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Taxonomic Revision of the Genus Fendlera (Hydrangeaceae)

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Abstract: Fendlera is treated as having five closely related species, four of which have been recognized by previous authors, and F. tamaulipana B. L. Turner, sp. nov., a newly described taxon from northeastern Mexico. Except for the latter, the species are all to some extent sympatric but their populations are relatively uniform and their diagnostic characters do not suggest that intergradation in a populational sense occurs. The taxa do not normally occur together, although they may occur in close proximity and probably do occasionally hybridize, this perhaps confounding taxonomic interpretations of the genus by previous workers. The five species recognized are: F. rupicola, so far as known, confined to three small populations in central Texas; F. falcata, occurring in northwestern Mexico and the southwestern United States; F. wrightii, having a distribution similar to that of the foregoing; F. linearis (including F. rigida), occurring mostly in northeastern Mexico and closely adjacent Trans-Pecos, Texas; and the newly described, F. tamaulipana, known by three collections from the vicinity of Miquihuana, Tamaulipas, Mexico. Distribution maps are provided for all of the species concerned.

Keywords: Fendlera, Hydrangeaceae.

The genus Fendlera was erected by Engelmann and Gray in 1852 with the description of F. rupicola in Plantae Wrightianae from collections made by Lindheimer along the Guadalupe River in Comal County, Texas. At the same time they also recognized a var. wrightii, this based upon collections made by Charles Wright in western Texas. The latter was elevated to specific rank by Heller in 1895. Thornber, in 1913, added two additional species, F. falcata and F. tomentosa. The latter taxon is treated as synonymous with F. wrightii in the present treatment. Rehder, in 1920, added F. linearis, a species largely confined to Mexico, the type from near Monterrey, Nuevo Leon. Johnston, in 1941, proposed an additional Mexican species, F. rigida, the latter treated here-in as synonymous with F. linearis. Four of the above proposed taxa are recognized as valid species. A fifth species, F. tamaulipana, is proposed in the treatment that follows.

Generic Relationships

Fendlera was initially placed in the large family Saxifragaceae but most recent workers position the genus in the Hydrangeaceae (e.g., Soltis et al., 1995; Holmgren and Holmgren, 1997) where its relationships appears to be with or near Philadelphus (in my opinion, based largely upon habitat, floral and ovarian features as well as ecogeographical considerations). I hypothesize that the present day, largely xerophytic, Fendlera was derived from the same ancestor as members of the large, mainly mesophytic genus, Philadelphus, becoming progressively modified as to stamen number (reduced from numerous to a set number, mostly eight), and filament modification (from terete to flattened with extended apical appendages). Soltis et al. (1995), however, using DNA (rbcL sequence data), suggest that Fendlera and Jamesia are sister taxa to the rest of the 16 or more genera of the Hydrangeaceae; following Fendlera and Jamesia, they found the remaining hydrangeoids to cluster into two large subclades that closely parallel the traditional division of the family into the tribes Philadelphoe and Hydrangeae.

Chromosome Numbers

Chromosome counts are available for only a single species of Fendlera, this re-
ported as *F. wrightii* (Fedorov, 1969). Two counts are reported in the compendium, one by Sax in 1931, listing a count of $2n = 22$, and another by Hamel in 1953, also reporting a count of $2n = 22$. Sax (1931) provided a camera lucida drawing of metaphase meiotic chromosomes of *F. wrightii* showing $n = 11$ pairs. He also noted that the plants concerned were obtained from the grounds of the Arnold Arboretum. I have not encountered vouchers for any of these early counts.

**SPECIES CONCEPTS**

I am an avid proponent of the biological species concept as elucidated by Mayr (1969, 1992), Levine (1981), and numerous other workers. While some botanical workers believe that “Plant species lack reality, cohesion, independence, and simple evolutionary or ecological values” (Levin, 1979), my many years of field work has led me to the conclusion that plant species, for the most part, are very much like animal species and with appropriate field work can be recognized as populational units having morphoecogeographic integrity. Mayr (1992) applied the biological species concept to plant populations at the local flora level and concluded that the concept applied equally well to plant taxa. I concur with Mayr’s assessment.

I freely admit that there are alternative ways to treat the five taxa recognized herein. For example, one might recognize two widespread species: 1) *F. rupicola*, with three varietal taxa; and 2) *F. linears* with but two varietal taxa. I have given reasons for their treatment as biological species under the taxa concerned. For a more extended account of my views on infraspecific categories and their hierarchical ranks see Turner and Nesom (2000).

The phyletic relationships of the five taxa of *Fendlera* recognized here, as inferred from morphoecogeographical considerations, is summarized in Fig. 1. I am reasonably sure that these relationships will be shored up by appropriate DNA studies.

**FENDLERA** Engelm. & A. Gray

Much-branched, usually thorny or “spinescent” shrubs (except for *F. tamaulipana*) mostly 1–3 m high. Leaves simple, opposite, short-petiolate to nearly sessile, entire, the blades 1–3 nerved, ovate to falcate or linear, mostly 1–3(4) cm long, 1–10 mm wide, variously pubescent above and below, rarely not. Flowers showy, mostly in clusters of 2 or 3, the pedicels 2–25 mm long; hypanthium narrowly to broadly turbinate; sepals 4, deltate to narrowly triangular; petals 4, white or tinged with pink or red, clawed, the blades broadly ovate to rhombic and having erose margins; stamens mostly 8, the filaments flattened and having lateral lobes which extend beyond the anthers, the latter apically appendaged; ovary about half inferior, 4–celled; styles 4, distinct or somewhat united below. Fruit a septicidal capsule, the seeds relatively few in each cell (mostly 1–6). Base chromosome number, $x = 11$. Type species, *Fendlera rupicola* Engelm. & A. Gray
The genus is named for Augustus Fendler (1813–1883), German-born naturalist of both North and South America, and one of the earliest plant collectors in the southwestern U.S.A. (mostly in New Mexico during the period 1846–1850).

**KEY TO SPECIES**

1. Leaves linear, 1–2 mm wide, the margins completely enrolled
2. Intricately branched "spinesent" or thorny shrubs mostly 0.5–2.0 m high; leaves mostly 1.0–1.5 mm wide; northcentral Mexico and closely adjacent U.S.A ........ 4. *F. linearis*
2. Strict, sparsely branched, shrubs mostly 1.5–4.0 m high; leaves 1.5–2.0 mm wide; Tamaulipas, Mexico, vicinity of Miquihuana ...........

1. Leaves narrowly lanceolate or falcate to ovate, mostly 2–10 mm wide, the margins incompletely enrolled, if at all
3. Upper surface of leaves glabrous; lower surfaces sparsely strigose; known from only three populations in Central Texas .... 1. *F. rupicola*
3. Upper surface to some extent pubescent; lower surfaces moderately to densely pubescent; widespread in the southwestern United States and northern Mexico
4. Undersurfaces of leaves with a single layer of coarse, appressed or ascending hairs ....

4. Undersurfaces of leaves with two layers of vestiture, a lower layer of minute frizzly or crinkled hairs, this overlain by a much coarser vestiture of appressed or ascending hairs ....... 3. *F. wrightii* 3. *F. falkata*

1. *FENDLERA RUPICOLA* Engelm. & A. Gray in A. Gray, Pl. Wright. 1: 77. 1852. (Fig. 2)

*Fendlera rupicola* var. *lindheimeri* A. Gray, Pl. Wright. 1: 77. 1852.

**TYPE:** United States, Texas: Comal Co., among "perpendicular rocks" along the upper Guadalupe River, ca. six miles above New Braunfels, May 1850, *F. Lindheimer 257* (HOLOTYPE: GH!; ISOTYPES: MO!, NY!, US!).
Lindheimer apparently first collected this species (in fruit only) in May of 1850. However, it was noted that the taxon concerned flowered “in April,” apparently a surmise provided by Engelmann, who transmitted the plants, since the authors note in the protologue itself that the illustration provided with the original description was comprised of fruiting material of var. *rupicola* (= var. *lindheimeri*) and flowering material of var. *wrightii*, adequate flowering material of var. *rupicola* not being available. Indeed, in the second volume of *Pl. Wright.* (1853, p. 61) the authors duly state that “Specimens [of var. *rupicola*] recently communicated by Lindheimer, in full flower, have their virgate branches loaded with the white blossoms, showing that the plant would be very ornamental in cultivation.”

Much-branched, brittle-stemmed SHRUBS mostly (0.5)1.0–2.5(3.0) m tall; vernal LEAVES lanceolate, 1–20 mm long, 3–6 mm wide, the upper surfaces glabrous, the lower, surfaces sparsely strigose. Vernal FLOWERS as described for the genus, being mostly 4–5 cm across the extended petals.

**Representative Specimens Examined:** UNITED STATES. TEXAS: Bandera Co.: Bandera [Bendera] Pass, Jun 1884, Reverchon 1577 (A, NY [year given as 1885], MO); Bear Dog Ranch, near west fork of Medina River, ca. 7 mi SW of Medina, ca. 600 m, 1 Apr 1991, Simpson & Tracy 4191 (SMU). Comal Co.: Comanche Spring, New Braunfels, Mar 1851, Lindheimer 793, 794 (TEX).

As noted above, this species is very rare and is known to date by only three populations (including the type), all collected within a 30 mile radius (Fig. 2). Other than material from the type locality, which has not since been re-collected, *F. rupicola* has been obtained from only two other localities, both in Bandera County: by Julian Reverchon in 1884, at Bandera Pass, a well known, rugged locality in NE Bandera Co., near the Kerr Co. line; and in central Bandera Co. by the late Benny Simpson (1928–1996) in April of 1991. The latter collector was well aware of his significant find, noting on the label itself, “not collected in over 150 years,” (being unaware of the aforementioned Reverchon collection).

*Fendlera rupicola* appears to be most closely related to *F. falcata* of far western Texas, New Mexico and closely adjacent states (Fig. 3), largely based upon their relatively large vernal flowers and sparsely to moderately pubescent leaves, shared characters that distinguish both from *F. wrightii*.

2. **Fendlera falcata** Thornber in Woot. & Standl., Contr. U.S. Natl. Herb. 16: 129. 1913. (Cover, Fig. 3)


**Type:** United States. New Mexico: San Juan Co.: Navajo Indian Reservation, Tunitcha Mts., 8 Aug 1911, P. C. Standley 7806 (HOLOTYPE: US!).

Resembling *F. rupicola*, but the leaves mostly 3–6 times as long as wide (vs 3–4), the upper surfaces to some extent pubescent (vs. glabrous), the lower surfaces mostly moderately to densely strigose (vs. sparsely strigose).

*Fendlera falcata*, like most of the species of its genus, is extremely variable in leaf shape and size. It is especially similar to *F. rupicola*, both sharing large vernal flowers and leaves having mostly a single layer of ascending and/or appressed hairs on the lower surfaces. Unlike *F. rupicola*, however, populations of *F. falcata* are widespread (Fig. 3), usually consisting of numerous individuals.

The latter taxon is partially sympatric with *F. wrightii* (Fig. 4), but only rarely do the plants occur together, if at all, although they may occur in close proximity. In the Trans-Pecos region of Texas populations of *F. falcata* occur at higher elevations than do those of *F. wrightii*. In the Davis Mts. of Jeff
Davis and Brewster counties *F. falcata* occurs mostly in igneous soils from 5000 to 7500 ft., whilst *F. wrightii* occurs at lower elevations in mostly rocky limestone soils from 2000 to 5000 ft. In Jeff Davis Co., numerous populations of *F. falcata* occur (LL, SRSC, TEX) but only a single population of *F. wrightii* is known, a Cory collection (TAES) from the lower eastern slopes of the Jeff Davis Mts., presumably from limestone outcrops near the Reeves County line. Again, numerous populations of *F. falcata* occur in the Guadalupe Mountains National Park of Culberson Co., mostly at mid-elevations (6000–7500 ft), whilst only two collections of *F. wrightii* are known to occur.
in this massif, these from populations in Dog Canyon from the more northern portions of the Park, one of these reportedly at 4800 ft. (Warnock 23653, SRSC). Actually, the latter collections were presumably collected in the state of New Mexico, Dog Canyon not reaching such low levels in the Park itself. Collections of *F. falcata* have also been made in Dog Canyon, but at much higher elevations (e.g. at 6500 ft, Warnock 21712, SRSC). Indeed, in Culber-son Co. *F. wrightii* occurs in the Delaware, Eagle, Quitman, and Sierra Diablo Mts., all of these much lower than the Guadalupes and none harboring known populations of *F. falcata*.

Early on, I thought that specimens re-ferrable to *F. wrightii* might be but forms of *F. falcata* having unusually pubescent leaves, but examination of populations of both taxa in the field show these to be quite uniform as regards leaf pubescence. Thus, a population of *F. falcata* along Limpia Creek in Jeff Davis Co. (Turner 20-501, TEX) consisting of 100 or more plants along a stretch of 300 meters or more was found to be quite uniform as regards leaf pubescence. Similarly, a population of *F. wrightii* at a much lower elevation along a rocky lime-stone escarpment of the Pecos River in Crockett Co., Texas (Turner 20-401, TEX) was also found to be quite uniform as regards leaf pubescence.

I have not examined populations of *F. falcata* and *F. wrightii* in yet other states but I infer from the numerous collections available that the two taxa occur in a similar fashion to that found in Texas. At least I have not discerned mixed collections of the two, although they occasionally occur in close proximity, most notably in southwestern New Mexico and southeastern Ar-izona. Occasional plants were noted in this region which appeared to approach one or the other species, suggesting that occasional hybridization between the species may have occurred, either past or present. Such plants also occur along the highway south of Pres-cott, Arizona, and more notably in the more northern border regions of Sonora and Chihuahua in northwestern Mexico; I have annotated several or more sheets in the latter region as more or less intermediates between the two species, these cited under *F. wrightii*. Whether this reflects an-cestral or extant hybridization between the taxa concerned, if that, can only be sur-mised.

**Representative Specimens Examined:**


**UNITED STATES. ARIZONA.**


3. **Fendlera wrightii** (Engelm. & A. Gray) A. Heller, Bull. Torrey Bot. Club 24: 537. 1897. (Fig. 4)


**TYPE**: Texas. Val Verde Co.: Crevices of rocks along the San Pedro [Devil’s] River, 7 Nov 1849, C. Wright 228a [field no. 1381]. (LECTOTYPE: GH; ISOLECTOTYPES: GH!, K, NY!).

In their protologue the authors note that the taxon was collected in “July, with old fruit; and a few flowering specimens were gathered on the return in November. (Sparingly distributed as No. 228a). Fine fruiting specimens have also come to hand since our figure was made, in the collection of 1851.” Clearly the description of var. **wrightii** was based upon the elements of several collections and is in need of lectotypification, as called to my attention by W. Kittridge of GH. Holmgren and Holmgren (1997), whom I initially followed, designated Wright 228a (GH) as the holotype, which I adopt here as a suitable lectotype, especially since the type locality is clearly stated.

Similar to F. rupicola but the vernal flowers smaller; upper surfaces of the leaves pubescent (vs glabrous), the under surfaces pubescent with a double layer of hairs, an upper layer of appressed or ascending coarse hairs and a lower layer of minute frizzly hairs (vs sparsely strigose).

Representative Specimens Examined: MEXICO. CHIHUAHUA: Ca. 25 mi S of St. Diego ranch, 1891, Hartman 586 (NY); Mpio. Juarez, Sierra Samalayca, 31 Mar 1985, Worthington 12857 (NY). Sonora: Sierra San Jose, 7 km. SSW of Naco, 30 Oct 1993, Felger 93-585 (ARIZ); Ignimbrite Canyon, 3 km. N of La Brisa, 22 Apr 1984, Martin & Rourke s. n. (ARIZ); Dead Bull Canyon, near Arzipe, 17 Mar 1982, Thompson & Davis 82-36 (ARIZ); Santa Rosa Canyon, near Bavispe, 31 Jul 1938, White 1530 (ARIZ); Arroya de la Galera, 27 Jul 1940, White 3055 (ARIZ); Sierra del Cumarito, 6 Oct 1941, White 4636 (ARIZ, NY); between Santa Rosa Canyon and Bavispe, 20 Jul 1938, White 626 (ARIZ); Rio de Bavispe, Canon del Carricito, 30 Jul 1940, White 3095 (ARIZ); El Rancho del Roble, NE of El Tigre, 2–13 Sep 1941, White 4299 (ARIZ). Most of the afore cited specimens from Sonora are more or less intermediate between F. wrightii and F. falcata, as noted under the latter.


While initially described as a variety of *F. rupicola*, Gray noted in his protologue that "[the two varieties] may belong to distinct species." Heller subsequently elevated var. *wrightii* to specific rank. Most subsequent workers have retained these as only varietally distinct, if that (e.g., Kearney and Peebles, 1951; Holmgren and Holmgren, 1997). Correll and Johnston (1970), however, maintained *F. wrightii*, as did Wooton and Standley (1915), (albeit as the newly described *F. tomentella*). The latter two workers also proposed *F. falcata*, but inexplicably maintained *F. rupicola* as distinct, distinguishing the former from the latter by its usually falcate and nearly glabrous leaves. Leaf shape and glabrousity are very variable in *F. falcata* and I have no hesitation in placing their concept of *F. rupicola* (type materials excluded) into my concept of a widespread highly variable *F. falcata*.

4. **FENDLERA LINEARIS** Rehder, J. Arnold Arb. 1: 72. 1920. (Fig. 5)

**TYPE:** MEXICO. NUEVO LEON: near Monterrey, 17 Jun 1889, C. G. Pringle s. n. (HOLOTYPE: A!).

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**Fig. 5.** Distribution of *Fendlera linearis* (closed circles) and *F. tamaulipana* (open circles).

Intricately branched, usually “spinescent” or thorny, SHRUBS or subshrubs 0.5–2.0 m. high. LEAVES linear, mostly 20–30 mm long, 1.0–1.5 mm wide; petioles mostly 0.5–1.0 mm long; margins completely enrolled, beneath these a dense frizzly or plumose-branched tomentum not readily observed unless the margins are upraised; surfaces sparsely to moderately pubescent with coarse appressed hairs, especially along the margins; apices short-apiculate. Flowers and fruits highly variable as to size, the FLOWERS mostly 1–2 cm across the expanded petals, the CAPSULES ovate, mostly 5–6 mm wide and 6–12 mm high.


This is a very distinct taxon and is well represented by numerous collections from northern Mexico on file at LL, TEX. Johnston's F. rigida was thought to differ from the earlier F. linearis in being more rigidly spinescent and possessed with shorter leaves, but a wide range of variation is found in these characters throughout the distribution of F. linearis (as well noted by Henrickson in his forth-coming Flora of the Chihuahuan Desert, in prep.).

5. Fendlera tamaulipana B. L. Turner, sp. nov. (Fig. 5)

Similis F. linearis Rehder sed altior, dendroidior, et non intricate ramosa, foliis leniter brevioribus et latioribus, petiolis habentibus callos auctos et brunelosus basibus.

Sparsely branched erect SHRUBS 1.5–4.0 m high, not at all intricately branched and/or spinulose. LEAVES mostly 10–15 mm long, 1.5–2.0 mm wide; petioles ca. 2 mm long, having a swollen cartilaginous, glabrous or sparsely pubescent base; blades with markedly enrolled margins, sparsely to moderately pubescent on the upper surfaces, especially along the margins, the apices short-apiculate. FLOWERS sessile or nearly so, 1.5–2.0 cm across the extended petals; calyces with 4 valvate sepals, ca. 7 mm long, their lobes 4–5 mm long, 3–4 mm wide, pubescent within and without by a vestiture of minute dendritic hairs, these over lain on the outer surfaces by an array of much coarser appressed hairs; petals white, 10–12 mm long, the claws ca. 4 mm long; stamens 8, 7–9 mm high; anthers 2.5–3.0 mm long. CAPSULES ovate, 4-carpellate, ca. 10 mm high, 6 mm wide, the calyces fused to its base for ca. 3 mm; seeds 1 or 2 per carpel, 3–4 mm long, ca. 0.6 mm wide.

TYPE: MEXICO. TAMAULIPAS: Ca.
46 km. WNW of Jaumave, 6.5 road km W of Miquihuana on road to La Perdida, along large limestone arroyo, ca. 1850 m [ca. 23 32 N, 99 50 W], 8 Oct 1982, James Henrickson 19133 (HOLOTYPE: TEX).

REPRESENTATIVE SPECIMENS EXAMINED: MEXICO. TAMAULIPAS: ca. 52 air km WNW of Jaumave, ca. 10 km NW of Miquihuana, 8–10 km N of La Perdido on limestone west-facing slopes along high road to Marcela, 8 Oct 1982, Henrickson 19151 (TEX); ca. 9 air mi NW of Miquihuana, 3 mi N of Servando Canales in limestone canyon on the way to Valle Hermosa, 9 Sep 1999, Henrickson 22452 (TEX).

When first examined I was inclined to treat this taxon as a varietal element of F. linearis, to which it is certainly related. Its habit differs markedly from that species, however, as aptly noted by Henrickson in collection data. The type label describes the plants concerned as "Woody shrubs to 12 ft tall." The two additional collections are described as strict erect, sparsely branched, shrubs, which appears to be the case judging from the relatively elongate internodes and strictly ascending secondary branches of the specimens concerned. In contrast, F. linearis is a very intricately branched usually spinescent shrub 1–2 m high. Additionally, the leaves of F. tamaulipana are somewhat shorter and broader, the petioles of which have enlarged callosities at their bases. These characters, along with its restricted distribution, suggest that it is deserving of specific recognition. Indeed, it is as distinct from F. linearis as F. rupicola is from F. falcata, if not more so.

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LITERATURE CITED