus* of the tribe Neillieae approached that which could be considered plesiomorphic although many character states found in these genera are considered advanced. The reduced and specialized growth habits and flowers of taxa such as *Kelseya* and its associates also provided guidelines for establishment of polarity, as it would hardly seem logical to consider cushionlike xeromorphic plants as *Kelseya* and *Petrophytum* as progeners of mesic shrubby spiraeas. Characters were omitted in the cladistic analyses if questions regarding polarity could not be resolved. The data were analyzed with the WAG-

Table 1. Character states of tribe Spiraeae, subfamily Spiraeoideae (Rosaceae), *Aruncus* excepted.*

CHARACTER	SPIRAEA Subg. Spiraea	SPIRAEA Subg. Metaspiraea	SIBIRAEA	PETROPHYTUM	KELSEYA	LUETKEA	XEROSPIRAEA
Growth Habit	Erect shrubs, rhizomes present, deciduous.	Erect shrubs, rhizomes absent, deciduous.	Erect shrubs, rhizomes present, Deciduous.	Prostrate shrubs, rhizomes absent, evergreen.	Cushion plants, rhizomes absent, evergreen.	Trailing herbs, rhizomes present, evergreen.	Thorny shrubs, rhizomes present, evrgreen.
Vegetative Shoots	Long shoots only.	Long shoots with some short shoots.	Long shoots only.	Short shoots.	Short shoots.	Short shoots.	Long shoots with axillary short shoots.
Leaves	Simple, serrate, dorsiventral.	Simple serrate or entire, dorsi-ventral.	Simple, entire, large, dorsiventral.	Simple, entire, isolateral.	Simple, entire, isolateral.	Bi-triternate, lobes entire, dorsiventral.	Simple, entire, rarely toothed, isolateral.
Inflorescences	Paniculate, terminating new shoots from old stems or base of plant.	Simple corymbs, terminating axillary shoots.	Paniculate, terminating new shoots from old stems or base of plant.	Simple racemes or with groups of racemes.	Solitary on short pedicels.	Simple racemes with leafy bracts.	Simple racemes, persisting at stem tip as thorns or of panicles of racemes.
Flowers	Perfect.	Perfect.	Polygamodioecious.	Perfect.	Perfect.	Perfect.	Perfect.
Hypanthium Nectary	On lobed disk at rim.	On larger lobed at rim.	10 very large lobes at rim.	On slightly lobed disk at rim.	On slightly raised smooth disk on rim.	With separate lobes below rim.	On upper hypanthium surface, no lobes.
Bracts	1-2, on pedicels.	1-2, on pedicels.	1, on pedicels.	1(-2) on pedicels.	Obscure.	1, on pedicels.	1 on pedicels, 2 on hypanthium.
Petals	White to reddish, obovate.	White, obovate.	White, obovate.	White, narrowly obovate.	Pink, narrowly obovate.	White, obovate.	White, obovate.
Stamen Number	20-40	20-40	19-22	20-40	7-12	16-20	15-20
Ovary Number	5(4-6)	5(4-6)	5(-6)	5(3-7)	3-4(-5)	5(4-6)	2-3(-5)
Ovules Per Ovary	5-6	6-8	5(-6)	2(-4)	3(2-5)	4-6	2
Fruit Dehiscence	Ventral.	Ventral.	Ventral.	Ventral-dorsal.	Ventral-dorsal.	Ventral-dorsal.	Ventral-dorsal.
Outer Seed Coat Extension	Slight.	Slight.	Slight.	Slight.	Slight.	Strong.	Slight.
Seed Number	2-4	2-8	2-4	1-2	1-4	2-5	1(-2)
Location	Temperate N.A. with 1 sp. also in Asia.	Asian, European.	Asian.	Limestone areas, Ore., S.Dak., s. to s. Calif., cen. Coah.	Limestone crevices, rare in mts. of Mont., Ida., Wyo.	Subalpine-alpine zones, Alas. to n. Calif., Ida. Mont.	Limestone, mountains of Pue., Oax. Ver., Hid., Dgo., Coah.

* Characteristics in common include: leaves alternate, exstipulate, enlarged and more or less decurrent at base; flowers perigynous, 5-merous, in terminal or axillary inflorescences; hypanthia obconic-hemispherical, smooth, entire or variously lobed with nectaries on upper rim, mostly sericeous at base inside; carpels alternating with sepals; ovules pendulous, epitropous; seeds fusiform; seed coat reddish brown, membranous; endosperm absent or scanty.

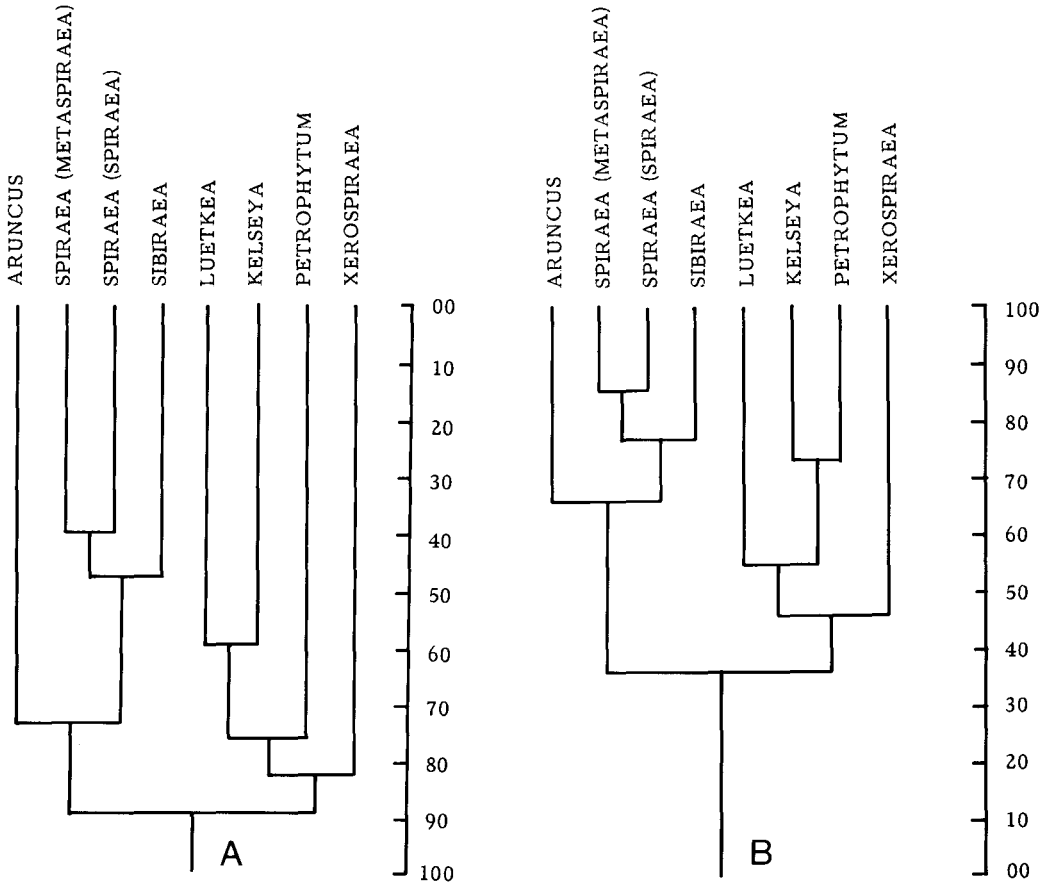


Fig. 1. Phenograms of genera of the tribe Spiraecae.—A. Derived from Euclidean distance and UPGMA clustering by PHYSYS program.—B. Derived from a simple similarity matrix formed by percent of total positive and negative matches.

NER option of PHYSYS. They presented an array of similar trees showing minor differences but with overall consistencies (C-index) in the high 70s to low 80s. This array of data was used as a guide to construct, by hand and by use of an algorithm of grouping by synapomorphies, the cladogram shown in Figure 2 that is consistent with a cladogram configuration commonly obtained from PHYSYS. These data indicate that *Spiraea* appears basal to the group, *Sibiraea* appears as diverged from the subgenus *Spiraea*, while *Petrophytum*, *Kelseya*, *Luetkea* and the proposed new genus *Xerospiraea* are shown to be derived from a common ancestor more closely related to the subgenus *Metaspiraea*. While in the various computer-run cladograms topologies between the four genera within this lineage were somewhat variable, in all analyses *Xerospiraea* always grouped with *Luetkea*, *Petrophytum* and *Kelseya*.

DISCUSSION

The xeromorphic taxa (*Petrophytum*, *Kelseya*, *Luetkea*, and the proposed new genus *Xerospiraea*) all appear most closely related to the Old World subgenus

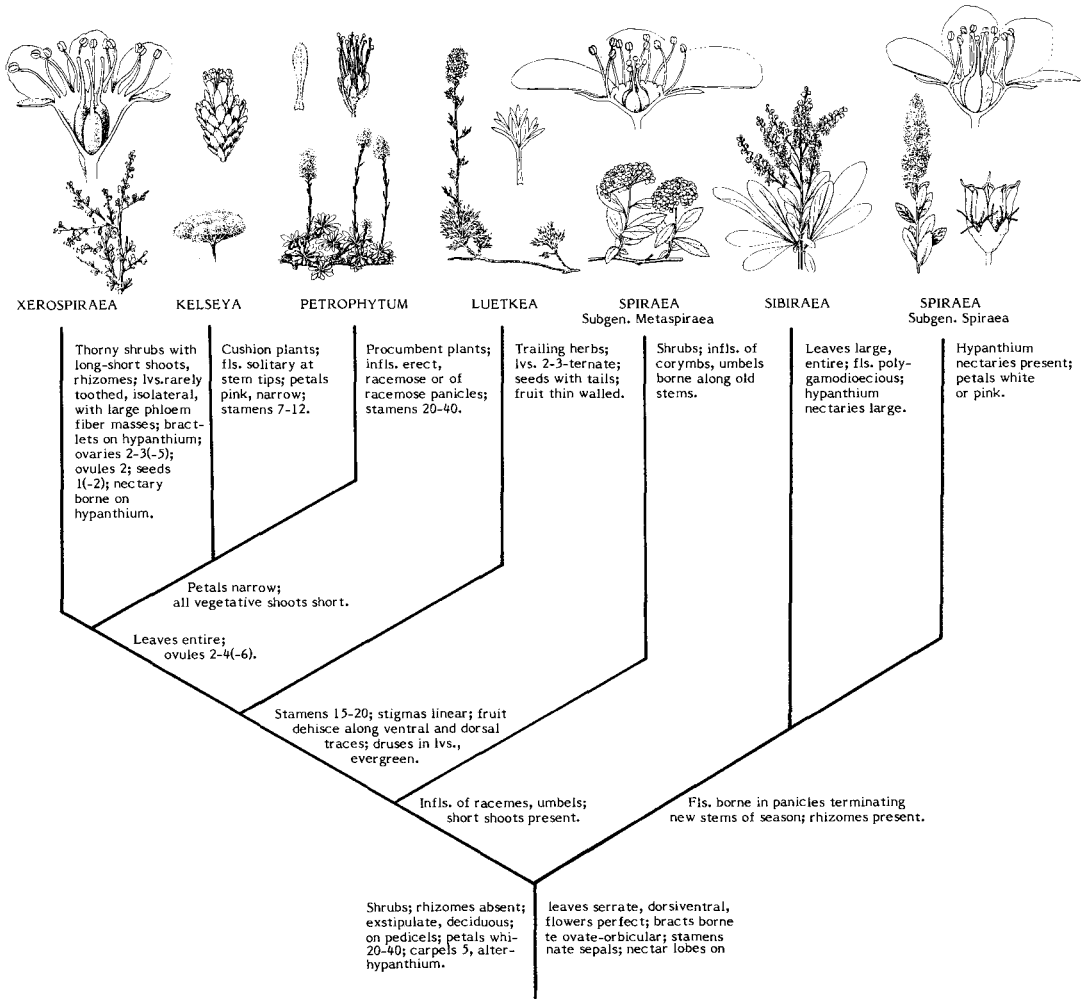


Fig. 2. Cladogram showing putative affinities of six selected genera of the tribe Spiraeeae. Basal characters listed at base of tree, synapomorphic traits are listed in lower portion of tree and autapomorphic traits are listed at top of tree branches. Note that *Petrophytum* and *Kelseya* can be rotated to the left of *Xerospiraea*. Representatives of all genera and subgenera of *Spiraea* are illustrated above.

Metaspiraea of *Spiraea*. *Sibiraea*, on the other hand, appears most closely related to *Spiraea* subgenus *Spiraea*. To preserve monophyly, all of these taxa must either be included in the same taxon (i.e., the genus *Spiraea*) or, if these genera are to be recognized, the two subgenera of *Spiraea* must be raised to the rank of genus. While it may be true that each of these two subgenera, in this relatively old and widespread genus, has given rise to diverse groups and should be placed in separate genera, it is not the intention of this paper to make major nomenclatural changes in the genus *Spiraea*. The subgenera of *Spiraea* differ in a few characteristics involving origin and types of inflorescences, presence or absence of rhizomes, and size and structure of nectaries on the hypanthium rim (see Table 1). In contrast, the two subgenera are similar in nearly all other floral and fruiting characteristics. I also do not see logic in combining the diverse *Luetkea* and *Kelseya* into *Spiraea*

s.l. I therefore find it necessary to accept the evidence indicated in the above analysis, which indicates that *Xerospiraea* is more closely related to *Petrophytum*, *Kelseya*, and *Luetkea* than to *Spiraea*, but I reject, at the present time, further subdivisions of *Spiraea*.

In this situation, if the old and diverse genus *Spiraea* is to be retained as a monophyletic group, it becomes a phylogenetic "black hole" that sucks in all the various derivative groups that may have evolved from its diverse branches as they adapted to various environments.

Megafossils of spiraeas are known from early Oligocene in Japan (Tonai 1972), which indicates that the genus is relatively old. This would encourage an interpretation that the Mexican *Xerospiraea* as well as *Petrophytum*, *Kelseya*, and *Luetkea* represent New World derivatives or progenitors to the otherwise Old World *Spiraea* subgenus *Metaspiraea*. These New World derivatives have then adapted to drying or cooler climates that developed in the post Oligocene in western North America eventually becoming part of the Madro-Tertiary Geoflora and undergoing strong modifications as they adapted to specialized dry habitats. In contrast, other native North American spiraeas of subgenus *Spiraea* appear to represent a separate more mesic lineage.

The genus *Xerospiraea* is herein described as new. It includes one species.

***Xerospiraea* Henrickson, gen. nov.**

Spiraea subgenus *Homoiospiraea* C. K. Schneider. *Illust. Handb. der Laubholz.* 1:484. 1905.

Frutices aculeati, rhizomatosi; ramis divergentibus; caules heteroblastici; folia simplicia, alterna et fasciculata, spathulata, isolateralia, exstipulata, integra, apicibus obtuso-rotundatis apiculata. Inflorescentiae terminales, in caulibus elongatis portatae, racemosae; pedicelli 3-bracteati, bracteis hypanthio adnatis. Flores bisexuales, perigyni; hypanthium obconicum, interne nectariferum (sine disco distincto); sepala 5, valvata; petala 5, ovata, alba; stamina 15–20, filamenta subulata, ad basem dilatata plus minusve connata; carpella 2–3(–5) libera; styli subterminali, glabri; ovula 2, pendulosa epitropa. Fructus erectus, fusiformis, coriaceus plus minusve follicularis sed simul ventraliter et dorsaliter dehiscens; semina 1–2.

Divergently-branched, thorny, rhizomatous shrubs; stems heteroblastic; leaves simple, alternate and in fascicles, spatulate, isolateral, exstipulate, entire, tip obtuse-rounded, apiculate. Inflorescence of lateral and terminal leafy-based racemes or panicles of racemes. Flowers perfect, perigynous, hypanthium obconic, nectariferous along inner margin (a distinct nectariferous disk absent); sepals 5, valvate; petals 5, ovate, white; stamens 15–20, filaments subulate, dilated and slightly connate at base; ovaries 2–3(–5), free; styles subterminal, glabrous; ovules 2, epitropic. Fruit erect, fusiform, coriaceous, dehiscent along ventral and part way along dorsal traces; seeds 1–2 per carpel. With 1 species.

***Xerospiraea hartwegiana* (Rydb.) Henrickson, comb. nov.**

Spiraea parvifolia Benth. *Plantae Hartwegianae*, 36. 1840 [*nom. illegit.* (a homonym) I.C.B.N. Arts. 64, 72 et al.], non *S. parvifolia* Rafinesque, *New Fl.* (3):63. 1838; *Spiraea hartwegiana* Rydb. *N. Am. Fl.* 22(3):246. 1900.—TYPE: México: Puebla: Puente de Dios, a little shrub 3–4 ft high. 1839. *Hartweg 284*. Holotype: K; isotype: (fragment of holotype) NY! *Spiraea northcraftii* I. M. Johnston. *J. Arnold Arbor.* 24:324. 1943.—TYPE: México: Durango: Summit of Mt. Jimulco, 13 kilo. e. of Jimulco, woodland association with oak, pine, juniper, thick underbrush, 3100 m, 29 Jun 1941, L. R. Stanford, K. L. Retherford and R. D. Northcraft 115. Holotype: GH!, Isotype NY!.

Intricately branched, thorny, calciphilous, colonial shrubs 2–9(–13) dm tall, spreading by woody rhizomes; young stems sparsely puberulent-hirtellous, soon glabrate, reddish brown; older stems with gray, fissured bark. Leaves simple, alternate and in axillary fascicles of 5–20, spatulate, 3–9(–13) mm long, (0.8–)1–3(–4.5) mm wide, obtuse-rounded, distinctly apiculate at tip, narrowly cuneate, short petiolate above a somewhat thickened, clasping, ciliate base, entire, rarely with 1–few acute marginal teeth, glabrous, gray-green to green, firm, isolateral, internally with thick masses of fibers along mid and secondary veins. Inflorescences terminating divergent, lateral woody long shoots, racemose or shortened into simple corymbs or branched into panicles of racemes, 5–10(–25)-flowered; pedicels 1–2 mm long, with 3 reduced, lanceolate to subulate bracts 1–2(–3) mm long, uppermost bractlets reduced, adnate to hypanthium; flowering shoots and pedicels becoming woody, persisting as thorns. Flowers complete, perigynous, 5.5–8 mm in diameter; hypanthium obconic, 1–2 mm high, 1.5–2.5 mm wide, green or tinged with maroon-red, glabrous to pubescent-hirtellous outside, sericeous at base or in lower half, nectariferous and yellowish-gold in lower half inside; sepals 5, deltate-ovate, valvate in bud, 1–1.9 mm long, 0.7–1.6 mm broad at base, acute to strongly apiculate, erect-spreading, glabrous to sparsely puberulent outside, villous near tip or nearly throughout inside, persistent; petals 5, ovate-orbicular, white, entire to erose, (1.2–)1.5–2(–3) mm long, (0.9–)1–1.5(–3) mm wide, briefly clawed at base; stamens 15–20, filaments white, 1–1.5(–2.2) mm long, dilated and joined together at base forming a short rim at edge of hypanthium, glabrous; anthers orbicular, 2-lobed, emarginate at both ends, 0.4–0.5 mm long, yellow gold; carpels 2–3 (4–5 in 1 collection), separate, radially compressed, ovoid, villous along ventral trace, otherwise glabrous; styles subterminal, 1–1.7 mm long, stigmatic at tips; ovules 2, pendulous. Fruit erect, coriaceous, each dehiscing along ventral and distal portion of dorsal sutures, 2.2–3 mm long, 0.9–1 mm wide; seeds solitary, fusiform-lanceoloid, 1.2–1.5 mm long, 0.5–0.6 mm wide; pericarp thin, reddish brown, smooth; endosperm absent, radicle inferior. Chromosome number $n = 9$ (R. Hilsenbeck, unpublished) (Fig. 3, 4).

Additional collections.—MEXICO. PUEBLA: La Cañada, 5 Aug 1897, *C. G. Pringle 6774* [ENCB, GH, LL (2 sheets), TEX]; 11 km despues de Cañada Morelos, por la carretera a Tecamachalco, 16 Jan 1981, *J. L. Villaseñor Rios et al. 115* (ENCB); 6 km al NW de Villa Morelos, sobre carretera a Techamchalco, 2350 m, 3 Feb 1974, *Rzedowski 31680* (ENCB); 30 km SW de Tehuacan hacia Esperanza, 31 Aug 1979, *F. Chiang C. et al. 250* (MEXU); 5 km al NE de San Nicolás Tepóztitlan, 2060 m, 24 Aug 1980, *F. González-Medrano 1417* (MEXU); 4 km NE de Tecamachalco, 2150 m, 1 May 1980, *F. González-Medrano et al. 918*; Cerro de Matzize, Jun 1908, *C. A. Purpus 2587* (GH, NY).—OAXACA: Vicinity of San Luis Tultitlanapa, Puebla near Oaxaca, Las Naranjos, Aug 1908, *C. A. Purpus 2587* (GH, NY); Camino El Carraizal, Macuiltiaquis, 1090 m, 29 Aug 1980, *R. Lucero L-70* (ENCB).—VERACRUZ: Cerros calizos al SW de Alchichica, cerca de limite con el estado de Puebla, 16 Jun 1968, *C. H. Ramos 174* (GH, MEXU); Cerros calizos entre Alchichica y Totalco, 12 Jul 1969, *C. H. Ramos A., F. González M. 298* (MEXU).—HIDALGO: 2 km al NE de Molanquito, Mpio. Cardonal, 26 Feb 1977, *P. Hiriart, A. Castellanos y O. Tellec 81* (MEXU); 2 km al W de Cardonal, Mpio. Cardonal, 1 May 1975, *F. González-Medrano et al. 8875* (MEXU).—DURANGO: Northwestern third of Sierra del Rosario; near 25°42'–45'N lat, 103°57'–104°00'W long, 1800–2655 m, 25 Jun 1973, *M. C. Johnston, F. Chiang C., and T. L. Wendt 11460* (TEX); N end of Sierra del Rosario about 20 km crowflight SW of Mapimí, near 25°43'–45'N lat, 103°57'–104°00'W long, 1800–2600 m, 2 Nov 1972, *T. L. Wendt, F. Chiang and M. C. Johnston 10010* (LL).—COAHUILA: 11 (air) miles WNW of Cuatro Ciénegas, Sierra de la Madera, above Cañon de la Hacienda, near 27°03'N lat, 102°24'W long, 8600 ft, 27 Sep 1973, *J. Henrickson 13602* (LL); Sierra de la Madera, along crest of range near head

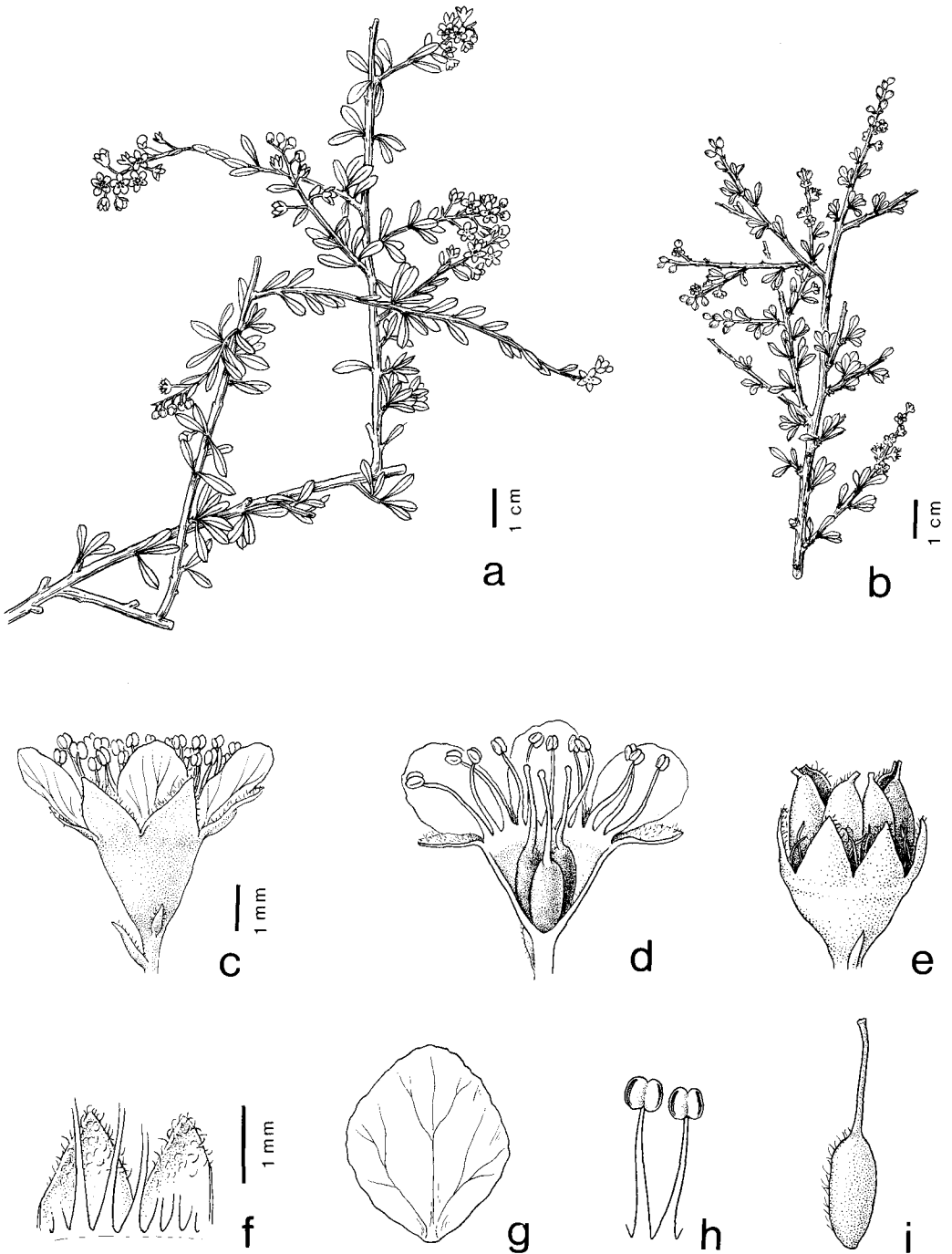


Fig. 3. *Xerospiraea hartwegiana*.—a-b. Growth habit.—a. Plants from Puebla tend to be taller, with more slender, elongate branches [copied from a portion of a pencil drawing of the holotype specimen from K located at NY and referred to by Rydberg (1908)].—b. Plant from the Sierra de la Madera in central Coahuila showing smaller, more branched habit (*Wendt and Lott 6.6A, LL*).—c-i.

of N-draining Cañon del Invierno (C. El Infiernillo), near 27°04'N lat, 102°23'W long, 2725 m, 28 Aug 1977, *T. Wendt and E. Lott 636A* (LL); Sierra de la Madera, Cañon de la Barrica, S cliffs of Picacho El Pajarito, near 27°01'N lat, 102°23'W long, 2300 m, 20 Aug 1975, *T. Wendt and E. Lott 1222* (LL, TEX); Sierra de la Madera, Rincon de las Derrumbes, near 27°01'W lat, 102°26'W long, 2080 m, *T. Wendt and E. Lott 1435* (TEX); 40 km WNW of Cuatro Ciénegas, along crest of limestone Sierra de la Madera, above cañon just W of Cañon de la Hacienda, near 27°03'N lat, 102°27'W long, 2700 m, 28 Sep 1980, *J. Henrickson and P. Bekey 18886* (TEX).

The species is known from a number of widely scattered populations in the mountains of Oaxaca, Puebla, and adjacent Veracruz, Hidalgo, eastern Durango, and Coahuila. This appears to be a relictual distribution pattern like that of the distinctive *Setchellanthus caeruleus* T. S. Brandeg. of the Capparaceae (Axelrod 1979). Each of these populations exhibits some distinguishing characteristics. Collections from Puebla and Oaxaca generally are taller, more slender stemmed with larger leaves and more strongly branched inflorescences (Fig. 3a). The *González-Medrano et al. 8875* collection from Hidalgo differs from all other collections in having four or five carpels per flower. Considerable intrapopulation variation exists in average leaf size, vestiture (i.e., whether young stems are glabrous or hirtellous, or bracts are glabrous or villous on the inner surfaces). The collection from the Sierra de Jimulco upon which I. M. Johnston based his *Spiraea northcraftii* was noted by Johnston (1943) to be distinctly smaller than specimens from southern Mexico but its small flowers exhibit only quantitative differences from those on the fragment of the type of *S. parvifolia* (Hartweg 285 at NY). The collection by M. C. Johnston et al. from the nearby Sierra del Rosario in eastern Durango, however, have larger, more hirtellous flowers, but with more acute sepals. These differences are considered in part due to genetic drift. The collections from the Sierra de la Madera in central Coahuila are relatively uniform all across the south-facing crest of the range, where it is encountered wherever the proper habitat of exposed limestone outcroppings occur (Fig. 4b). It is there associated with *Cercocarpus montanus* Raf. var. *paucidentatus* (Wats.) F. Martin, *Cupressus arizonicus* Greene, *Nolina cespitifera* Trel., *Comarostaphylis polifolia* (H.B.K.) Zucc. ssp. *coahuilensis* Henrickson, *Allium kunthii* G. Don, *Petrophytum caespitosum* (Nutt.) Rydb., *Quercus greggii* (D.C.) Trel., and *Rhus virens* Lindh. ex Gray, etc. Generally, the collections from the Chihuahuan Desert Region exhibit smaller-sized leaves and inflorescences (Fig. 3b) in comparison to the southern Mexican populations. But no qualitative differences exist that would support recognition of these populations as a distinct taxon.

While *Xerospiraea* is similar to *Spiraea* in its shrubby habit, it is distinguished by a number of unique characteristics (Table 1; Fig. 3, 4). It is the only genus of tribe Spiraeae that has isolateral leaves (Fig. 4e). Major veins also have very

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Flowers and flower parts drawn from greenhouse-grown plants of *Henrickson and Bekey 18886* (TEX).—c. External view of flower showing sepals, petals, and bracteoles at base of hypanthium.—d. Longitudinal section of flower showing ovaries and lack of any nectary lobes at rim of hypanthium.—e. Mature fruit showing three carpels that have dehisced along ventral trace and part way along dorsal trace.—f. Inner view of sepals showing hairs and filaments.—g. Petal.—h. Anthers and filaments that are partially united at base.—i. Carpel showing linear style. (Scale in c holds for c–e; in f holds for f–i. Illustration by Bobbi Angell.)

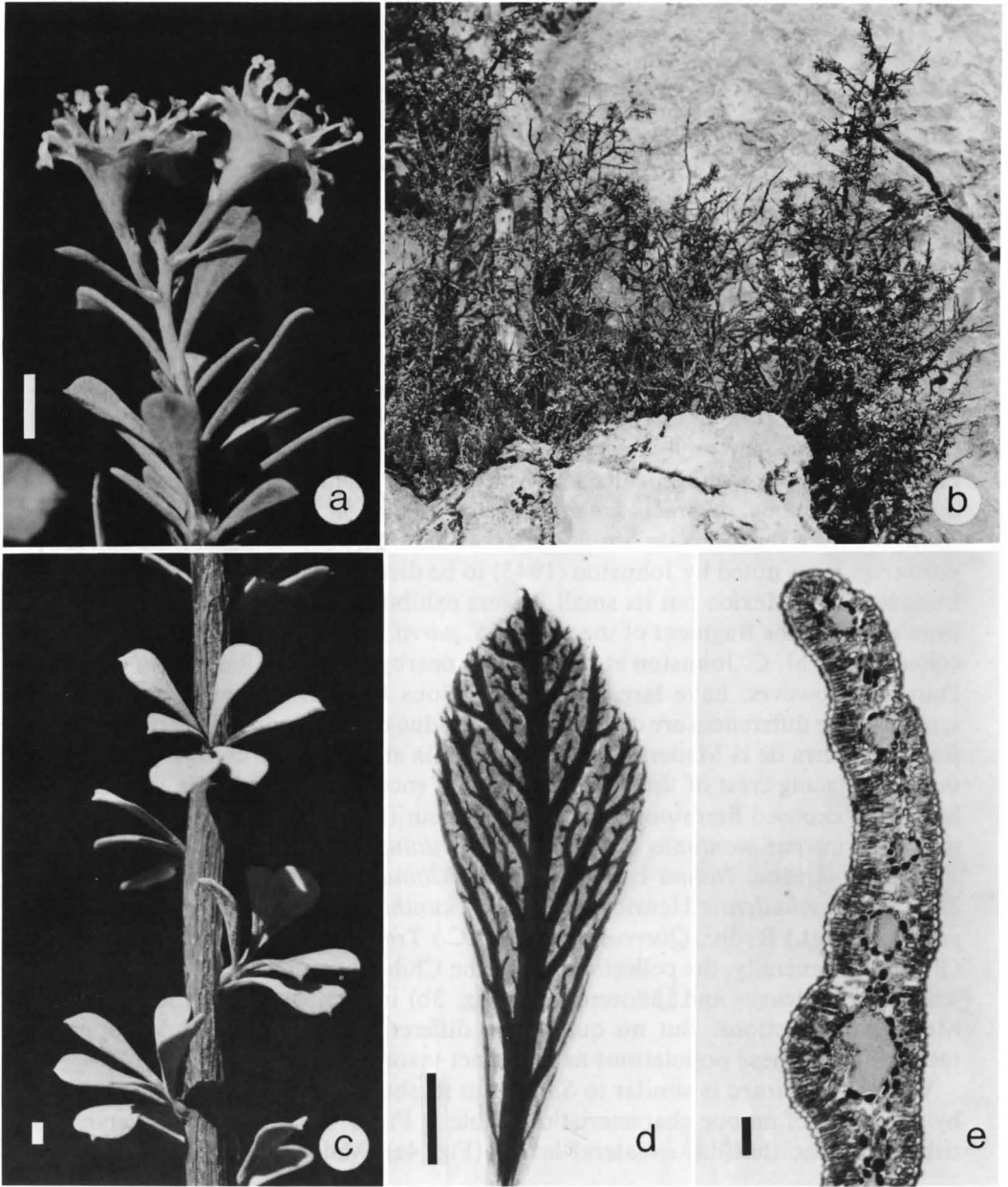


Fig. 4. *Xerospiraea hartwegiana*.—a. Flowers and stem tips of cultivated plant showing leaves, hypanthium, and spreading sepals.—b. Growth habit of plant spreading by rhizomes between limestone rocks at crest of Sierra de la Madera in central Coahuila. Plant is about 30 cm tall (*Henrickson and Bekey 18886*).—c. Stem of cultivated plant showing fascicles of spatulate, apiculate leaves.—d. Leaf clearing showing pattern of fibers that parallel major veins.—e. Cross section of leaf showing isolateral structure and large bundles of phloem fibers along veins. (Vertical bars in a, c, d = 1 mm; in e = 0.1 mm.)

large strands of phloem fibers that can be seen in both clearings (Fig. 4d) and cross sections (Fig. 4e). Unlike other taxa considered here, the upper bracteoles are borne on the hypanthium (Fig. 3c), the hypanthium is nectariferous along the inner surface—a distinct nectariferous rim or series of lobes is not present, and ovary number is usually reduced to 2–3 (Fig. 3d). In growth habit, several species of *Spiraea* subgenus *Metaspiraea* (*S. canescens* D. Don, *S. hypericifolia* and others) are somewhat similar to *Xerospiraea* having narrow, spatulate, entire, fasciculate leaves. But the *Spiraea* species consistently differ in their enlarged nectaries along the inner hypanthium rim, dorsiventral leaf structure, bracts only on pedicels (not on the hypanthium) and flowers with five carpels, each with 5–6 ovules and 2–4 seeds per fruit (see Table 1).

The chromosome number of $n = 9$ for *Xerospiraea* is the same as that reported in McArthur and Sanderson (1985) for *Kelseya uniflora* and occurring in *Luetkea*, *Petrophytum*, and through most of *Spiraea* [see McArthur and Sanderson (1985)].

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