Phytotaxa 124 (1): 37–42 (2013)
www.mapress.com/phytotaxa/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

http://dx.doi.org/10.11646/phytotaxa.124.1.4

Heuchera lakelae (Saxifragaceae), a new species from the Sierra La Marta and Sierra Coahuilón, Coahuila and Nuevo León, Mexico

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Abstract

Described herein is a new species from high-elevation limestone outcrops in the northern Sierra Madre Oriental, closely allied to *Heuchera sanguinea*, from which it is distinguished on the basis of 6 morphological characters (external flower surface color and indumentum, petal color, petal shape, stamen exsertion, and overall flower shape) as well restriction to high elevations and a geographical range restricted to the Sierra la Marta and Sierra Coahuilón.

Introduction

Heuchera is the largest by far of a series of North American endemic genera of the Saxifragaceae, with about 43 species. It is also the most widely distributed, occurring from Kodiak Island, Alaska, south to the Sierra Madre de Oaxaca of southern Mexico, and from the Atlantic forests to the Pacific coastal bluffs within meters of the sea. It has its greatest diversity in the western Cordillera, where it is well-known for its difficult morphological patterns and frequent hybridization both ancient and recent (Wells & Shipes 2009, Rosendahl, Butters & Lakela 1936, Soltis *et al.* 1991, Folk & Freudenstein unpublished). My own morphological investigations have indicated that there is significant diversity within the genus in the mountains of Mexico that has yet to be described, particularly in the north, owing to a high natural diversity and to the paltry work that has been devoted to them in this area.

During recent inspections of Mexican herbarium material a highly distinct plant of restricted occurrence has come to my attention, which is here described as a new species and placed within the subgeneric taxonomy of Rosendahl, Butters & Lakela (1936).

Materials and Methods

Herbarium loans were obtained from ASU, BRIT, CAS, F, MEXU, MICH, MO, NY, RSA, TEX, US, VT, and XAL, comprising 765 sheets of *Heuchera* from Mexico. I have reviewed types belonging to all species of *Heuchera* that have been described from Mexico and the adjacent US, either in person, or where necessary through high resolution digital images. The names that have been examined are: *H. acutifolia, H. amoena, H. halstedii, H. hemsleyana, H. leptomeria, H. longipetala, H. mexicana, H. minutiflora, H. orizabensis, H. pulchra, H. reglensis, H. rubescens, H. sanguinea, H. townsendii,* and *H. versicolor.* A phylogenetic species concept (Nixon & Wheeler 1990), in which a species is the most restrictive collection of populations with a unique combination of character states, was applied in the context of the most recent treatment of Mexican *Heuchera* species (Rosendahl, Butters & Lakela 1936) to revise and delimit taxa.

Accepted by Maximilian Weigend: 17 July 2013; published: 15 August 2013

Taxonomy

Heuchera lakelae Folk, *sp. nov.* (Fig. 1)

A *Heuchera sanguinea* Engelm. flore albo-rubescenti cylindracei vel leviter bucciniformi, hypanthio et sepalo dense glanduloso-hirsuto, petalis albis valde exsertis rhomboideo-spatulatis vel ovato-spatulatis, staminibus leviter inclusis, crescenti supra 3200 m altitudinis differt.

Type:—MEXICO. Coahuila: Sierra La Marta E of Cerro Moro [Cerro el Morro], ca. 3400 m alt., 22 July, 1985. S. Ginzbarg 134. (Holotype NY!, isotypes MO!, TEX!, MEXU!)

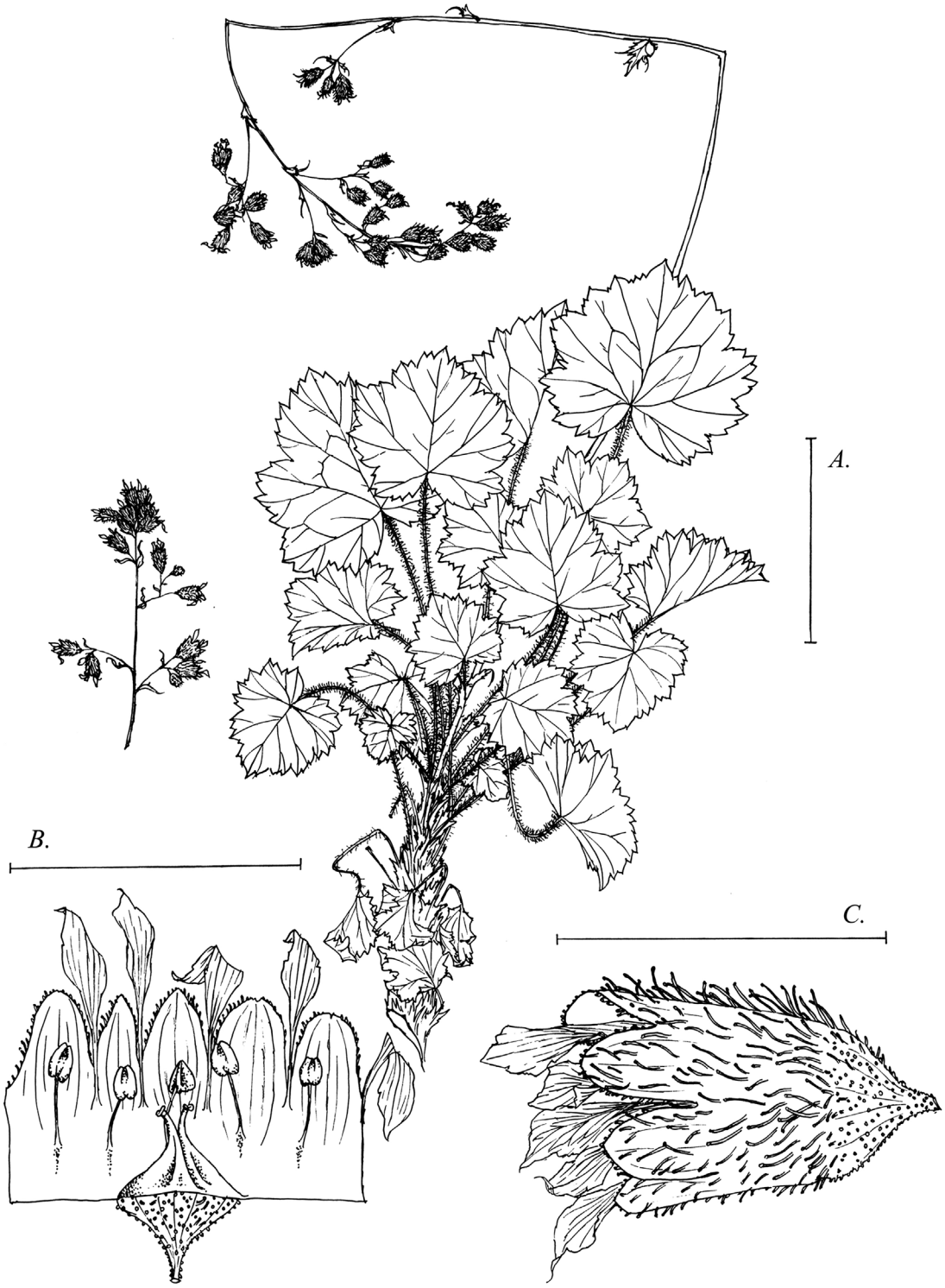

FIGURE 1. Drawing of *H. lakelae,* prepared from the type material at NY and TEX by the author. A. Habit and inflorescence; scale represents 4.5 cm. B. Dissected flower; scale represents 6 mm. C. Side view of flower; scale represents 6 mm.

Description:—*Perennial herb,* subcaulescent from a multicipital thick caudex. *Petioles* glandular-villous and glandular-pulverulent, (1.5–) 3–10 cm long. *Leaf blades* (1–) 2–5 cm wide and (1.25–) 1.5–4 cm long, orbicular to ovate, deeply cordate with a narrow or wide sinus, shallowly divided into 5–7 lobes with narrow sinuses; teeth large and coarse, triangular to crenate and mucronate; adaxial surface sparsely to densely glandular-villous as well as glandular-puberulent, abaxial surface similarly vestitured but the longer hairs restricted mainly to the veins. Margin moderately ciliate. *Inflorescences* indeterminate scapiform thyrses (11.5–) 18.5–45 cm long, the flowers rather crowded and becoming interrupted proximally, the bracts highly reduced, rarely having a large leaf-like bract, the lowest pair of bracts subopposite, primary axis glandular-hirsute proximally to glandular-puberulent distally; cymules 2–7 flowered, 1.5–5.5 cm long, monochasial or often dichasial at the first branching. *Flowers* 5–7 mm long, external surface white aging to pale pink, puberulent proximally and becoming strongly hirsute-glandular distally; *hypanthia* campanulate, moderately zygomorphic, 2.5–3.5 mm long on the adaxial side, (2.5–) 3–6 mm wide; *sepals* rounded, (1–) 1.5–3 mm long; *petals* 2–3 mm long, white, ovate-spatulate to rhombic-spatulate with a prominent claw, exceeding the sepal tips, adnate to free hypanthium just below the sepal sinuses; *stamens* 1.5–2 mm, slightly or strongly included, filaments adnate to free hypanthium about halfway between the base and the level of the sepal sinuses, anthers ovate; closed true *styles* about 1 mm, stigmas capitate. *Capsule* 8–10 mm long, 4–5 mm wide, ovoid, exceeding slightly the accrescent calyx. *Seeds* about 0.7–0.8 mm long, fusiform but somewhat lunular, beset with short spines.

Phenology:—Flowering June–September (–October), fruiting August–October.

Distribution:—The rocky slopes of El Coahuilón and Cerro El Morro in the Sierra Coahuilón and Sierra la Marta, along the border between Coahuila and Nuevo León just south of Monterrey, northern Sierra Madre Oriental, Mexico.

Habitat:—Moist north-facing rock outcrops or talus slopes, mostly on limestone, 3250–3700 m, subalpine or alpine zone. Alpine specimens much dwarfed. Some plants, including the type collection, are reported from the pioneer vegetation of recently burned pine forests.

Associates:—*Pseudotsuga menziesii, Pinus rudis, P. culminicola, P. hartwegii, Abies vejari, Holodiscus* sp., *Salix* sp., *Quercus* sp., *Garrya* sp., and *Symphoricarpos* sp.

Conservation:—Known from only an extremely narrow range of about 6 km in width; a possible candidate for conservation listing, but field work is needed to establish the size and stability of these populations.

Etymology:—For Olga Lakela, whose dissertation work led to an exemplary and well-regarded 1936 monograph on *Heuchera*, the most recent such work to include Mexican species.

Other specimens examined:—MEXICO: **Coahuila:** El Coahuilón, Sierra de la Marta, mpio. Arteaga, 25°14'12 N, 100°18'40" W, 3600 m, 9 October 1986, *J.A. Villareal 3467* (MEXU, BRIT); El Coahuilón, Sierra de la Marta, mpio. Arteaga, 25°14'12 N, 100°18'40" W, 3600 m, 6 August 1987, *J.A. Villareal 3818* (TEX); El Coahuilón, Sierra de la Marta, mpio. Arteaga, 25°14'12 N, 100°18'40" W, 3600 m, 17 October 1989, *J.A. Villareal 5471* (TEX); El Coahuilón, Sierra de la Marta, 25°14'12 N, 100°18'40" W, 3600 m, 17 October 1989, *J.A. Villareal 5473* (XAL); Rocky knoll, Sierra la Marta, 3450 m, 6 September 1981, *G.B. Hinton 18331* (TEX); Cliff in pine forest, S. del Coahuilón, mpio. Arteaga, 3250 m, June 2, 1985, *G.B. Hinton 18855* (TEX); Estepa alpina, Cerro del Morro en ladera sur, Sierra la Marta, ca. 3700 m, 17 June, 1985, *McDonald 1470* (TEX); Ladera sur, zona subalpina, Sierra Coahuilón, ca. 3400–3500 m, 18 June 1985, *McDonald 1521* (TEX). **Nuevo Leon:** Sierra la Marta, mpio. Galeana ?, 3400 m, 4 August 1980, *G.B. Hinton 17912* (TEX, MEXU);

Discussion

Heuchera lakelae is represented by a number of collections from high elevations in a very narrow area in northeastern Mexico, the Sierra la Marta and Sierra Coahuilón just south of Monterrey. Judging from the large number of geographically representative specimens I have seen for the genus in Mexico, *H. lakelae* appears to

be locally abundant, but quite absent outside the documented range. Specimens of this taxon to date have mostly been identified in herbaria as *H. sanguinea* Engelmann (1848: 107), though a recent floristic list (Villareal-Quintanilla 2001) for Coahuila lists the type collection as *H. mexicana* Schaffn. ex Rydberg (Rydberg 1905: 108), a plant to which it does not appear to be as closely related, and a few have been annotated even more remotely as *H. rubescens* Torrey (1852: 388). One specimen collected by G.B. Hinton at TEX was anonymously annotated "n. sp.?", indicating that other botanists have been struck by its appearance as well.

Heuchera lakelae is assigned to the previously monotypic subsection *Sanguineae* (section *Rhodoheuchera*; currently containing only *H. sanguinea*). Though *H. lakelae* is strikingly different in gross appearance from *H. sanguinea,* they share a number of technical characters: relatively large flowers with broadly campanulate, slightly zygomorphic hypanthia, relatively wide petals, included stamens, adnation of the filaments to the hypanthium well below the sepal sinuses, and very short true closed styles. They are also similar in their summer flowering (other Mexican *Heuchera* species bloom in early spring). *Heuchera lakelae* differs from *H. sanguinea* by having the external flower surface white but tinged with pale pink as the flowers age (as opposed to a vivid, darkening cerise) and strongly glandular-hirsute distally (rather than uniformly glandular-puberulent or sparsely glandular-hirtellous), petals white, ovate-spatulate to rhombic, large and showy, and considerably surpassing the sepal tips (as opposed to cerise or pinkish, miniscule lanceolate-spatulate petals not exceeding the sepal tips). The overall flower shape of *H. lakelae* is squatly cylindrical or very slightly flaring (rather than strongly flaring-conical). Variegation of the upper leaf surface, apparently caused by a secondary thickening of epidermal cell walls, is polymorphic and common across the range of *H. sanguinea,* but wholly absent in *H. lakelae.* The habitat is also quite different: *Heuchera sanguinea* in Mexico occurs at 1500–2300 (rarely to 3600) m, whereas *H. lakelae* is known from 3250–3700 m and is completely absent from lower elevations. *H. lakelae* is obviously close to *H. sanguinea* but it approaches the geographically proximate species *H. mexicana* in having exserted petals and a pale calyx color; *H. lakelae* differs from *H. mexicana* in having short included true styles, included stamens which are attached well below the level of the sepal sinuses on the abaxial side, rather wide petals, and a broadly campanulate flower, as well as a later flowering period (Table 1).

The rank of species is chosen because of the striking morphological distinctness between *H. lakelae* and *H. sanguinea,* its apparent closest relative, in 6 morphological characters (external flower surface color and indumentum, petal color, petal shape, stamen exsertion, overall flower shape) as well as an altitudinal difference and parapatric distribution. On the other hand, I have discovered a few specimens of *H. sanguinea* with flowers that are unusually pale in appearance, and therefore resemble the color of *H. lakelae.* These unusual specimens occur near the tiny range of *H. lakelae,* a region in which *H. sanguinea* is rare and far-disjunct (about 600 km) from its more extensive range in the northern Sierra Madre Occidental (Figure 2). Overall these specimens are strikingly variable, but they have in common with *H. sanguinea* larger flowers, small petals terminating below the sepal tips, and inserted anthers; their flowers, while opening pale, eventually darken to the cerise color of typical *H. sanguinea*. Pale *H. sanguinea* has been seen only from the periphery of the range of *H. lakelae:* the lower slopes of El Coahuilón, the Sierra de la Nieve, Sierra de la Viga, and Sierra de los Lirios, at higher elevations than typical *H. sanguinea* in the west (2700–3600 m versus 1500–2300 m). The pale phase does not occur in the Sierra Madre Occidental. The typical forms of *H. lakelae* and *H. sanguinea* are at a glance strikingly different and easily distinguished by morphology, and these unusual specimens seem to fall within the range of variation of *H. sanguinea* in characters examined other than color.

Material of *Heuchera lakelae* (from *Hinton 17912* TEX) has been included in studies on the phylogenetics of *Heuchera* using molecular data (results in progress). It has not been possible to resolve the relationships of *H. lakelae* to other species on the basis of molecular data owing to the difficulty in obtaining more variable single-copy nuclear loci from herbarium material. The loci recovered, ITS, ETS, and *rpl32-trnL,* are not sufficient to resolve the relationships of *H. lakelae.* However, two of these loci provide molecular diagnostic characters: *H. lakelae* was differentiated from two collections of *H. sanguinea* (from the Dragoon and Chiricahua mountains) and all other species of section *Rhodoheuchera* on the basis of a single base mutation (ITS), and a 3 base pair insertion (*rpl32-trnL*), apomorphic character states in both cases.

TABLE 1. Comparison among *Heuchera* taxa known to occur in northeastern Mexico.

Taxon	***Heuchera sanguinea***	***H. lakelae***	***H. mexicana***
Flower length (anthesis)	6–12 mm	5–7 mm	3–4.5 mm
Flower shape	Flaring-conical	Squatly cylindrical or slightly flaring	Long-tubular
External flower color	Cerise, darkening with age*	White, turning pink with age*	White, turning pale pink with age*
External flower indumentum	Puberulent or rarely hirtellous distally	Becoming strongly hirsute distally	Becoming long–villous distally
Hypanthium zygomorphy	Weak	Moderate	Very strong
Petal color	Cerise to pink	White	White
Petal shape	Lanceolate-spatulate	Ovate-spatulate to rhombic-spatulate	Narrowly lanceolate-spatulate
Petal exsertion	Included	Exserted	Exserted
Stamen exsertion	Included	Included to slightly included	Strongly exserted
Filament adnation (abaxial side)	Well below the sepal sinuses	Well below the sepal sinuses	Near the level of the sepal sinuses
True style	Very short, inserted	Very short, inserted	Long, exserted
Variegation	Often present	Always absent	Always absent
Phenology (blooming)	Summer	Summer	Early spring
Elevation	1500–2300 (–3600) m	3250–3700 m	1000–3700 m
Range	Northern Sierra Madre Occidental, disjunct and rare in the northern Sierra Madre Oriental	Sierra la Marta and Sierra Coahuilón	Broadly distributed in Northern Mexico, Sierra Madre Occidental and Oriental.

* The tendency of the external flower surface becoming darker pink with age ("rubescence") seems to be a synapomorphy of section *Rhodoheuchera,* but species differ widely in the overall amount of pink. The hypanthium tends to be paler than the rest of the external flower surface.

The phylogenetic position of *Heuchera lakelae* seems to be as sister to or perhaps derived from *H. sanguinea* on the basis of morphological similarity. It may have originated allopatrically when previously continuous mesic habitats across northern Mexico were cut off by the aridification of what is now the Chihuahua Desert. Current populations of *H. sanguinea* in the Sierra Madre Oriental may represent more recent incursions eastwards, either through long-distance dispersal or more likely through migration corridors created during a recent glacial maximum. However, some of the features of *H. lakelae*, such as flower size, hair length on the external flower surface, and degree of zygomorphy, are intermediate between *H. sanguinea* and *H. mexicana.* Since *Heuchera* is well-known for its propensity to form hybrids (Soltis *et al.* 1991 and citations therein), it is possible that *H. lakelae* arose from hybridization between *H. sanguinea* and *H. mexicana,* both of which are peripherally distributed very near its range. More data, especially using molecular characters and cytology, are needed to resolve the position of *H. lakelae* and explore the possibility of its origination by hybridization.

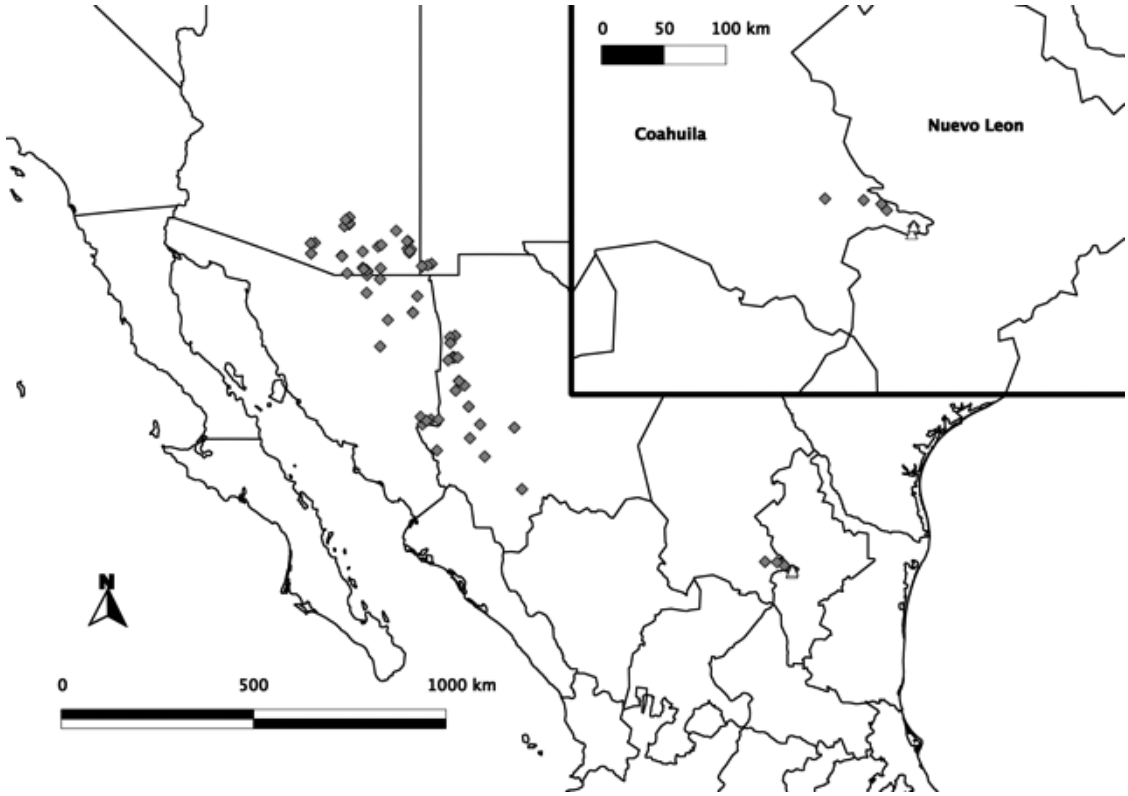

FIGURE 2. Occurrence map of *Heuchera lakelae* (white triangles) and *H. sanguinea* (gray diamonds). Inset shows the Sierra la Marta and adjacent regions.

Acknowledgements

I thank the directors of ASU, BRIT, CAS, F, MEXU, MICH, MO, NY, RSA, TEX, US, VT, WIS and XAL for assistance in obtaining loans, Mesfin Tadesse for assistance in specimen curation, Brandon Sinn for assistance with GIS programs, and John Freudenstein for discussion and criticism of the manuscript.

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