Species Status for a Sonoran Desert Annual Member of *Oenothera* sect. *Anogra* (Onagraceae)

Warren L. Wagner
Department of Botany, MRC 166, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.
Email: wagner.warren@nmnh.si.edu

ABSTRACT. The taxon most recently known as *Oenothera avita* W. Klein subsp. *arizonica* (Munz) Klein is here elevated to species level. It is easily distinguished from the perennial taxa of this complex, currently treated as three subspecies of *O. californica*, by its annual habit with a taproot, stems thickened near the base and tapering toward the apex, buds with conspicuous purple spots, each spot at the base of a long hair, longer attenuate capsules, and pinnatifid leaves.

In preparation of treatments for the *Flora of Arizona* and *Flora of North America* I here raise to specific level an annual member of *Oenothera* sect. *Anogra*. It has been most recently known as *Oenothera avita* Klein subsp. *arizonica* (Munz) Klein (Klein in Munz, 1965). In this paper I will review the biosystematic information about the plant and discuss why it should be treated at the rank of species.

Munz (1931) described *Oenothera deltoides* Torrey & Frémont var. *arizonica* Munz for the distinctive plants of *Oenothera* sect. *Anogra* with an annual habit from a taproot, stems thickened near the base and tapering toward the apex, buds with conspicuous purple spots, each spot at the base of a long hair, longer attenuate capsules, and pinnatifid leaves from the Sonoran Desert in central and southwestern Arizona. That these distinctive populations deserved formal recognition has never been questioned; rather the controversy has been at what taxonomic level they should be recognized and to what taxon they were most closely related. Because of its annual habit Munz (1931) included it in the annual desert species *O. deltoides*. William Klein transferred it, based on detailed biosystematic study of several species of *Oenothera* sect. *Anogra* from the western United States (1962, 1964, 1970, in Munz, 1965), to the perennial species *O. californica* (S. Watson) S. Watson in 1962. This species included four subspecies: subsp. *californica* from southern California, subsp. *avita* Klein from interior California to northern Arizona, Nevada, and southwestern Utah, subsp. *eurekensis* (Munz & Roos) Klein, and subsp. *arizonica*. He later restricted the circumscription of *O. californica* to include only the more western taxon (subsp. *californica*) of the complex because it was an autotetraploid, and the other taxa were diploid. He described a new species for the three diploid taxa, *O. avita* Klein. I have reviewed all of the information from past studies and compared the morphology in limited field studies and extensive herbarium study of all taxa included within *O. deltoides*, *O. californica*, and its segregate *O. avita*. Recently, I treated the perennial autotetraploid populations (*O. californica* s. str.) and the diploid ones (*O. avita*) as one species (Wagner, 1993) because they share many morphological features, the differentiating characters intergrade extensively, and the polyploid taxon is an autotetraploid of apparent recent origin. Here I discuss the data on the Arizona annual populations and provide justification for proposing the new combination to recognize it as a distinct species.

Klein transferred *Oenothera deltoides* var. *arizonica* to *O. californica* and then to *O. avita* primarily because it shared a high level of chromosomal end arrangements, differing from *O. californica* subsp. *avita* by only a single reciprocal translocation (5_{II} + ⊙ 4) in experimental crosses (1962, 1964, 1970). Additional data for his decision were obtained from pollen fertility of experimental hybrids. He easily obtained hybrids between the Arizona annual and both the perennial *O. avita* subsp. *avita* and *O. avita* subsp. *eurekensis*. The hybrids had 62–96% and 54–99% pollen fertility, respectively, a similar level of fertility found in crosses between the perennial taxa of the complex, but more variable and usually somewhat lower fertility than interpopulational within-taxon crosses (Klein, 1964, 1970). He also obtained hybrids between *O. avita* subsp. *arizonica* and two of the subspecies of *O. deltoides*, where this taxon had been originally placed by Munz. These hybrids had reduced pollen fertility ranging from 24% to 60%

(Klein, 1964, 1970). I concur with Klein that these data suggest that the Arizona annual appears to be less genetically differentiated from the perennial taxa of *O. avita* (= *O. californica*) than the annual taxa of the *O. deltoides* complex. Because crossability represents a plesiomorphic trait, these data do not necessarily reflect the relationships among the taxa and should be used with caution.

The primary reason I propose species-level recognition for the Arizona plants is that they are morphologically divergent from both *O. deltoides* and the perennial taxa I treat as *O. californica*, and are genetically differentiated based on crossing relations and chromosome end arrangements from *O. deltoides*. They are strikingly divergent morphologically from *O. californica* in the annual habit from a taproot, stems thickened at base and tapering toward the apex, buds with conspicuous purple spots, each spot at the base of a long hair, longer attenuate capsules, and pinnatifid leaves. They are at odds with placement back into *O. deltoides* because of the presumed relationships derived from Klein's work, although they share with it an annual taprooted habit, long attenuate capsules, and stems thickened basally.

Klein indicated allopatry for *Oenothera californica* and *Oenothera arizonica*, but also mentioned naturally occurring intermediates between them (1964, 1970), though he did not cite any collections or localities. I have studied material from throughout the range of *O. arizonica* and have not found any intermediates. *Oenothera arizonica* occurs in the northern portion of the Sonoran Desert east of the Colorado River from Maricopa and Yuma Counties east to Pima, Pinal, and Cochise Counties and scattered collections from northwestern Sonora, Mexico. *Oenothera californica* occurs exclusively west of the Colorado River in the southern part of its range and to the east of it only in Mohave County, Arizona, and southwestern Utah. I surmise that Klein's comment about intermediates must mean that he thought they approached each other morphologically.

Klein's study was done at a time when crossing studies and chromosome cytology were relatively new tools being successfully applied to a wide variety of systematic questions. At that time, the combination of limited knowledge of crossing patterns in *Oenothera* other than in section *Oenothera* and a strong emphasis on the phylogenetic value of the fertility of hybrids and cytological information led Klein to develop a classification that was more natural than previous ones, but that had very broadly delimited species. We now know that in *Oenothera* interspecific hybrids within a section nearly always are highly fertile (Stubbe & Raven, 1979; Wagner et al., 1985; Dietrich et al., 1985, 1997; Dietrich & Wagner, 1988; Wagner, unpublished), and thus high crossability alone usually is not a good basis for delimiting species in *Oenothera* or most other genera of the Onagraceae. I have not seen any intermediates between *O. arizonica* and any other taxa of the section, and see no reason to include *O. arizonica* within any other species, despite the viable hybrids that can be obtained experimentally, especially with the perennial *O. californica*. Another reason to treat them as distinct species is that they are geographically allopatric. By contrast, there is a broad range of intermediacy between the diploid *O. californica* subsp. *avita* and the autotetraploid *O. californica* subsp. *californica*. The single reciprocal translocation difference found by Klein between *O. arizonica* and *O. californica* would not be sufficient to treat *O. arizonica* as a distinct species since translocations are very common within many species of *Oenothera*. The distinctive annual habit along with the other morphological characters show that *O. arizonica* has differentiated relative to *O. californica*.

Oenothera arizonica (Munz) W. L. Wagner, comb. et stat. nov. Basionym: *Oenothera deltoides* Torrey & Frémont var. *arizonica* Munz, Amer. J. Bot. 18: 315. 1931. *Oenothera californica* (S. Watson) S. Watson subsp. *arizonica* (Munz) Klein, Aliso 5: 179. 1962. *Oenothera avita* (Klein) Klein subsp. *arizonica* (Munz) Klein, in Munz, N. Amer. Fl. ser. II, 5: 116. 1965. TYPE: U.S.A. Arizona: Pima Co., Grosetta Ranch near Tucson, 730 m, 28 Apr. 1903, *J. J. Thornber 509* (holotype, UC-128066 not seen; isotypes, MO, US-661488).

Oenothera deltoides Torrey & Frémont f. *floccosa* Munz, Amer. J. Bot. 18: 315. 1931. TYPE: U.S.A. Arizona: Maricopa Co., Tempe, 18–27 May 1903, *D. Griffiths 4317* (holotype, US-660165; isotype, MO).

Winter or spring taprooted, annual herb; stems 1–3.5(–6) dm long, thickened at the base and tapering toward the apex, unbranched or with few to several decumbent branches arising from the base, the older stems glabrate and the epidermis exfoliating, the younger portions sparsely to densely strigillose and sparsely to densely hirsute, the longer hairs straight or curved, erect or spreading, 1.3–2 mm long, sometimes the inflorescence and the flowers densely hirsute, the hairs then often crinkled or somewhat curled, and up to 2.5 mm long. Rosette leaves 5–10(–26) cm long, 0.6–1.5(–3.5) cm wide, lanceolate to oblanceolate, pinnatifid, apex acute,

base attenuate to the petiole, petiole 1.5–12 cm long. Cauline leaves 5–8(–15.5) cm long, 1–2 cm wide, lanceolate or oblanceolate, pinnatifid or sometimes coarsely serrate, the lobes sometimes widely spaced, apex acute to long-acute, base attenuate, petioles 0–5 cm long. Flowers axillary in the upper half of the stem, opening near sunset. Floral tube 2.6–3.1 cm long, yellowish green or flushed with red. Buds oblong to narrowly oblong-oblanceoloid, 1.2–1.6 cm long, without free sepal tips. Sepals 1.9–2.6 cm long, green, flushed with red and conspicuously purple-spotted, each spot at the base of a long hair, pubescence same as the floral tube. Petals 1.6–2.6(–3.6) cm long, white, yellow to pale yellow at the base, obcordate, fading pink to deep pink. Anthers 7–9 mm long; pollen 90–100% fertile. Filaments 9–15 mm long. Ovary 2.1(–6) cm long. Style 4.5–5 cm long; stigma elevated above the anthers at anthesis, the lobes 5–10 mm long. Capsules 3–8 cm long, 2.5–3.5 mm diam. at the base, woody at maturity, 4-angled especially toward the base, curved upward, cylindrical attenuate to the apex, pubescence similar to that of the ovary but less dense, the valves separating to the base, sinuous with the upper 5–7 mm often recurved. Seeds 1.6–1.9 mm long, the testa minutely ridged under magnification, light brown to yellowish brown with dark purple splotches. Chromosome number, $n = 7$ (7_{II}; ⊙4 and 5_{II}; 2 ⊙4 and 3_{II}; based on 6 individuals from one locality; Klein, 1964, 1970). Self-compatible, but mostly outcrossing (Klein, 1964, 1970).

Phenology. Flowering from February through May, but mostly in April, rarely in October (*Felger et al. 14982*).

Distribution. Occurring in gravelly or sandy soils, usually along watercourses or other disturbed sites, 270–1370 m elevation, in southern Arizona from Maricopa and Yuma Counties to Cochise County, and from scattered localities in northern Sonora, Mexico, including Cerro Tepopa, Puerto Libertad, and Tastiota. The populations from southwestern Arizona (Yuma Co.) southward to Sonora often grow on low dunes (R. Felger, pers. comm.).

Specimens examined. MEXICO. **Sonora**: NW side of Cerro Tepopa, ca. 10 mi. S of El Desemboque San Ignacio, dunes (29°22′N, 112°24′W), *Felger et al. 14982* (ARIZ, MO); coastal dunes 1 km S of El Desemboque San Ignacio (vicinity 29°30′N, 112°28′W), *Felger et al. 12443* (ARIZ), *Felger & Edmundson 16995* (ARIZ); desert plain near N side of Cerro Tepopa, 0.5 mi. W of 9.2 mi. by road S of El Desemboque San Ignacio (29°23′N, 112°25′W), *Felger et al. 14122* (ARIZ); 13.2 mi. by road S of El Desemboque San Ignacio, middle bajada, *Felger & Bezy 14173* (ARIZ); 6 km S of Puerto Libertad, edge of big dune, 24 Feb. 1978, *Martin* (ARIZ); 1.8 km NNE of Punta Cirio, Sierra Bacha, 7.2 km (by air) SE of Puerto Libertad, on Pleistocene dunes, 30 m, 29°51′10″N, 112°38′20″W, *Van Devender et al. 91–27* (ARIZ); ca. 1 mi. NW of Tastiota, high beech dunes, vicinity 28°20.5′N, 111°30.3′W, *Felger et al. 20872* (ARIZ). U.S.A. **Arizona**: Maricopa Co., Gila River Canyon, *Mohr 273* (US); near Marinette [33°35′44″N, 112°16′47″W], *Peebles & Loomis 6709* (US); Salt River bottom lands near Phoenix, *Nelson & Nelson 1683* (MO), *Gillespie 5627* (US); Stewart Mt., near Salt River [33°34′55″N, 111°33′25″W], *Gillespie 5465* (US); 1.3 mi. SE of Surprise, along Hwy. 60–89–93 in Sun City [33°35′51″N, 112°16′16″W], *Wagner & Mill 4567* (MO), *Mill & Wagner 8* (MO); vicinity of 91 Ave. and the Gila River, SW Phoenix, *Lehto & Schuessler 18050* (MO); Jct. Baseline Rd. and 91st Ave. growing with *O. deltoides* subsp. *deltoides*, *Rea 790* (ARIZ). Pima Co., near Growler Pass [32°11′N, 112°55′W], *Kearney & Peebles 10856* (US); sparingly on mesa about Tucson, *Toumey 157* (US); Tucson, 4 May 1905, *Wilcox s.n.* (US); vicinity of Tucson, *Rose 11878* (US); near Tucson, *Peebles, Harrison & Kearney 1273* (US); Santa Cruz Valley, Grosetta's Ranch, 29 Apr. 1902, *Thornber & Thornber s.n.* (MO), 12 May 1903, *Thornber & Thornber s.n.* (MO). Pinal Co., near Florence [33°15′34″N, 111°20′11″W], *Peebles 1688* (US); near Sacaton [33°04′N, 111°44′W], *Peebles 1730* (MO); Casa Grande, *Peebles & Harrison 3536* (US); Gila River near Casa Grande Ruins [National Monument, 32°59′49″N, 111°31′53″W], *Nelson & Nelson 1678* (MO, US). Yuma Co., Pinta Sands along Camino del Diablo, Cabeza Prieta National Wildlife Refuge (32°08′N, 113°33′W), dunes, *Felger & Huddy 92–36* (ARIZ [2], MO). Without further locality, *Palmer 596* (US).

The specimen from Yuma Co., Pinta Sands along Camino del Diablo, Cabeza Prieta National Wildlife Refuge (*Felger & Huddy 92–36*) is a large phenotype of *Oenothera arizonica*. It differed from all other specimens only in the size of both the vegetative parts and the flowers, and all of the atypical measurements given in the description are from this specimen except for stem length. It may represent a robust form that grows on dunes. *Oenothera arizonica* typically grows on dunes in Sonora, but rarely so in Arizona. Populations growing on dunes should be studied further and compared to non-dune populations in the northern and eastern portion of the range.

Acknowledgments. I appreciate the useful comments on a draft of this manuscript by Werner Dietrich, Peter Hoch, and Robynn Shannon. Richard Felger kindly provided copies of the specimen records from ARIZ and useful comments on the species distribution and ecology.

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