
Resolving a Nomenclatural and Taxonomic Problem in Mexican *Oenothera* sect. *Hartmannia* (Tribe Onagraceae, Onagraceae)

Warren L. Wagner

United States National Herbarium, Department of Systematic Biology, Botany, MRC-166,
P.O. Box 37012, Smithsonian Institution, Washington, DC 20013-7012, U.S.A.
wagner.warren@nmnh.si.edu

ABSTRACT. Study of type material from the trans-volcanic region of Mexico of two species of *Oenothera* sect. *Hartmannia* (tribe Onagraceae, Onagraceae), currently known as *Oenothera deserticola* (Loesener) Munz and *O. purpusii* Munz, indicates that they represent the same species. Thus, the latter name *O. purpusii* becomes a new synonym of *O. deserticola*. Also, a neotype is designated herein for *O. deserticola*. The only available name for the second species, previously incorrectly called *O. deserticola*, is *Hartmannia montana* Rose, but since *O. montana* is already occupied, a new name, *O. orizabae*, is here proposed. A previously unreported chromosome count of $n = 7$ is given for *O. deserticola*. While examining collections to resolve this problem, a series of specimens from the Sierra Madre Occidental was determined to represent a third species here described as *O. luciae-julianiae*. These three species can be distinguished by a suite of characters involving habit, petal color, and capsules. *Oenothera deserticola* is characterized by decumbent stems, morning-opening flowers, rose purple petals, and angled, but unwinged capsules with an attenuate apex, while *O. luciae-julianiae* has erect or ascending stems, evening-opening flowers, white petals, and narrowly winged capsules with an abruptly acuminate apex. *Oenothera orizabae* has decumbent stems, evening-opening flowers, white petals, and large-winged capsules with a rounded apex.

RESUMEN. El estudio de los tipos de *Oenothera deserticola* y *O. purpusii* de la sección *Oenothera* sección *Hartmannia* procedentes de la región tras-volcánica de México, indica que ambos representan la misma especie. Como resultado, *O. purpusii* es considerado sinónimo de *O. deserticola*. Una segunda especie, originalmente descrita como *Hartmannia montana*, pero cuyo epíteto específico está ocupado en *Oenothera*, es substituido por el nombre *O. orizabae*, el cual es aquí propuesto. El estudio de las colecciones procedentes de la Sierra Madre Occidental determinó que existe una tercera es-

pecie, la cual es aquí descrita como *O. luciae-julianiae*. Estas tres especies pueden ser distinguidas por una serie de caracteres relacionados al hábito, color de pétalo y de las cápsulas. *Oenothera deserticola* es caracterizada por tallos decumbentes, flores de apertura matutina, pétalos purpúreo-rosados y cápsulas angulosas, ápteras y atenuadas hacia el ápice, mientras que la especie de la Sierra Madre, aquí descrita como *O. luciae-julianiae*, tiene tallos erectos o ascendentes, flores que abren al anochecer, pétalos blancos y cápsulas estrechamente aladas con un ápice abruptamente acuminado. *Oenothera orizabae* tiene tallos decumbentes, flores que abren al anochecer, pétalos blancos y cápsulas aladas, grandes, con el ápice redondeado.

Key words: evening-primrose, Mexico, *Oenothera* sect. *Hartmannia*, Onagraceae.

Nearly one third of the 120 species of the genus *Oenothera* L. occur in Mexico. Recent focus on the phylogeny of the family Onagraceae, especially of the most diverse tribe Onagraceae (Levin et al., 2003), along with analyses of biogeographic patterns of tribes Epilobieae, Gongylocarpeae, and Onagraceae (Katinas et al., in press) have resulted in the need to resolve a nomenclatural problem and describe a new species.

Two relatively uncommon species from the trans-volcanic region of Mexico, *Oenothera deserticola* (Loesener) Munz and *O. purpusii* Munz, have had a confused application of names since the latter was described in a revision of *Oenothera* sect. *Hartmannia* (Munz, 1932). A brief history leading up to the confusion clarifies the problem. The first species was described as *Hartmannia montana* J. N. Rose (1905). The second was published as *Xylopleurum deserticolum* Loesener (1913). Both of these species were included in Munz's revision of *Oenothera* sect. *Hartmannia* (Munz, 1932), but for some reason he was confused on the correct application of *Xylopleurum deserticolum*. Munz's description of *O. deserticola* clearly fits the taxon that J. N. Rose described as *Hartmannia montana* (1905).

It was characterized by decumbent stems, white petals, and large-winged capsules with a rounded apex. Munz cited a number of collections of it, including the type of *Hartmannia montana*, and placed Rose's name in synonymy of *O. deserticola*. Munz also cited all four syntype collections given in the original publication of *Xylopleurum deserticolum* (Loesener, 1913). It is not clear if Munz had actually seen any of the syntype collections or if he merely cited them from Loesener's protologue, while at the same time selecting one of them as the type. For reasons unknown to me, Munz was confused because at least one of the syntypes, Seler 5614 (photo US), and likely all four judging from Loesener's description, is clearly the same taxon as the one he described in the same paper (1932) as the new species *O. purpusii* Munz. This species was characterized by decumbent stems, rose-purple petals, and smaller, angled, but unwinged capsules with an attenuate apex.

A photo of one of the four syntypes was taken before all four were destroyed in the Berlin herbarium during World War II. This photo is reproduced here in Figure 1. I had hoped to confirm the characteristics of original material of *O. deserticola* by either locating duplicates of the lectotype, other syntype collections, or photographs of any of the other three syntypes, but none were found by the collections managers who kindly searched for them at the herbaria known to have received Seler collections (A, B, CAS, F, GH, K, MEXU, NY, US). Despite not having any of Loesener's original material, it is clear from the leaves and dehisced capsule shown in the photograph that *O. deserticola* represents the same taxon that has gone under the name *O. purpusii* since 1932. The name *Oenothera deserticola* has priority over *O. purpusii*, and therefore is the correct name. This conclusion is further supported by Loesener's original description (1913), as characterized earlier.

The other species in question was first described in 1905 as *Hartmannia montana* Rose. Since the specific epithet *montana* is already occupied in *Oenothera*, a new name, *O. orizabae*, is proposed here.

During the course of study of these two species using material from a number of primarily American and Mexican herbaria, it became clear that a significant number of Mexican collections from the Sierra Madre Occidental, from Chihuahua south through Durango to Jalisco and Guanajuato that were identified as *O. deserticola* by P. H. Raven, myself, or others over the past three decades represents an undescribed species characterized by erect or ascending stems, white petals, and narrowly winged capsules with an abruptly acuminate

apex. It is here described as *O. luciae-julianiae*. It has a distribution allopatric from both *O. orizabae* and *O. deserticola*. The following key distinguishes them from one another.

KEY TO SPECIES OF MEXICAN *OENOTHERA* SECT. *HARTMANNIA*

- 1a. Capsules winged, acuminate to rounded at apex; petals white at anthesis, fading purple.
2a. Stems decumbent, ascending toward the apex; caudine leaf blades 1–3 cm wide, narrowly ovate, occasionally elliptic, subentire to subdenticulate; capsule body 15–26 mm long, ovoid, apex rounded, the margins winged, the wings 2.3–4 mm wide, the sterile stipe stout, 15–50 mm long; capsule body apparently dehiscing only at apex *O. orizabae*
- 2b. Stems erect to ascending; caudine leaf blades 0.5–1.1(–3) cm wide, elliptic to lanceolate or narrowly elliptic-ovate, denticulate to serrulate; capsule body 8–18(–25) mm long, clavate or narrowly ovoid, apex obtuse to bluntly acuminate, the wings 1.3–2 mm wide; the sterile stipe slender, 7–35 mm long; capsule body dehiscing from about half its length to nearly throughout
..... *O. luciae-julianiae*
- 1b. Capsules angled, but not winged, attenuate at apex; petals rose-purple at anthesis, fading darker *O. deserticola*

Oenothera deserticola (Loesener) Munz, Amer. J. Bot. 19: 758. 1932. *Xylopleurum deserticolum* Loesener, Repert. Sp. Nov. 12: 238. 1913.
TYPE: Mexico. Distrito Federal: Contreras, Lyonnet 532 (neotype, designated here, MEXU-238843; isoneotypes, GH, K not seen, MEXU [3], MO, NY, US). Figure 2.

Oenothera purpusii Munz, Amer. J. Bot. 19: 759. 1932.
Syn. nov. TYPE: Mexico. Ixtaccihuatl, open woods, 1903, C. A. Purpus 1839 (holotype, POM 32827 not seen; isotypes, F, G not seen, GH, MO, NY, UC, US).

Perennial herb with usually several or sometimes more, decumbent or sometimes ascending when short, branched or occasionally simple stems 5–20(–36) cm long, usually reddish purple or occasionally pale purple, strigillose, rarely with a few longer erect hairs, often producing new rosettes via rhizomes up to 6–7 cm long, from a thick somewhat woody caudex; root fleshy and thickened in age. Rosette leaf blades 4–6 × 1–1.7 cm, oblanceolate to elliptic, sparsely to moderately strigillose, apparently quickly deciduous; petiole 0.4–1.6 cm; caudine leaf blades 1–6.5 × 0.5–1.8 cm, elliptic to elliptic-oblanceolate or narrowly so, subserrate to weakly sinuate-toothed, apex obtuse to acute, sparsely to moderately strigillose; petiole 0.1–1.1 cm long. Flowers opening near sunrise (Iltis et al.



Figure 1. Reproduced photograph of Seler 5614, a Berlin (B) syntype of *Xylopleurum deserticolum* Loesener no longer extant, taken as part of the Field Museum's (F) Types of the Berlin Herbarium project. Copies of the photograph are in MICH, MO, NY, POM, and US. The photograph was scanned into Photoshop 6.5, and then a dehisced capsule showing the long apex of the valves allowing for unambiguous identification was cut, enlarged, and pasted into the upper left-hand corner (obscuring two small branches evident in the original). A white box on the full photograph indicates the part cut and enlarged. The leaves and part of a stem were removed from the inset for clarity.

202 says evening); floral tube, sepals, and ovary densely strigillose, and ovary usually also densely hirtellous with hairs up to 2 mm long; floral tube 4.5–11 mm long; sepals 7.5–16 mm long; free tips

in bud absent or rarely present and ca. 0.1–0.2 mm long; petals 8.5–17 mm long, rose-purple fading darker after pollination; filaments 5.5–8 mm long, rose-purple; anthers 2.5–4.5 mm long, cream; pol-

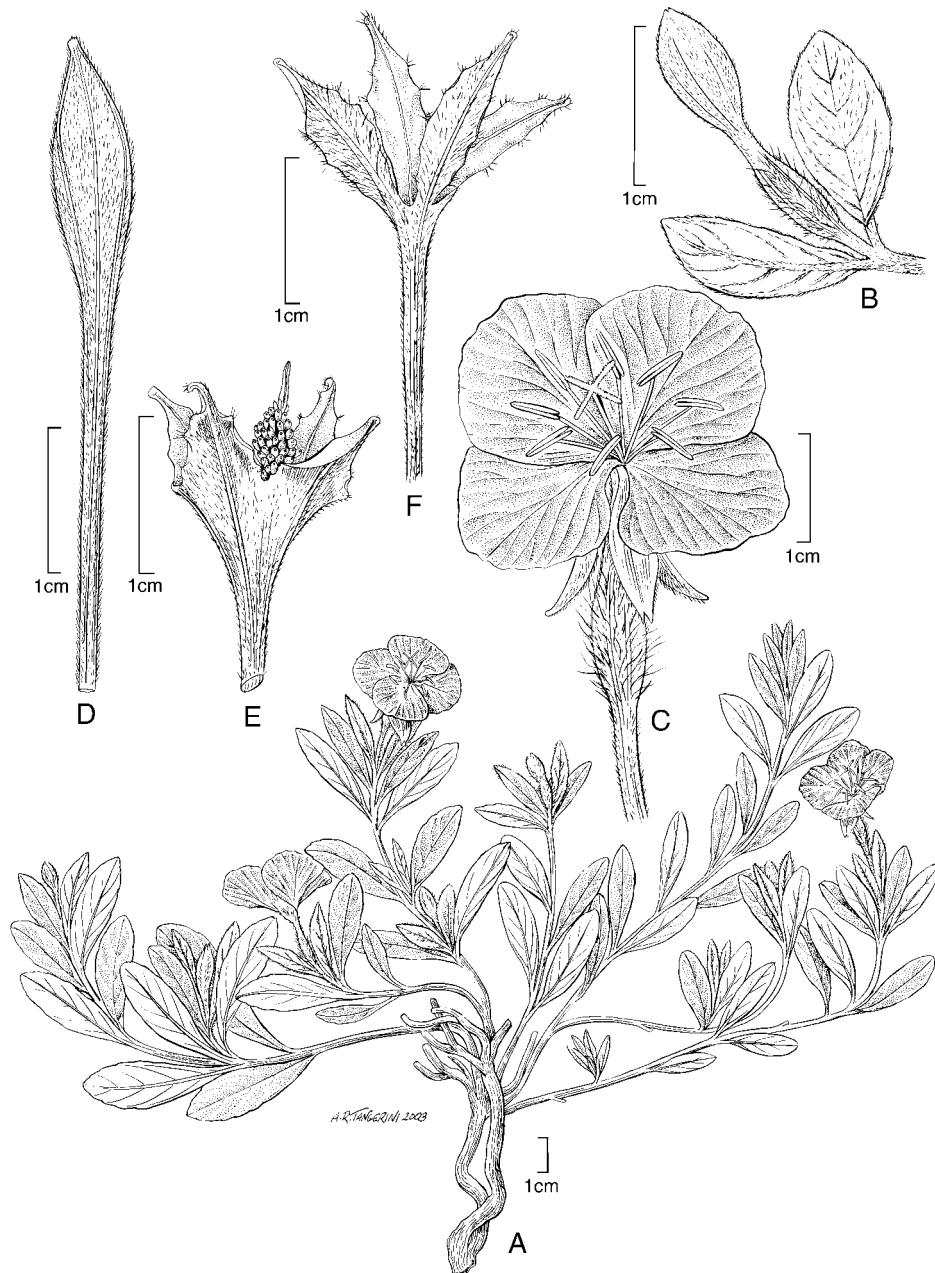


Figure 2. *Oenothera deserticola* (Loesener) Munz. —A. Habit, showing decumbent stems from a branched rhizomatous base (Arroyo 182, MO, and Balogh 1005, US). —B. Bud, floral tube, and ovary, showing the lack of free sepal tips and pubescence pattern (Arroyo 182, MO). —C. Flower, showing petal shape and overlap of petals (Hinton 9104, US). —D. Young capsule showing shape, attenuate apex, and sterile stipe (Lyonnet 532, MEXU). —E. Dehisced capsule showing length of dehiscence and seeds clustered on placentas (Straw & Gregory 1116, GH). —F. Dehisced capsule showing shape of open valves (Lyonnet 532, US).

len cream, > 90% fertile; style 12–21 mm long; stigma surrounded by the shedding anthers at anthesis or slightly elevated above it; stigma lobes 2.5–4 mm long. Capsule body 10–22 mm long,

rose-purple to green with purple tinge, the body narrowly ellipsoid to clavate, apex attenuate, angled or rarely with a narrow wing up to 0.5 mm wide; sterile stipe slender, 7–17 mm long; capsule body

dehiscing nearly throughout; seeds clustered in each locule, 1–1.2 mm long, 0.4–0.6 mm thick, brown. Gametic chromosome number, $n = 7$ (Raven, unpublished).

Distribution. *Oenothera deserticola* occurs in open forests of *Pinus*, *Pinus-Quercus*, or occasionally *Abies*, *Alnus*, and *Salix*, on sandy open sites or steep banks, in the mountains of the Trans-Mexican Volcanic region from the northeastern Michoacán and central Hidalgo south to México and Orizaba, Veracruz, from (2100)2500 to 3400 m.

The lectotype selected by Munz (1932), but now destroyed, was collected in Mexico, D.F., El Desierto de los Leones, May 1909, W. Höpfer s.n. (C. & E. Seler 5280) (B destroyed). The lectotype and three additional syntypes (without further locality Uhde 1222; El Desierto de los Leones, W. Höpfer s.n. (labeled as Seler 5614) [photos: MICH, MO, NY, POM, US]; and San Rafael, Tlalmancalo, Seler 5319) were destroyed during World War II (Christopher Oberprieler, pers. comm. 2001).

Oenothera deserticola is a member of section *Hartmannia*, which can be subdivided into three groups of species based on petal color and time of flowering. With its rose-purple petals and morning flowering, *O. deserticola* appears to be in a group with other morning-flowering species with purple petals, including *O. platanorum* P. H. Raven & D. R. Parnell, *O. rosea* L'Héritier de Brutelle ex Aiton, and *O. texensis* P. H. Raven & D. R. Parnell. These species share angled, but not winged capsules and no free sepal tips in bud or tips free and minute (0.1–0.2 mm long).

The geographic and elevational range of *Oenothera deserticola* broadly overlaps the range of *O. orizabae*. One collection (Barkley et al. 2438) is a mixed collection of *O. deserticola* and *O. orizabae* suggesting that they occur sympatrically at some localities; however, there is no documentation of hybridization. Hybridization must be strongly limited by the different timing of flowering, with flowers of *O. deserticola* open during the day and those of *O. orizabae* open at night.

Specimens examined (those marked by * are chromosome determination vouchers). MEXICO. **Distrito Federal:** Desierto de los Leones, *Raven 15424 (also flavonoid voucher) (TEX); hwy. 190, betw. Puebla & Mexico City, Ahshapanek 701 (TEX); Contreras Canyon, SW of Mexico City, Munz 15000 (GH, MO); Chapultepec III, Valle del Silencio, Wonderly 217 (MEXU, NMC); Cerro de Esquihuil, delegación de Mipa Alta, Ventura 2804 (MEXU, MO, NY); Río Frío, Russell & Souviron 82 (US); Volcán Pelado, ladera E, Mondragón s.n. (MEXU); near Estación La Cima, Serranía del Ajusco, Rzedowski 19840 (MICH, MO, TEX); Tlalpan, Volcán Ajusco, Reyes s.n. (MEXU); lava fields ca. 2 km SSW of La Cima R.R. Station on either

side of old Hwy. 95 on top of Serjana de Ajusco, Iltis et al. 202 (MICH, RSA); Cerro Tepetlahualo, delegación de Milpa Alta, Ventura 1412 (MEXU); Santa Rosa, delegación de A. Obregón, Ventura 2720 (MEXU, MO); 1 mi. SE of Puerto del Aire, Barkley et al. 2438 (MICH, TEX) [both sheets mixed collection with *O. orizabae*]. **Hidalgo:** Cerro de los Pitos, Matuda 21562 (MEXU [2]); El Chico, Cerro de Las Ventanas, Gentry et al. 32180 (MO); Parque Nacional El Chico, Ortiz 10 (MEXU); Metzquititlan, Carpinteros, 20 km E Metzquititlan, Hernandez 6806 (MO); Sierra de Pachuca, Rose & Hay 5611 (US). **México:** on hwy. México to Puebla, Munz 15064 (POM); Monte de Río Frío, km 49, road from Mexico City to Pueblo, Mexia 2696a (UC); near Salazar, Rose & Painter 7027 (US); Neiva de Tolucá, Rose & Painter 7873 (US); El Crucero, Temascaltepec, Hinton 521 (POM); Cerro de León, Valle de Mexico, Matuda 19128 (MEXU [2]); Paraje Provincial, Balls 4173 (UC, US); San Rafael, ladera W del Iztaccíhuatl, Sánchez 8 (MEXU); Ixtapaluca, Estación Experimental de Enseñanza y Investigación de Zoquiapan, Koch & Magaña 75242 (MEXU, MO, NY); Llano Grande Gap, near Río Frío, Sharp 4496 (MEXU, RSA); Nat. Park Lagunas de Zempoala, Cole 49 (MEXU), McAdams 57 (MICH), Taylor 55 (MEXU); Comunidad, Temascaltepec, Hinton 860 (GH, NY, POM); Cumbre, Temascaltepec, Hinton et al. 7478 (GH, LL, MICH [2], MO, NY, POM, TEX, UC, US); Cumbre Trojes, Temascaltepec, Hinton et al. 8272 (MEXU, MICH, NY, UC, US); Mt. Popocatapetl, Nelson 10 (US); 10 km al NE del Entronque a Sultepec, Flores & Terpán 829 (MEXU); Vallee de Bravo, 0.8 mi. S of Cajones, 9500 ft., Balogh 1005 (US); 55 km SE of Mexico City, 10,500 ft., Weaver 712 (POM, US); near Toluca, Schery 64 (MO); Ocuilan, Matuda 32454 (MEXU). **Michoacán:** near base of Cerro de Tecolote near Zacapu, Sharp 45531 (RSA); Cerro del Burro, Santa Clara del Cobre, Pérez 53 (MEXU, MO), Escobedo 1400 (MO); Cerro Prieto, Nuevo Parangaricutiro, Medina 2684 (MEXU); En El Salto, a 7 km al E de Ocampo, Melchor Ocampo, Martínez & Torres 419 (MEXU); Ocampo, 11 km al SE de Ocampo, en el Cerro El Chivati, Soto Núñez & Solórzano 12609 (MEXU); Queréndaro, cerca de San José de la Cumbre, Santos 1301 (MEXU); ladera SW del Cerro San Andrés, Zinapécuaro, Zamudio 5520 (MEXU, MO); lado N de La Presa La Gachupina, Jasso 1029 (MEXU); ca. 18 mi. S of Pátzcuaro, King & Soderstrom 5189 (TEX, US); near Paricutín volcano, Eggler 34 (US). **Morelos:** km 48, carretera federal, Vázquez 1871 (MEXU [2]); Lagunas de Zempoala, *Straw & Gregory 1068 (GH, MEXU, MICH, RSA, UC); Huitzilac, ladera NE del Lago Hueyapan, Parque Nacional Lagunas de Zempoala, Avonce s.n. (MEXU). **Puebla:** 4 km E of Río Frío, Roe et al. 343 (MICH, US); side of Popocatepetl, Miranda & Barkley 17M200 (F, TEX); El Salto, Río Frío, Boeve 3073 (MEXU). **Veracruz:** Lomogrande, Mt. Orizaba, Balls 4377 (UC, US). Without locality: Gregg 697 (MO).

***Oenothera orizabae* W. L. Wagner, nom. nov.**
Hartmannia montana Rose, Contr. U.S. Natl. Herb. 8: 329. 1905, non *Oenothera montana* Nuttall, in Torrey & Gray, Fl. N. Amer. 1: 500. 1840. TYPE: Mexico. El Cima, on the railroad between México, D.F., and Cuernavaca, México, 19 Sep. 1903, J. N. Rose & J. H. Painter 7170 (holotype, US-00450745; isotypes, GH, MEXU, NY, US). Figure 3.

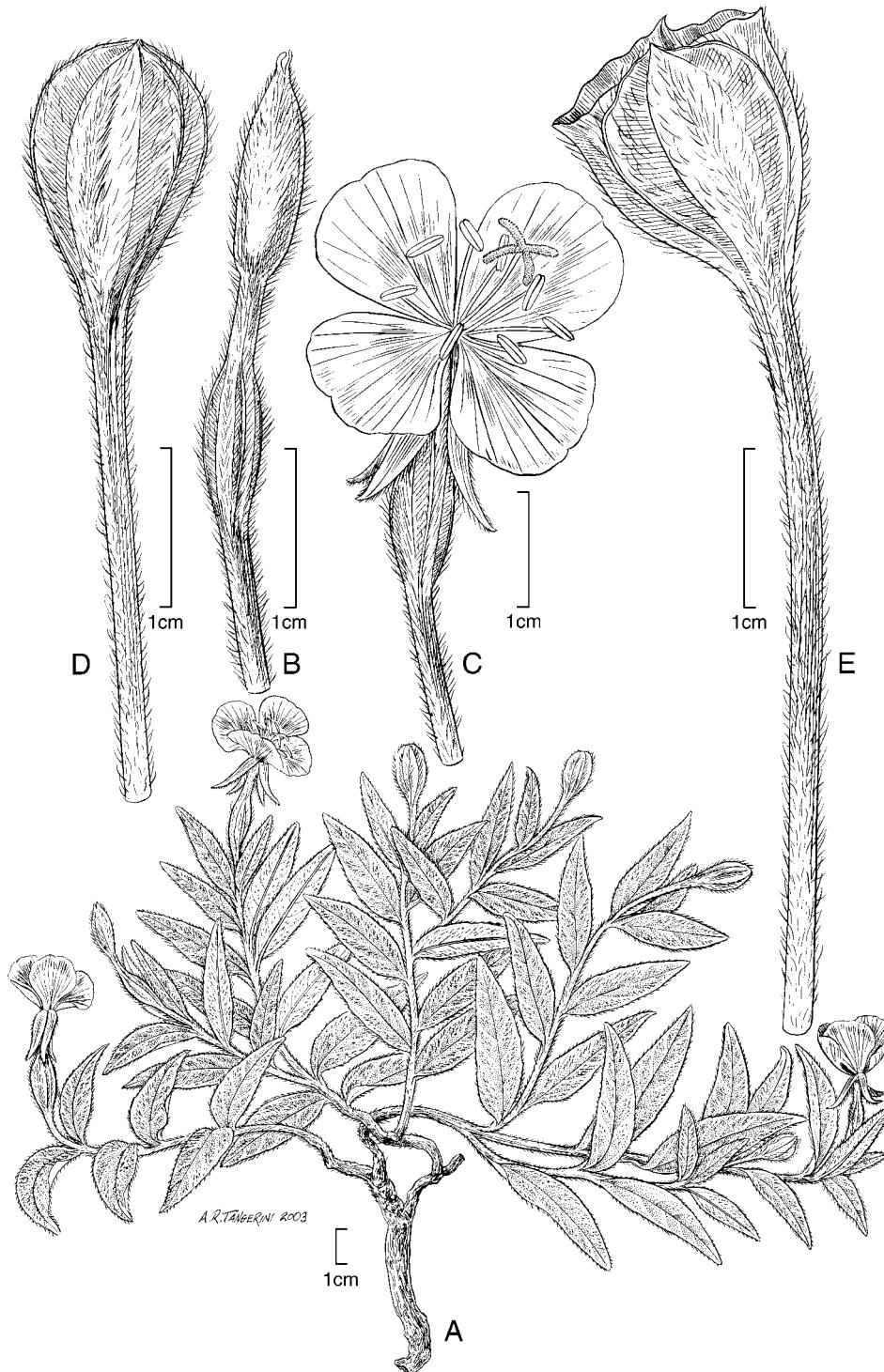


Figure 3. *Oenothera orizabae* W. L. Wagner.—A. Habit, showing decumbent stems from a multi-stemmed base (*Straw & Gregory* 1120, GH).—B. Bud, floral tube, and ovary, showing the free sepal tips and pubescence pattern (*Straw & Gregory* 1120, GH).—C. Flower, showing petal shape and expected non-overlap of petals (*Straw & Gregory* 1120, MICH).—D. Young capsule, showing shape, wings, rounded apex, and sterile stipe (*Rose & Painter* 7170, holotype, US).—E. Dehisced capsule, showing known length of dehiscence (*Rose & Painter* 7170, isotype, US).

Perennial herb with several decumbent to ascending, simple or usually branched stems, 6–46 cm long, the plant hirtellous throughout. Rosette leaf blades 3–5 × 0.9–1.5 cm, elliptic to oblanceolate, hirtellous; petioles 0.3–1 cm long. Cauline leaf blades 3–9 × 1–3 cm, narrowly ovate, occasionally elliptic, subentire to subdenticulate; petiole 0.1–2.2 cm long. Flowers opening near sunset; floral tube, sepals, and ovary densely hirtellous with hairs up to 1.5 mm long; floral tube 9–15 mm long; sepals 15–20 mm long; free tips in bud 1.7–2 mm long; petals 18–22 mm long, white, fading purple; filaments 15–16 mm long, pale maroon; anthers 3–7 mm long, cream; pollen cream-colored, > 90% fertile; style 20–28 mm long; stigmas held above the anthers at anthesis, the lobes 4–5 mm long. Capsule body 15–26 mm long, obovoid, apex rounded, the margins winged, the wings 2.3–4 mm wide; the sterile stipe stout, 15–50 mm long; capsule body apparently dehiscing only at apex; seeds 1–1.4 mm long, 0.5–0.7 mm thick, brown. Gametic chromosome number, $n = 7$ (forming 7 pairs at meiotic metaphase I; Gregory & Klein, 1960; Raven, unpublished).

Distribution. *Oenothera orizabae* is scattered in rocky grasslands in *Pinus-Quercus* forest at middle elevations in the Trans-Mexican Volcanos from Morelos and México to El Chico to the north in Hidalgo, and Pico Orizaba in Veracruz, at 2980–3000 m.

Oenothera orizabae appears to be allied to a group of evening-flowering species with white petals currently assigned to section *Hartmannia*, including *O. kunthiana* (Spach) Munz, and *O. tetrapetala* Cavanilles, but based on recent molecular studies this white-petaled group may need to be distinguished as a separate section (Levin et al., 2004). Another white-flowered species, *Oenothera dissecta* A. Gray ex S. Watson, may also belong in this group, but was most recently assigned to section *Gauropsis* (Wagner, 1984). A single collection was examined for pollen fertility using Alexander stain (Alexander, 1969).

*Specimens examined (those marked by * are chromosome determination vouchers and voucher for pollen fertility indicated by +).* MEXICO. **Distrito Federal:** 1 mi. SE of Puerto del Aire, Barkley et al. 2438 (MICH, TEX) [both sheets mixed with *O. deserticola*]; Estación La Cima, Pringle 10293 (F, GH, MEXU [2], MICH [2], MO, NY, UC, US), *Raven s.n. (Stanford greenhouse #67-354; flavonoid voucher) (TEX); Colonia del Valle, Lyonnet 198 (US); ca. 2 km SSW of La Cima R.R. Station, old Hwy. 95, Iltis et al. 200 (MICH, RSA); Volcán Pelado, ladera W, Sanderval 230 (MEXU). **Hidalgo:** El Chico, Lyonnet 2205 (MEXU). **México:** S of Mexico City, Leavenworth & Leavenworth 954 (F); 55 mi. SE of Mexico City, Weaver 713 (POM); near Gap, near Río Frío, Sharp 4495 (MEXU, RSA); pub-

lic park area W of divide betw. México & Puebla at the Estacionamiento, Pennell et al. 125 (MO); 1 km al N de Llano Grande sobre la ladera S del Telapón, Espinosa 542 (MO); Llano Grande, Telapón, +Lyonnet 689 (MEXU [2], US); near Río Frío, Puebla hwy., *Straw & Gregory 1120 (GH, MEXU, MICH [2], RSA); Río Frío, Kenoyer 2485 (GH); just W of Río Frío, 40 mi. E of Mexico City, Manning & Manning 53656a (GH). **Morelos:** Cuernavaca, Kenoyer A422 (F); 6 mi. W of Yautepec, Walther 133 (MICH). **Veracruz:** Pico de Orizaba, Rose & Hay 5672 (US).

Oenothera luciae-julianiae W. L. Wagner, sp. nov. TYPE: Mexico. Durango: San Dimas, Mesa del Roble, San Miguel de Cruces, 24.99°N, 105.99°W, 2740 m, 26 May 1990, A. García & S. Acevedo 345 (holotype, US-3441077; isotypes, ANSM, CHAPA, CIIDIR, ENCB, IEB, MEXU, UAMIZ (none seen)). Figure 4.

Ab *Oenothera orizabae* caulinibus erectis ad adscendentes, laminis foliorum caulinorum 0.5–1.1(–3) cm latis ellipticis ad lanceolatas et denticulatis ad serrulatas, corpe capsulae 8–18(–25) mm longo clavato vel anguste obovoideo ad apicem obtuso vel acuminato alis ejus 1.3–2 mm latis stipite sterili tenui 7–35 mm longo.

Perennial herb with few to several, ascending to erect, simple or occasionally branched stems, the longer ones becoming decumbent and often developing lateral branches, 20–50(–90) cm long, sparsely (very sparsely) to moderately hirtellous, the hairs 1.5–2.5 mm long, also strigillose throughout or only in the upper portions of the stem, the hairs mostly 0.3–0.4 mm long; root a thickened, often branched taproot. Rosette leaf blades 4–10 × 0.5–2.5 cm, oblanceolate, denticulate to serrulate, or weakly sinuate-toothed, sparsely to moderately strigillose, apex obtuse to rounded; petiole 0–1.5 cm long; cauline leaf blades (1.8–)3–7 × 0.5–1.1(–3) cm, elliptic to lanceolate or narrowly elliptic-ovate, denticulate to serrulate, apex attenuate, acute, sparsely to moderately strigillose; petiole 0–0.5 cm long. Flowers opening near sunset; floral tube, sepals, and ovary moderately to occasionally densely strigillose and rarely with scattered hirtellous pubescence with hairs up to 1.5 mm long; floral tube 12–21 mm long; sepals 14–24 mm long; free tips in bud 1–2 mm long; petals 16–26 mm long, white fading deep purplish red; filaments 7–10 mm long, rose-purple or yellow; anthers 4.8–6.5 mm long, cream; pollen cream, ca. 50–60% fertile (range 26–94%); style 20–30 mm long; stigma elevated above to surrounded by the shedding anthers at anthesis, the lobes 3.6–6 mm long. Capsule body 8–18(–25) mm long, gray-green, clavate or narrowly obovoid, apex obtuse to bluntly acuminate, winged in the upper part or throughout the



Figure 4. *Oenothera luciae-julianiae* W. L. Wagner. —A. Habit, showing ascending to erect stems from a several-stemmed base (*García & Acevedo* 345, US). —B. Bud, floral tube, and ovary, showing the free sepal tips and pubescence pattern (*Reveal & Harley* 4095, NY). —C. Flower, showing petal shape and apparent slight overlap (*García & Acevedo* 345, US). —D. Young capsule, showing shape, wings, obtuse to bluntly acuminate apex, and sterile stipe (*Reveal & Harley* 4095, TEX). —E. Dehisced capsule, showing known length of dehiscence, and valves (although they can be spreading) (*García & Acevedo* 345, US).

body, the wings 1.3–2 mm wide; sterile stipe slender, 7–35 mm long; capsule body dehiscing in upper half to nearly throughout; seeds clustered in each locule, 1.4–1.5 mm long, brown.

Distribution. *Oenothera luciae-julianiae* is scattered to common in open *Pinus* or *Pinus-Quercus* forests or mixed forests of *Abies*, *Pseudotsuga*, *Pinus*, *Quercus*, and sometimes with *Arbutus*, *Juniperus*, or *Cupressus*, on rocky or open sites, steep slopes, or moist flats or along streams in the Mexican mountains of the Sierra Madre Occidental from Chihuahua south through Durango, Guanajuato, Nayarit, Jalisco, Michoacán, and Querétaro, from 2100 to 2800(–3250) m. Flowering nearly throughout the year, and documented from February through November.

Etymology. It is a pleasure to name this attractive Sierra Madre Occidental species in honor of my wife, Lucy C. Julian, on the occasion of our 10th wedding anniversary.

Oenothera luciae-julianiae has gone undetected for decades of collecting in the Sierra Madre Occidental. The collections cited herein were determined most commonly as *O. deserticola* by P. H. Raven, myself, or others, but also occasionally as *O. pusilla*, *O. tetraptera*, or *O. kunthiana*. It was treated as part of *O. deserticola* (now correctly known as *O. orizabae*) by Raven and D. Parnell (pers. comm.) in their unpublished revision of section *Hartmannia*. Munz, who revised the section in 1932, never annotated any of the collections, as very few were made before 1960. J. N. Rose, however, annotated a single collection from Chihuahua (Nelson 4848) as a new species, but he never published it. *Oenothera luciae-julianiae* appears to be allied to a group of evening-flowering species with white petals currently assigned to section *Hartmannia*, including *Oenothera orizabae*, *O. kunthiana* (Spach) Munz, and *O. tetraptera* Cavanilles.

Like *Oenothera kunthiana* of this white-flowered species group of section *Hartmannia*, *O. luciae-julianiae* appears to be a permanent translocation heterozygote (PTH) species. In PTH species a ring of 14 chromosomes is usually formed in meiotic metaphase. I have not yet been able to obtain cytological material to examine meiosis in this species, and thus current data are only suggestive of this condition in *O. luciae-julianiae*. PTH species in the Onagraceae are nearly always autogamous (Raven, 1979). The stigma is usually surrounded by the shedding anthers at anthesis in *O. luciae-julianiae*, suggesting that it is predominately autogamous. Another feature of PTH species is the balanced lethals in pollen and ovules, which can be

observed in lowered pollen fertility and fewer mature seeds (see Cleland, 1972). I examined pollen fertility of as many collections as possible of *O. luciae-julianiae*. In the 15 collections I examined with Alexander stain (Alexander, 1969; vouchers noted with brackets in the exsiccatae) pollen fertility ranged from 26% to 94%, a very wide range, but suggestive nevertheless that *O. luciae-julianiae* is probably a PTH species. Typically, PTH species have about 50% pollen fertility on average, but all exhibit a range of fertility. For example, *Oenothera nutans* G. F. Atkinson & Bartlett exhibited a similar wide range of fertility (48% to 84%) in a detailed study (Wasmund, 1990). Raven (1979) pointed out that most PTH species are annuals or biennials, with about 10% of the known PTH species in Onagraceae being perennial. If *O. luciae-julianiae* proves to be a PTH species, it will represent another atypical species, as it clearly has a perennial habit from an enlarged root. *Oenothera luciae-julianiae* does not appear to be closely related to other species of the white-flowered species group of section *Hartmannia*. It may share a common ancestor with *O. tetraptera*, an outcrossing pair-forming species that appears to be directly related to the other PTH species in this group, *O. kunthiana*.

Paratypes (those used to study pollen fertility have % fertile pollen given in square brackets). MEXICO. **Chihuahua:** ca. 51 mi. S of Creel, Straw & Forman 1900 (RSA) [26%]; Llano Grande, Pennington 181 (TEX) [37%]; Guachochi, 8 km al W de Cabórachi, Hernández 8778 (MEXU); Ocampo, Cascada de Basaseachi, Tenorio & Torres 4510 (MEXU); Urique, Bye et al. 15612 (MEXU) [90%], Tenorio et al. 9935 (MEXU) [62%]; base of Mt. Mohinora, 8 mi. from Guadalupe y Calvo, Nelson 4848 (US). **Durango:** Canelas, Bolaños 1565 (MEXU); 55–60 km SW of Durango City on road to La Flor, Breedlove 44134 (MO); from the Sierra Madre, W of Durango, Forrer 12 (UC); ca. 77 rd. km S of Durango by hwy. to La Flor, Worthington 8826 (MO); 48 km NW of Huejuquilla El Alto, Jalisco to Canoas, Breedlove & Almeda 59165 (MO); 6 mi. E of Buenos Aires tow. El Salto, Straw & Forman 1795 (RSA) [83%]; 31 mi. N of Estacion Coyotes, Breedlove 18741 (MO); 54 mi. N Estacion Coyotes, just NW of Guachichilas, Breedlove 18783 (MO) [59%]; 71 mi. W of Durango, E of La Campaña, Oliver 715 (MO); 11 km SW of La Ciudad near Buenos Aires, Breedlove 36465 (MO) [27%]; Hwy. 40, 11.5 mi. W of La Ciudad, Wagner & Solomon 4303 (MO); Hwy. 40, at La Campana, Reveal et al. 2689 (MO) [74%]; Hwy. 40, about 81 mi. W of Durango, Reveal & Atwood 3477 (MO) [39%]; betw. Pinos Altos & Concheño, Hewitt 118 (GH) [88%]; El Salto, El Tapextle, Tenorio & Romero 816 (MEXU); 1 km al SW de El Salto, Tenorio & Romero 927 (MEXU); “Arroyo de El Salto” al N de El Salto, Tenorio & Romero 759 (MEXU); 17 mi. W of El Salto, Waterfall 12693 (GH, US) [35%]; 25 mi. E of El Salto along Mexican Hwy. 40, Breedlove 15753 (MO); 7 km W of Llano Grande, Hendrickson 1704 (RSA) [72%]; ca. 120 road mi. NW of Santiago Papasquiaro, Spellenberg & Zimmerman 6683 (MO, NMC); 10

mi. W of El Salto on Mazatlan rd., *Straw & Gregory* 1270 (RSA); Sierra Madre Occidental, 5.1 rd. mi. by hwy. 40 SW of El Salto at Arroyo de Agua, *Worthington* 8902 (MO); Durango, Ejido Ciénega de Los Caballos, *Ortega & Pacheco* 81 (CIIDIR, IEB, MEXU, US); Ejido, Encina, *Ortega* 20 (CIIDIR, US); El Mezquital, El Zapote, *Solís* 902 (CIIDIR, US); La Guajolota, *García* 260 (CIIDIR, US); Laguna del Chivo, *Acevedo* 445 (CIIDIR, IBUG, US); Las Minas, *Solís* 11 (CIIDIR, US); Nombre de Dios, San José de La Parrilla, *Sánchez* 455a (US), 544 (CIIDIR, US); Pueblo Nuevo, El Salto, *Valenzuela* 3–25 (CIIDIR, US); Predio Las Bayas de la UJED, *García & Acevedo* 980 (US); San Bernardino de Milpillas Chico, *Sánchez* (INI) 9 (US), 19 (CIIDIR, US); San Francisco de Lajas, *I.N.I.* 31 (CIIDIR, US); Santa Bárbara, *García* 1137a (US); San Dimas, Los Aposentos, *García* et al. 435 (CIIDIR, US). **Guanajuato:** Guanajuato, Rincón del Toro, *Martínez* 760 (MEXU [2]); Cañada de la Virgen, Agua Sabrosa, *Martínez* 935 (MEXU); 34–35 mi. E of San Luis de la Paz tow. Xichu, *Straw & Forman* 1474 (MEXU, RSA). **Jalisco:** 14–18 km SW of Tequila on Volcán de Tequila, *Breedlove* 39226 (MO) [47%]; Volcán Tequila, *Reveal & Harley* 4095 (F, MEXU, MO, NY, TEX) [94%]. **Michoacán:** betw. Los Cabras & Pueblito, Chilchota to Zacapú, *Sharp* 45507 (RSA). **Nayarit:** 105 km WNW of Huejuquilla El Alto along road to Jesus María, *Breedlove* 61508 (MO) [94%]. **Querétaro:** Colón, parte alta del Cerro Zamorano, *Rzedowski* 44449 (MICH).

Acknowledgments. The holotype and the distribution of isotypes of *Oenothera luciae-julianiae* were kindly provided by S. González. Thanks are given to Alice Tangerini for the preparation of the three excellent plates that amply demonstrate the distinctions among these difficult species of *Oenothera* sect. *Hartmannia*. I thank Denise Mix for comments on the manuscript, compilation of the specimens examined, assistance with the loans, and preparation of Figure 1. I appreciate translations of the diagnosis of *O. luciae-julianiae* to Latin provided by Dan Nicolson, and the translation of the abstract into Spanish by Pedro Acevedo. I greatly appreciate the help of Socorro González in obtaining

an excellent set of collections of *O. luciae-julianiae* from the region surrounding Durango, including the type. Finally, I am grateful to Peter Hoch for his excellent comments during the review process, which improved the clarity and accuracy of this paper.

Literature Cited

- Alexander, M. P. 1969. Differential staining of aborted and non-aborted pollen. *Stain Technol.* 44: 117–122.
Cleland, R. E. 1972. *Oenothera* Cyogenetics and Evolution. Academic Press, London.
Gregory, D. P. & W. M. Klein. 1960. Investigations of meiotic chromosomes of six genera in the Onagraceae. *Alioso* 4: 505–521.
Katinas, L., J. Crisci, W. L. Wagner & P. C. Hoch. In press. Geographical diversification of tribes Epilobieae, Gongylocarpeae, and Onagreae (Onagraceae) in North America. *Ann. Missouri Bot. Gard.*
Levin, R. A., W. L. Wagner, P. Hoch, M. Nepokroeff, J. C. Pires, E. A. Zimmer & K. J. Sytsma. 2003. Family-level relationships of Onagraceae based on chloroplast *rbcL* and *ndhF* data. *Amer. J. Bot.* 90: 107–115.
_____, _____, _____, W. J. Hahn, A. Rodriguez, D. A. Baum, L. Katinas, E. A. Zimmer & K. J. Sytsma. 2004. Evolutionary relationships among and within Tribes Onagreae and Epilobieae (Onagraceae). *Syst. Bot.*, in press.
Loesener, L. E. T. 1913. Mexikanische und zentralamerikanische Novitäten. IV. *Repert. Sp. Nov.* 12: 217–244.
Munz, P. A. 1932. Studies in Onagraceae VIII. The subgenera *Hartmannia* and *Gauopsis* of the genus *Oenothera*. The genus *Gayophytum*. *Amer. J. Bot.* 19: 755–778.
_____. 1965. Onagraceae. N. Amer. Fl. II. 5: 1–278.
Raven, P. H. 1979. A survey of reproductive biology in Onagraceae. *New Zealand J. Bot.* 17: 575–593.
Rose, J. N. 1905. Studies of Mexican and Central American plants—No. 4. *Contr. U.S. Natl. Herb.* 8: 281–339.
Wagner, W. L. 1984 [1985]. Reconsideration of *Oenothera* subg. *Gauopsis* (Onagraceae). *Ann. Missouri Bot. Gard.* 71: 1114–1127.
Wasmund, O. 1990. Cytogenetic investigations on *Oenothera nutans* (Onagraceae). *Pl. Syst. Evol.* 169: 69–80.