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# Systematics of *Oenothera* Sections *Contortae*, *Eremia*, and *Ravenia* (Onagraceae)

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ABSTRACT. Previous classifications based on morphology recognized a distinctive but poorly delimited group of species from western North America as *Oenothera* subg. *Pachylophus*. In earlier papers, I split this group into four sections more comparable to others in the genus, but nevertheless assumed the whole group was monophyletic based on morphological analyses. Recent molecular analyses indicate that the morphological analysis was incorrect, however, and suggest instead that the sections are part of a basal grade within the genus. The two yellow flowered sections are shown by the molecular study to be sister taxa, yet because of highly distinctive morphology, especially of the capsules and seeds, I maintain them as separate sections, sect. *Contortae* (*O. xylocarpa*) and sect. *Eremia* (*O. primiveris*) comparable to others in the genus. The two white flowered sections, sect. *Pachylophus* (*O. brandegeei*, *O. cespitosa*, *O. cavernae*, *O. harringtonii*, and *O. psammophila*) and sect. *Ravenia* (*O. muelleri*, ***O. riskindii***, and *O. tubifera* with two subspecies, *tubifera* and ***macrocarpa***), are not so closely related and the shift to white petals appears to have been independent. Detailed taxonomic descriptions are given for the species of sects. *Contortae*, *Eremia*, and *Ravenia*. Taxonomic treatment of the species of sect. *Pachylophus* was given elsewhere.

The species treated in this paper were most recently included in *Oenothera* subg. *Pachylophus* (Munz 1965; Raven 1970). Spach (1835a, 1835b, 1835c) established the name when he segregated *Oenothera cespitosa* from *Oenothera* as the genus *Pachylophus*. He did this as part of a generic revision of the Onagraceae that divided the family into small homogeneous groups of species. His narrow generic concept generally was not accepted by others at that time, although, in his *Genera Plantarum*, Endlicher (1840) treated 10 of Spach's genera, including *Pachylophus*, as sections of *Oenothera*. In fact, Spach's genera continue to form the basis of most of the current sectional classification of the genus (Wagner et al. 1985; Dietrich et al. 1997).

The first detailed evaluation of *Pachylophus* and related species was made by Munz (1931) as one of his series of revisionary studies of *Oenothera*. He followed Jepson (1925) in recognizing *Pachylophus* as a subgenus, but expanded it to include, in addition to *O. cespitosa*, the white-flowered *O. tubifera* and two yellow-flowered species, *O. xylocarpa* and *O. primiveris*. He later (Munz 1941) added *O. cavernae* to subgenus *Pachylophus*. Munz characterized the subgenus primarily by its cylindrical to ovoid, thick-walled capsules and seeds with a raphial groove. When Munz (1965) summarized his work on *Oenothera* in the *North American Flora,* he recognized *Oenothera* subg. *Pachylophus* as one of the nine subgenera with stigmas divided into four linear lobes.

Subsequently, Raven (1970) considered the relationships of the subgenus and suggested adding another white-flowered species, *Oenothera muelleri*, and the yellow-flowered *O. macrosceles*, both previously placed in subg. *Raimannia* by Munz (1965). Raven also raised *O. brandegeei* of central Baja California to specific level and included it in the subgenus. These rearrangements gave *Oenothera* subg. *Pachylophus* a total of eight species, which he tentatively divided into four subgroups: *O. cespitosa*, *O. cavernae*, and *O. brandegeei* with white flowers and stout, tuberculate capsules; *O. xylocarpa* and *O. primiveris* with yellow flowers and stout, acutely angled, nontuberculate capsules; *O. macrosceles* with yellow flowers and slender, quadrangular, nontuberculate capsules; and *O. muelleri* and *O. tubifera* with white flowers and stout, obtusely angled, nontuberculate capsules. Raven (1970) suggested that these eight species were related and could be treated as constituting one somewhat heterogeneous subgenus or alternatively as four distinct sections. He emphasized that further detailed biosystematic studies were necessary to determine the best classification.

A survey of crossing relationships of *Oenothera* sect. *Oenothera* (Stubbe and Raven 1979) showed that fertile hybrids could be obtained between *O. macrosceles* and both *O. maysillesii* and *O. organensis*. Further, *O. macrosceles* shares a number of morphological features with these species including long decumbent stems, yellow flowers, slender, nontuberculate capsules and seeds with a small cryptic internal cavity at the distal end (Dietrich et al. 1985). Based on these similarities, *O. macrosceles* was transferred to *Oenothera* sect. *Oenothera* subsect. *Emersonia* (Stubbe and Raven 1979; Dietrich et al. 1985). Recent molecular study (Levin et al. 2004) confirmed the placement of *O. macroseles* within sect.*Oenothera* but not the monophyly of subsect. *Emersonia*.

Detailed studies of crossing relationships, cytology, and seed morphology and anatomy in a phylogenetic context supported the distinctiveness of Raven's subgroupings of subg. *Pachylophus* (Stockhouse 1973; Wagner et al. 1985; Wagner 1986; Tobe et al. 1987). Wagner (1986) choose to recognize each of them as sections with *O. cespitosa* and four related species in sect. *Pa-*

*chylophus*, *O. muelleri* and *O. tubifera* in a new sect. *Ravenia*, and *O. primiveris* and *O. xylocarpa* each assigned to new unispecific sections, *Eremia* and *Contortae* respectively. The Morphological phylogenetic analyses, especially of seed features by Wagner et al. (1985) suggested that *O. cespitosa*, *O. cavernae*, *O. brandegeei*, and two species described in that paper formed a monophyletic group (sect. *Pachylophus*) mostly closely related to *O. primiveris* (sect. *Eremia*) and *O. xylocarpa* (sect. *Contortae*). The analyses suggested that these lineages were related in turn to *O. muelleri* and *O. tubifera* (sect. *Ravenia*). Species of subsect. *Emersonia* were used as the outgroup for this study.

The primary focus of this paper is to present details of this revised sectional classification of the group delimited as ''subg. *Pachylophus*'' based on the studies by Raven (1970), Stockhouse (1973), and Wagner et al. (1985), and on new data from capsule and seed morphology, cytology, crossing relationships, breeding systems, herbarium study of over 500 collections, and field and greenhouse study of most of the species during 1979–1981. Especially significant data comes from a genus-wide study of seed anatomy (Tobe et al. 1987) and from recent molecular phylogenetic studies (Levin et al. 2003, 2004). An expanded taxonomic treatment of all of the species in this group is presented, except the white flowered, tuberculate-capsuled *O. cespitosa* group (sect. *Pachylophus*). A full systematic account of the species of sect. *Pachylophus* has been presented by Wagner et al. (1985).

Lewis and Lewis (1955) established a narrow sectional concept in their studies of *Clarkia*. This concept has been adopted subsequently in all systematic studies in the family Onagraceae by P. H. Raven and various collaborators. Sections are composed of very closely related species that share numerous morphological and anatomical features, and based on crossing studies, have similar genomes and plastomes.

Revisionary studies of most of the sections of *Oenothera* have been published, with each publication of the series usually covering one or more sections (Dietrich 1977; Straley 1977; Raven et al. 1979; Wagner 1984; Dietrich et al. 1985, 1997; Wagner et al. 1985; Dietrich and Wagner 1988). The completion of the sections revised in this paper leaves only revisions of sects. *Anogra*, *Hartmannia*, *Lavauxia*, and *Megapterium* unpublished, although these sections have been studied in detail (Klein 1964, 1970; Raven and Parnell 1969 unpubl.; Wagner unpubl.).

An important conclusion emerging from the detailed studies of *Oenothera* is that although there are groups of closely related species of *Oenothera* that have been treated as sections, grouping sections into distinctive higher level taxa (i.e., subgenera) has not seemed possible, or, at least at present, desirable. The study of seed anatomy (Tobe et al. 1987) and molecular phylogentic study (Levin et al. 2004), however, suggested that eventually it may be possible to subdivide the genus into two monophyletic groups.

## DISTRIBUTION AND HABITAT

The species of sects. *Pachylophus*, *Eremia*, *Contortae*, and *Ravenia* occur in western North America, the geographical region with the highest concentrations of sections of the genus (Fig. 1). The evolution of each of these sections has involved ecological specialization. They are also isolated geographically from each other except that *Oenothera cavernae* and sometimes *O. cespitosa* (both sect. *Pachylophus*) occur together with *O. primiveris*, the only member of the sect. *Eremia*. Moreover, species of sections *Ravenia* and *Contortae* have disjunct distributions. Based on their occurrence in xeric and submesic vegetation types derived from generalized Madro-Tertiary vegetation, the diversification of these sections may well have been linked to the Pliocene spread of dry climates, especially from the mid-Pliocene onward (Wagner et al. 1985). During this time, many plant groups radiated from the more southern, warm Madro-Tertiary vegetation into the cooler, drier climates that were rapidly spreading in western North America.

The species of sect. *Pachylophus* s.s., consisting of *Oenothera cespitosa* and four closely related species, occur in a wide variety of habitats (Wagner et al. 1985) centering around the Great Basin region, but they have spread widely to the Great Plains, to all three North American deserts, and to montane habitats in the Rocky Mountains and desert mountains of Nevada, Utah and California. Two of the species, *O. cavernae* and *O. brandegeei*, are narrow endemics in xeric desert vegetation types. *Oenothera cavernae* occurs in desert scrub throughout the Grand Canyon and in and around the low calcareous mountains of Clark County, Nevada. Similarly, *O. brandegeei* is known only from among volcanic rocks above Bahia de los Angeles and Isla Angel de la Guarda in central Baja California.

*Oenothera harringtonii* occurs in slightly more mesic silty clay soils in the foothill grasslands along the Front Range in southeastern Colorado. *Oenothera psammophila* is extremely restricted, known only from one sand dune system in Fremont County, Idaho, where populations occur only on the interface between lava rocks and the unstable sand dunes.

The polymorphic *Oenothera cespitosa* is one of the more widespread species of the genus, ranging from southern Canada and North Dakota south to southeastern California, Trans-Pecos Texas, and northern Chihuahua, Mexico. The five subspecies of this polymorphic species occur in Mojave and Great Basin Desert scrub, pinyon-juniper woodlands, Great Plains grasslands, various kinds of Rocky Mountain conifer-

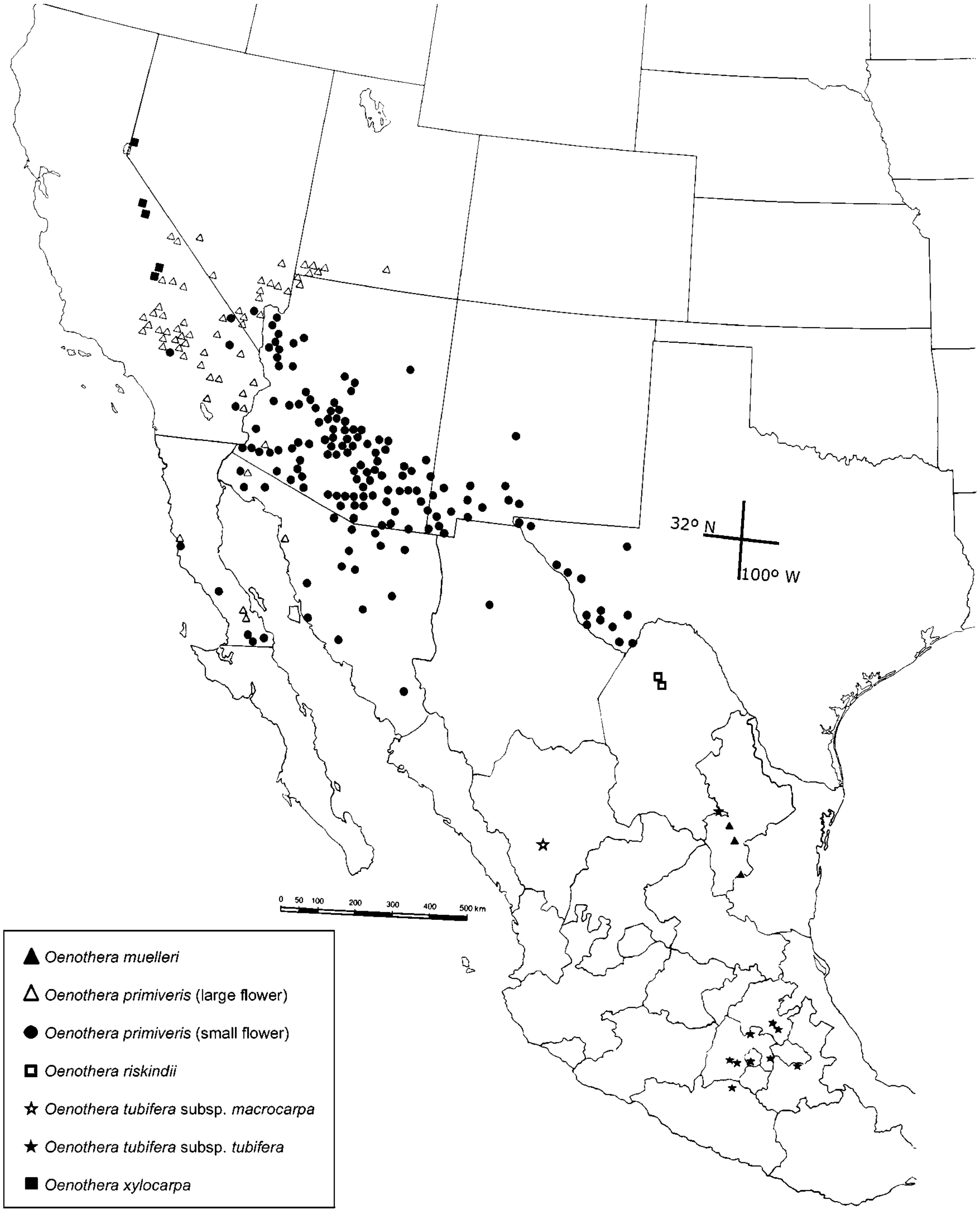

FIG. 1. Map of western North America showing the distributions of sections *Eremia*, *Contortae*, and *Ravenia*.

ous forests, and even subalpine forest of *Pinus longaeva* and *P. flexilis*.

The single species of sect. *Contortae*, *Oenothera xylocarpa*, has a presumably relictual distribution in the Sierra Nevada of California and Nevada, at 2250–3050 m. It is restricted to granitic gravels, sand, or pumice in forests of *Pinus jefferyi* or *Pinus contorta* subsp. *murrayana*/*Abies magnifica*. It must have been more widespread at one time but now occurs in three disjunct areas: 1) Mount Rose, Nevada; 2) southern Sierra Nevada, Mono County from Crestview to Casa Diablo; and 3) southern Sierra Nevada, primarily Inyo County, Big Whitney Meadows to Volcano Meadows and Casa Vieja. *Oenothera xylocarpa* may have been more widespread in the past and subsequently with episodes of mountain building and cooling and drying of the climate, populations of *O. xylocarpa* have become progressively more restricted to marginal substrates not inhabited by other species. Now it occurs only on very porous substrates, and has a disjunct range corresponding to the distribution of those substrates.

*Oenothera primiveris*, the only species of sect. *Eremia*, is widespread in sandy xeric habitats in all three of the warm North American deserts at elevations ranging from 30 m in Baja California to 1600 m in southwestern Utah. The only populations retaining the plesiomorphic character of self-incompatibly occur in the Mojave Desert and on the western edge of the Sonoran Desert. At its upper elevational range, *O. primiveris* extends marginally into Great Basin type vegetation consisting of plants like *Ericameria*, *Artemisia* and *Juniperus*.

The three species of sect. *Ravenia* occur in montane, mesic to relatively dry habitats in forests dominated by *Pinus*, *Abies*, *Quercus*, *Arbutus*, and *Tilia*, and are often found in rocky or grassy sites at 2300–3200 m. The species have disjunct ranges in Madrean woodland vegetation. *Oenothera muelleri* is known from three disjunct areas in the Sierra Madre Oriental of northeastern Mexico: 1) Cerro Potosi, Nuevo León; 2) near Pablillo, Nuevo León; and 3) Pena Nevada, Tamaulipas. The closely related *O. riskindii* is known only from Rincon de Maria and adjacent Serranias del Burro, Coahuila, nearly 500 km north of the range of *O. muelleri*. The third species, *O. tubifera*, has the widest distribution in the section, but it is highly disjunct, occurring in Coahuila, central Mexico, and Durango. It is subdivided here into two subspecies: Subsp. *tubifera* from southern Hidalgo east to Puebla and south to Guerrero, and disjunct in Coahuila; and subsp. *macrocarpa* only from the Sierra Madre Occidental in Durango. Although species of sect. *Ravenia* occur in montane vegetation, their ecological and geographical ranges are very similar to, but at slightly higher and cooler altitudes than the species of northern Mexican sect. *Oenothera* subsect. *Emersonia*, which are presumably early-diverging species in the large related sect. *Oenothera* (Stubbe and Raven 1979; Dietrich et al. 1985). Thus sect. *Ravenia* appears to have evolved in response to a shift to a cooler montane element of the Madrean woodland vegetation early in the evolution of the genus from a common ancestor with sects. *Eremia* and *Contortae*.

Major diversification of Onagraceae tribes Onagreae, Gongylocarpeae, and Epilobieae may have occurred during the Miocene and Pliocene (Raven and Raven, 1976; Raven and Axelrod 1978; Raven, 1979). Thus the timing of the origin of *Oenothera* was likely after the mid-Miocene around 14 Ma as the climate became drier and summer rains decreased (Raven and Axelrod 1978).

## Breeding System

***Self-incompatibility.*** Tests for self-incompatibility were made by repeatedly self-pollinating cultivated strains in the greenhouse. Plants were classified as self-incompatible only if seed was never set following self-pollination. Plants of *Oenothera primiveris* were analyzed by self-pollination and also by the study of pollen tube growth in selfed styles by means of fluorescence microscopy.

Flowers were collected in the field, brought indoors, selfed and placed in water overnight (ca. 9–10 hours) to allow for possible pollen tube growth. The following methods of examination are those of Martin (1959) and Kho and Baer (1968). The styles were removed from the flowers, fixed in FAA (90 parts 70% ethanol: 5 parts acetic acid: 5 parts formalin) rinsed in deionized water, softened in 8 N NaOH for ca. 4–6 hours, placed on a standard slide, and stained in a solution of 0.1% water-soluble aniline blue dissolved in 0.1 N $K_3PO_4$. The styles were then carefully spread for viewing by gently tapping the coverslip.

This technique depends on the formation of callose in pollen tubes during their growth down the style. The aniline stain is selectively taken up by the callose which is absent in the surrounding stylar tissue, and it fluoresces when illuminated by a mercury-vapor light source between 350–400 nm.

In *Oenothera*, pollen tube growth is inhibited in the surface layers of the stigma (Emerson 1938; Bills 1968; Dickinson and Lawson 1975), so if pollen tubes are present in the style then the plant is self-compatible.

The results of the self-incompatibility tests on sects. *Ravenia*, *Eremia*, and *Contortae* are presented in Table 1. The single strains of *Oenothera riskindii* and *O. muelleri* studied were self-incompatible (SI). Stockhouse (1973) used the same strain of *O. meulleri* in his study and also found it to be SI. In contrast, Raven (1970) reported *O. muelleri* to be self-compatible (SC). However, this seems to have been an error since subsequent study of the only strain in cultivation has uniformly produced results of SI. *Oenothera tubifera* is SC as would be expected from its relatively small flowers and stigma that is surrounded by the anthers at anthesis. Contrary to the prediction based on its large flowers, the strains of *O. xylocarpa* tested were SC. More strains should be studied, but *O. xylocarpa* is extremely difficult to maintain in cultivation.

The results of the self-incompatibility tests in *Oenothera primiveris* are more complex. The populations of *O. primiveris* from Nevada and some from California were SC, an unexpected result for these large-flowered populations. Interestingly, two populations from California consisted of both SI and SC individuals. Typi-

TABLE 1. Self-incompatability tests in *Oenothera* sects. *Ravenia, Eremia* and *Contortae.* All vouchers deposited at MO unless otherwise indicated. Compatability is SC (self-compatible) or SI (self-incompatible); N = number of individuals tested. An asterisk (*) indicates test performed by fluorescence microscopy and aniline blue stain on wild populations; all others tested by success of seed-set following self-pollination in the greenhouse.

Sect. *Ravenia* - *Oenothera riskindii*: Mexico, Coahuila, *Wagner 6933, 6937*; SI N = 4. *Oenothera muelleri*: Mexico, Nuevo León, *Lloyd 4081*; SI N = 6. *O. tubifera* subsp. *macrocarpa*: Mexico, Durango, *Breedlove 14321*; SC N = 2.

Sect. *Eremia* - *O. primiveris*: Arizona, Mohave Co., *Wagner & Mill 4584*; SC N = 4*. Arizona, Mohave Co., *Jordan 362* (MNA); SC N = 4. Arizona, Pima Co., *Stockhouse 290*; SC N = 3. Arizona, Pima Co., *Wagner & Mill 4566*; SC N = 4*. Arizona, Yavapai Co., *Wagner & Mill 4571*; SC N = 7*. Arizona, Yavapai Co., *Wagner & Mill 4573*; SC N = 7*. California, Inyo Co., 1979, *Pavlik s.n.*; SI N = 6. California, Inyo Co., *Klein s.n.* (no voucher located); SI N = 2. California, Kern Co., *Wagner & Mill 4555*; SI N = 3*, SC N = 5*. California, San Bernardino Co., *Wagner & Mill 4557*; SI N = 4*, SC N = 1*. Nevada, Clark Co., *Wagner & Mill 4591*; SC N = 4* + 10. Nevada, Clark Co., *Wagner & Mill 4592*; SC N = 3*. Nevada, Clark Co., *Wagner & Mill 4593*; SC N = 4*.

Sect. *Contortae* - *O. xylocarpa*: California, Mono Co., 1979, *DeDecker s.n.*; SC N = 5.

cally most species of *Oenothera* are either entirely SC or SI. A few species, such as *O. deltoides* (sect. *Anogra*), consist of both SI and SC populations (Klein 1964, 1970). In this case, however, the two compatibility types are not found in the same population or even the same taxon, but rather characterize different subspecies. The only other species known to have populations of mixed SC and SI individuals is *O. grandiflora* L'Her. (Steiner and Stubbe 1984). *Oenothera grandiflora* of the southeastern United States is modally outcrossing and until recently was thought to consist entirely of SC individuals, but recent studies (Steiner and Stubbe 1984, 1986; Stubbe and Raven 1979) detected a number of SI individuals mixed with SC ones.

Why should this intermediate pattern be so uncommon? Possible explanations can be sought in an understanding of how the *Oenothera* self-incompatibility system operates. Genetic self-incompatibility in *Oenothera* is of the gametophytic type (Crowe 1955; Raven 1979). Emerson (1938, 1939) and Crowe (1955) suggested that the system is controlled by a single multiallelic locus. When the pollen has the same allele as the maternal tissue of the style (the case in self-pollination) fertilization is prevented by pollen tube growth inhibition in the surface layers of the stigma (Dickinson and Lawson 1975). When the alleles are different in the pollen and style, then pollination is successful. When large numbers of alleles are present, self-pollination is rare and potential outcrossing combinations maximized. The studies of *Oenothera* suggest that this is indeed the case. For example, the most detailed study of S-alleles in *Oenothera* was made on *O. organensis* (Emerson 1938), which has at least 45 S-alleles known in a species consisting of as few as 5000 individuals (Dietrich et al. 1985). A single population of *O. cespitosa* studied by Bills (1968) contained at least five S-alleles.

The development of self-compatibility will not result from merely a reduction of the number of S-alleles, but requires the mutation of a self-compatible allele or a mutation of a gene linked to the S-locus. The subsequent spread of self-compatibility then depends upon the ability of an outcrossing individual to successfully outbreed the self-incompatible individuals or to migrate to new habitats. Our evidence suggests that both factors have been involved in the spread of self compatibility in *O. primiveris*.

A model proposed by Charlesworth and Charlesworth (1979) suggests that there is always a critical number of active S alleles that ensures the elimination of mutant alleles. Furthermore, they state that polymorphism for (SI/SC) alleles is usually obtained within a narrow range of situations, and would therefore be unlikely to be commonly found, except for a transient stage while self-compatible alleles are spreading (which may be on the order of hundreds of generations when there are many active S alleles).

Populations of *Oenothera primiveris* from only one area, Eureka Dunes, California (the two Inyo County populations) apparently consist of all SI individuals. This suggests that population is these areas are relictual in the more equable sandy habitat. In these populations there presently is no estimate of the number of SI alleles present, but examination of several selfed styles where some pollen tubes penetrated the style while the majority did not suggest the existence of individuals heterozygous for SI and SC alleles.

Aside from these California populations, all individuals tested were SC, suggesting that SC and progressive autogamy appear to have been favored in conjunction with the modern spread of desert habitat in Holocene times. In the eastern part of its range *O. primiveris* represents the other end of the spectrum with its much smaller flowers and stigmas completely surrounded by the anthers at anthesis. Small flowered populations of *O. primiveris* may be outcrossed occasionally by hawkmoths, but judging from the reduced amounts of nectar in the floral tube and weak scent, presumably they are usually autogamous.

Three of the species of sect. *Pachylophus*, *Oenothera cespitosa*, *O. harringtonii*, and *O. psammophila*, were uniformly self-incompatible, and the two small-flowered species, *O. cavernae* and *O. brandegeei*, were self-compatible and autogamous (Wagner et al. 1985).

These results for self-incompatibility found in all three sections except for sect. *Contortae* (although plants from each disjunct area of the distribution of *O. xylocarpa* should be examined for self-incompatibility) indicate that self-incompatibility was present in the common ancestor of the genus. There is a clear trend in three of the sections for evolution from the self-incompatibility and mandatory out-crossing to self-compatibility and predominant autogamy. In both sects. *Ravenia* and *Pachylophus* self-compatible, autogamous species have evolved, while *O. primiveris* is apparently in a transitional state where there are mixed populations of SC and SI individuals, a situation thus far found elsewhere in the genus only in *O. grandiflora*.

***Pollination.*** Pollination has been observed in most of the species of sect. *Pachylophus* (Gregory 1963, 1964; Wagner et al. 1985) with several incidental observations in species of the other sections (Linsley et al. 1964; Gregory 1963, 1964). Two patterns are evident: the large-flowered species with strong fragrance are pollinated by hawkmoths, and the smaller-flowered species with faint floral fragrance are normally self-pollinating (Wagner et al. 1985). Gregory (1963, 1964) showed this to be the primary pattern for the genus.

## CYTOLOGY

Cytological observations to determine chromosome number and usually meiotic configuration were made on buds collected in the field or from greenhouse-grown progeny from seed collected in nonflowering populations. Buds were fixed and stored in 1:3 acetic acid: absolute ethanol under refrigeration. Prior to staining in 1% acetocarmine, buds were hydrolyzed in a mixture of concentrated HCl and 95% ethanol for 20 minutes.

A total of 13 strains representing all species of sects. *Ravenia*, *Contortae*, and *Eremia* are presented in Table 2, including unpublished reports provided by P. Raven, C. Peng and S. Seavey. Cytology of the species of sect. *Pachylophus* was reported in Wagner et al. (1985).

All species of sects. *Ravenia*, *Eremia*, and *Contortae* are diploid, $2n = 14$, as are most species of *Oenothera*. At least some plants of *O. muelleri* and *O. primiveris* had seven bivalents at meiotic metaphase I, but translocation heterozygosity with formation of small rings was more frequent in both species. The widespread occurrence of reciprocal translocations in natural populations, especially translocations involving only two to four bivalents as found here, is a characteristic feature occurring only in several genera of the tribe Onagreae, especially *Oenothera* (Cleland 1972; Raven 1979; Deitrich et al. 1997).

The five species of sect. *Pachylophus* are also all diploid, $2n = 14$, except for the sporadic occurrence of autotetraploids in *O. cespitosa* (Wagner et al. 1985). Translocation heterozygosity was likewise uncommon in the species of sect. *Pachylophus*.

## PHYLOGENETIC RELATIONSHIPS

Raven (1970) suggested that the species of *Contortae*, *Eremia*, *Pachylophus*, and *Ravenia* were closely related. He also tentatively recognized four subgroups corresponding to the four sections here recognized. Sects. *Contortae*, *Eremia*, and *Pachylophus* were thought by Wagner et al. (1985) to be related through sect. *Ravenia* to sect. *Oenothera* subsect. *Emersonia*. Wagner et al. (1985) developed the first morphological phylogenetic analysis of relationships for this group. The results of their study suggested that: 1) The group of four sections was monophyletic; and 2) sect. *Ravenia* was sister to the remaining three sections. Wagner et al. (1985) used as the outgroup species of sect. *Oenothera* subsect. *Emersonia* (Dietrich et al. 1985), thought based on crossing studies (Stubbe and Raven 1979) to be an early-derived group within sect. *Oenothera*, and perhaps the entire genus. Another phylogentic analysis using seed anatomy (Tobe et al. 1987) identified similar relationships among these four groups, but they did not form a monophyletic clade, but rather a grade. Recently, Levin et al. (2004) found in a molecular study (Figs. 2, 3) results similar to these earlier analyses, but more consist with the seed anatomical study. In their analysis of combined sequence variation in nrITS, *trnL-F,* and *rps16,* Levin et al. (2004) found that sect. *Pachylophus* branches off above the first node in the genus, whereas sect. *Oenothera* subsect. *Emersonia* is a member of the terminal clade containing all of the subsections of sect. *Oenothera* as well as sects. *Anogra* and *Kleinia*. Significantly, all of the phylogenetic studies identified the same basic network of taxa.

## TAXONOMIC TREATMENT

The following taxonomic section provides details for the species of sects. *Contortae*, *Eremia*, and *Ravenia*. For convenience I also provide a summary account of sect. *Pachylophus*. In the revision of the species of the latter group were published (Wagner et al 1985) no sectional description was provided for sect. *Pachylophus* because a decision had not been made for its delimitation pending completion of the work presented here. Thus, a sectional treatment of sect. *Pachylophus* is provided below.

## KEY TO THE SECTIONS

1. Valves of capsule thickened at the margin to form conspicuous tubercles or a ridge; petals white; raphial (adaxial) face of seed with an enlarged hollow chamber, or rarely filled with large spongy cells, if so then seed triangular, the area above the raphe

TABLE 2. Chromosome observations of plants in *Oenothera* sects. *Eremia, Contortae,* and *Ravenia.* All specimens deposited at MO unless otherwise indicated. $_{\text{II}}$ = bivalent; $\odot$ = translocation ring.

| Species | Locality | Collection | Source or investigator | Meiotic chromosome observations[a] |
|---|---|---|---|---|
| Sect. *Eremia* | U.S.A.: | | | |
| *O. primiveris* | Arizona | | | |
| | Mohave Co. | *Wagner & Mill 4581* | W.L. Wagner | $4_{\text{II}} + \odot 6$ |
| | Pima Co. | *Stockhouse 290* (no voucher located) | Stockhouse, 1973 | $5_{\text{II}} + \odot 4$ |
| | California | | | |
| | Inyo Co. | *Klein s.n.* (no voucher located) | Stockhouse, 1973 | $4_{\text{II}} + \odot 6$ |
| | | 1979, *Pavlik s.n.* | W.L. Wagner | $7_{\text{II}}$ |
| | Nevada | | | |
| | Clark Co. | *Gregory 380* (RSA) | W. Klein | $7_{\text{II}}$ |
| | | *Wagner & Mill 4592* | W.L. Wagner | $4_{\text{II}} + \odot 6$ |
| | | *Wagner & Mill 4593* | W.L. Wagner | $5_{\text{II}} + \odot 4$; 2 plants |
| | Mexico: | | | |
| | Sonora | *Breedlove 15891* (DS) | P. Raven | $7_{\text{II}}$ |
| Sect. *Contortae* | U.S.A.: | | | |
| *O. xylocarpa* | California | | | |
| | Mono Co. | 1979, *DeDecker s.n.* | W.L. Wagner | $5_{\text{II}} + \odot 4$ |
| | | *Raven 14263* (GH, RSA, UC) | P. Raven | $3_{\text{II}} + 2\ \odot 4$ |
| Sect. *Ravenia* | Mexico: | | | |
| *O. muelleri* | Nuevo León | *Lloyd 4081* | Stockhouse, 1973 | $7_{\text{II}}$ |
| *O. riskindii* | Coahuila | *Wendt et al. 1289* | W. L. Wagner | $2n = 14 + 3\text{-}5b$'s |
| *O. tubifera* subsp. *macrocarpa* | Durango | *Breedlove 14321* | S. Seavey | $n = 7$ |

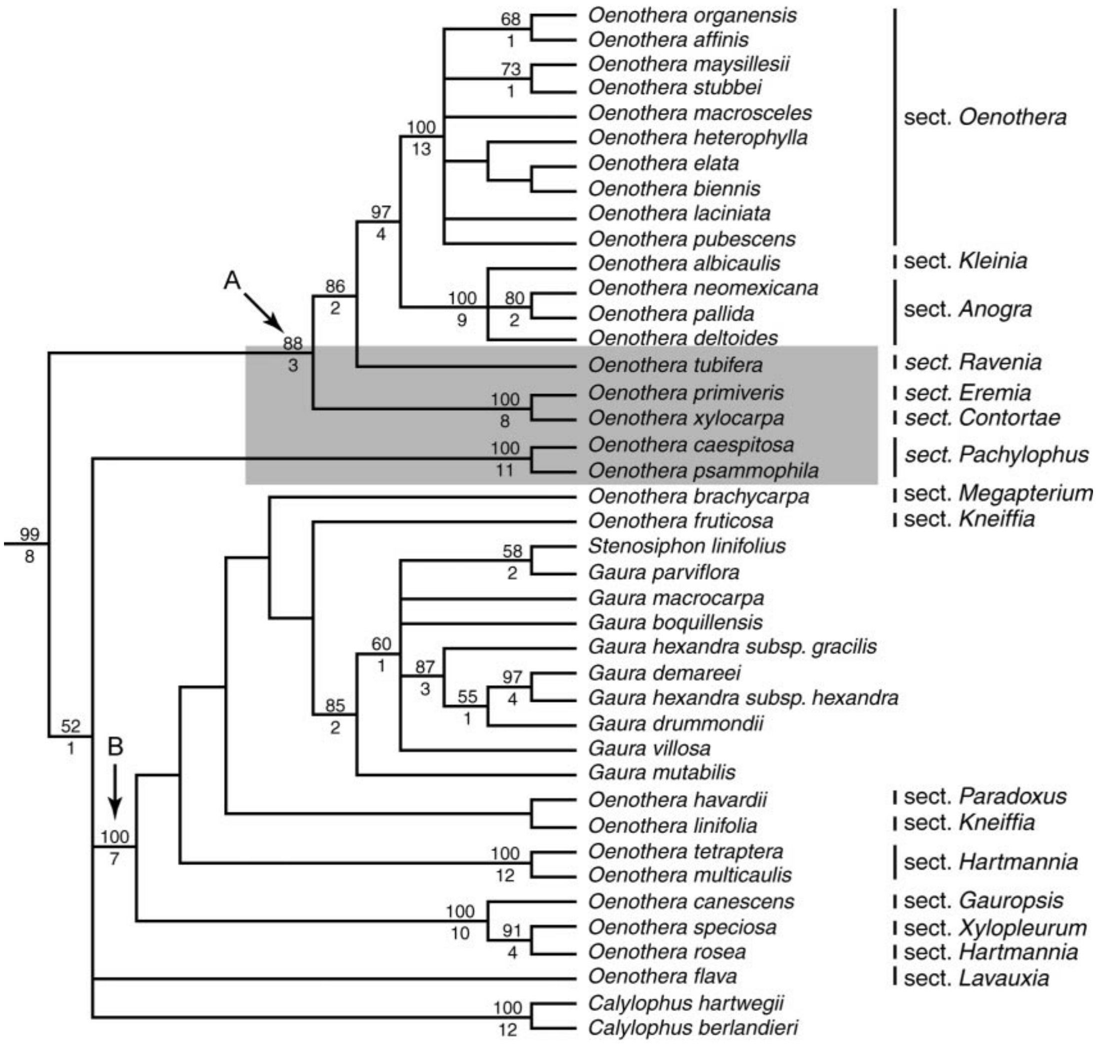

FIG. 2. Portion (*Oenothera* clade) of strict consensus of 18,200 MP trees (TL=2018, rescaled CI=0.47, RI=0.73) of Onagraceae showing relationships in *Oenothera* from analyses of Levin et al. (2004) based on combined nrITS, *trn*L-*trn*F and *rps*16 sequences (75 taxa). Nodes with bootstrap values (BS) >50% and decay indices (DI) >0 are indicated, with BS listed above the node and DI below. Current sectional affiliations are listed to the right for all species. The two main lineages within *Oenothera* are indicated as A and B.

± with a unicellular translucent membrane; southern Can., eastern WA, eastern to SD & ND, south to southeastern CA, Chih., Mex. & Trans-Pecos TX, also Baja California. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . sect. I. *Pachylophus*.

1. Valves of capsule uniformly thickened, without tubercles or a ridge; petals white or yellow; raphial (adaxial) face of seed enlarged, but only with a small, internal, distal cavity and a visible longitudinal groove, the raphe ± with a unicellular membrane toward the distal end, which is split and often disintegrates at maturity, or seed not especially thickened on raphial face and only with two longitudinal ribs.
   2. Stems several arising from the rosette, decumbent or rarely erect; petals white, fading pink and drying purple; seeds 3–7 mm long, the surface dull, appearing smooth to unaided eye, the abaxial surface with longitudinal ribs; northeastern to central Mexico . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . sect. IV. *Ravenia*.
   2. Stems absent or if present then at least central stem erect; petals yellow, fading and drying red, reddish orange or purple; seeds 2.4–3.5 mm long, the abaxial and sometimes adaxial surface coarsely rugose and papillose.
      3. Plants winter annuals of deserts; pubescence of three types: long-hirsute, strigillose and glandular puberulent; petals fading reddish orange to purple; capsules never twisted, the surface not wrinkled; seeds with a conspicuous raphial groove and a pore at the distal end of the raphial face; Mojave, northern Sonoran and northern Chihuahuan deserts . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . sect. II. *Eremia*. i.
      3. Plants stout perennial herbs from a thick fleshy taproot; pubescence usually exclusively short-hirsute, occasionally also sparsely long-hirsute; petals fading salmon-red; capsules twisted, the surface conspicuously wrinkled; seeds lacking a raphial groove and pore; Mt. Rose, southern NV; southern Sierra Nevada, CA . . . . . . . . . . . . sect. III. *Contortae*.

I. OENOTHERA L. sect. PACHYLOPHUS (Spach) Endl., Gen. Pl. 2(15): 1190. 1840. *Pachylophus* Spach, Hist. Nat. Vég. 4: 365. 11 April 1835. *Oenothera* L. subg. *Pachylophus* (Spach) Jeps., Man. Fl. Pl. Calif. 680. 1925; ex Munz, Amer. J. Bot. 18: 728. 1931.—TYPE: *Pachylophus nuttallii* Spach, nom. illeg. (= *Oenothera cespitosa* Nutt.). Munz attributed the combination at the subgeneric level to Jepson, but, Jepson merely mentioned ''subgenus *Pachylophus*'' as part of his key with no indication of the author of the basionym nor the place of original publication. Thus, Munz was the validating author of the subgeneric combination.

Perennial or sometimes annual herbs from a stout, sometimes fleshy taproot, sometimes slender lateral roots producing adventitious shoots along their length, acaulescent or with ascending to erect leafy stems. Pubescence nearly always of two types: glandular puberulent and one non-glandular type, either hirsute, hirtellous, villous, or strigillose, or occasionally glabrous or pubescent exclusively with either glandular or strigillose pubescence. Leaves forming a basal rosette, stem leaves, if present alternate, oblanceolate to rhombic or spatulate, rarely linear-oblanceolate, rather coarsely dentate to pinnatifid or sometimes serrate or subentire, tapering to a winged petiole. Buds erect or sometimes curved downward by the recurved floral tube, quadrangular in cross section, occasionally obtusely angled, without free sepal-tips. Flowers opening near sunset and fading the following morning, borne singly in the axils of the leaves, congested on relatively short axes, fragrance sweet with background rubbery odor. Floral tube variable in length, flaring to a wide mouth. Sepals separating individually or in pairs, reflexed at anthesis. Petals white fading to rose purple, rose, or light pink. Capsule thick-walled and rather woody, lanceoloid or elliptic-ovoid to cylindrical, falcate, sigmoid, or straight, each valve with a row of tubercles or a thickened ridge along margins, tapering to a sterile beak, the base asymmetrical to nearly symmetrical, sessile or sometimes long-pedicellate. Seeds usually in two rows in each locule, occasionally in two overlapping rows or rarely one irregular row, obovoid to orbicular or triangular, the adaxial face typically with a hollow chamber (seed-collar), rarely (in *O. brandegeei*) the chamber filled with large spongy cells, the area above the raphe consisting of a unicellular, thin, translucent membrane running the length of the seed, either intact or split at maturity; embryo portion constituting 1/5–2/3 of the seed volume; the surface papillose, reticulate, or irregularly roughened. Three species self-incompatible, two self-compatible and largely autogamous. Basic chromosome number, $x = 7$. Fig. 4a, b, c.

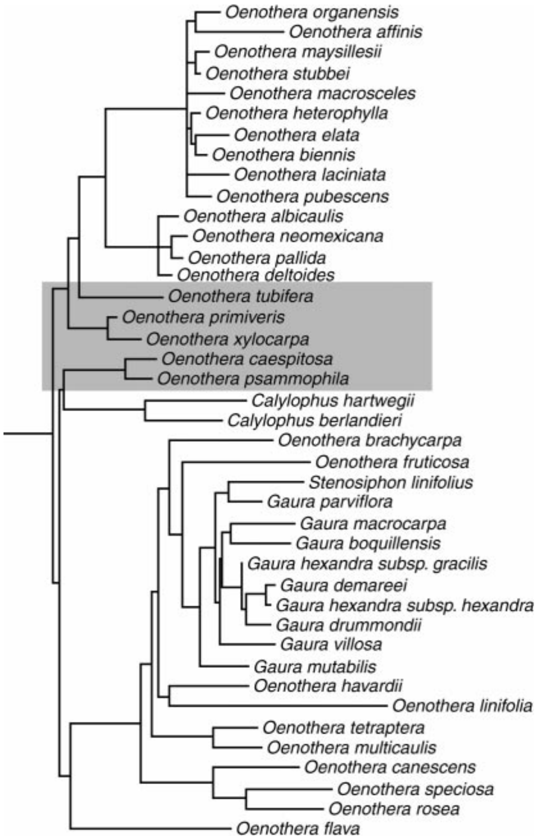

FIG. 3. Partial phylogram (*Oenothera* clade) from maximum likelihood (ML) analysis of the combined nrITS and cp *trnL-trnF* and *rps*16 data (75 taxa; −ln = 16321.085) from Levin et al. (2004).

*Oenothera* sect. *Pachylophus* with five species is widespread in a large number of habitats of western North America. It is centered in the Great Basin region, but occurs widely in the Great Plains, in all three North American deserts, and in montane habitats in the Rocky Mountains and desert mountains. The species of sect. *Pachylophus* were treated in detail by Wagner et al. (1985). Synonyms are cited here only if not included in Wagner et al. (1985).

Spach's original spelling (1835a) of the name was *Pachylophus*, which appears to be correct when the Greek words pachys (thick) lophos (crest) are Latinized. In two subsequent publications Spach (1835b, 1835c) changed his original spelling to *Pachylophis* without giving any reason. This has caused some subsequent confusion. I here use his original spelling since it was properly formulated and thus can not be corrected under Art. 60.1 of the ICBN (Greuter 2000).

1. OENOTHERA CESPITOSA Nutt.

I have here corrected the spelling, *Oenothera caespitosa*, long used for this species by dropping the ''a'' to *O. cespitosa*. The reason is that *O. cespitosa* was originally published in a relatively obscure publication

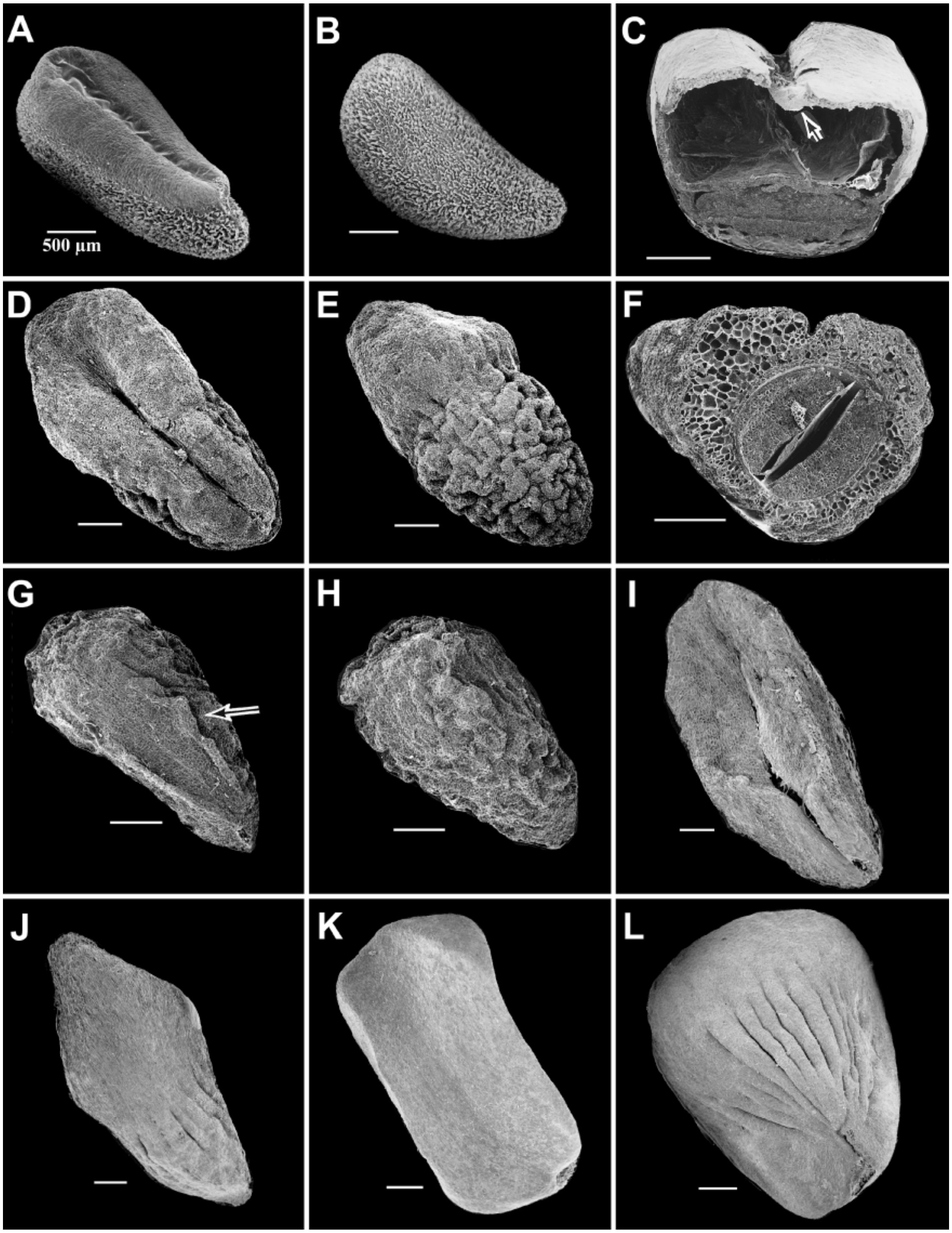

FIG. 4. Scanning electron micrographs of seeds of *Oenothera*. A–C. *O. cespitosa* (sect. *Pachylophus*). A. Adaxial view of *O. cespitosa* subsp. *navajoensis* from *Wagner 4509* (MO). B. Abaxial view of *O. cespitosa* subsp. *navajoensis* from *Wagner 4509* (MO). C. Cross-section of *O. cespitosa* subsp. *marginata* from *Wagner et al. 4401* (MO). D–F. *O. primiveris* (sect. *Eremia*) from *Maguire & Blood 4446* (UTC). D. Adaxial view. E. Abaxial view. F. Cross-section. G–H. *O. xylocarpa* (sect. *Contortae*) from *DeDecker, s.n.* in 1979 (MO). G. Adaxial view. H. Abaxial view. I–J. *O. riskindii* (sect. *Ravenia*) from *Wendt et al. 1289* (MO). I. Adaxial view. J. Abaxial view. K–L. *O. muelleri* sect. *Ravenia* from *Lloyd 4081* (MO). K. Adaxial view. L. Abaxial view.

(Nuttall 1813) using the spelling without the ''a,'' Sims (1813) only a few months later published on this species in the *Botanical Magazine.* Because this was a more widely accessible publication his spelling became universally adopted, including in my revision of this group (Wagner et al. 1985). Because either spelling is acceptable the original spelling without the ''a'' must be adopted.

1a. OENOTHERA CESPITOSA Nutt. subsp. CRINITA (Rydb.) Munz

1b. OENOTHERA CESPITOSA Nutt. subsp. CESPITOSA

1c. OENOTHERA CESPITOSA subsp. NAVAJOENSIS W. L. Wagner, Stockh. & W. M. Klein.

*Oenothera cespitosa* var. *navajoensis* (W. L. Wagner, Stockh., & W. M. Klein) Cronquist in Welsh, Great Basin Naturalist 46: 259. 1986.

1d. OENOTHERA CESPITOSA subsp. MACROGLOTTIS (Rydb.) W. L. Wagner, Stockh. & W. M. Klein.

*Oenothera cespitosa* var. *macroglottis* (Rydberg) Cronquist in Welsh, Great Basin Naturalist 46: 259. 1986.

1e. OENOTHERA CESPITOSA subsp. MARGINATA (Nutt. ex Hook. & Arn.) Munz

2. O. PSAMMOPHILA (A. Nelson & J. F. Macbr.) W. L. Wagner, Stockh. & W. M. Klein
3. O. HARRINGTONII W. L. Wagner, Stockh. & W. M. Klein
4. O. CAVERNAE Munz
5. O. BRANDEGEEI (Munz) P. H. Raven

II. OENOTHERA L. sect. EREMIA W. L. Wagner, Ann. Missouri Bot. Gard. 73: 477. 1986.—TYPE: *Oenothera primiveris* A. Gray.

*Oenothera* subg. *Pachylophus* sensu Munz, Amer. J. Bot. 18: 728. 1931, pro parte; N. Amer. Fl. II. 5: 98. 1965, pro parte.

Winter annual herbs from a somewhat fleshy taproot, acaulescent or caulescent; stems, if present, 0.5–3.5 dm long, erect, usually simple but occasionally with ascending secondary branches arising from near the base, densely leafy. Pubescence of three types: strigillose, glandular puberulent, and hirsute, these often with reddish purple pustulate bases. Leaves forming a basal rosette, oblanceolate to linear-oblanceolate, pinnatifid to sinuate-dentate, rarely bipinnatifid, or sometimes smaller leaves subentire, gradually tapering to a winged petiole. Buds curved downward by the recurved floral tube, becoming erect before anthesis, quadrangular in cross-section, without free sepal-tips. Flowers opening near sunset and fading the following morning, borne singly in the axils of the leaves, congested on relatively short axes, fragrance strongly scented with a sweet lemony fragrance or a pungent semen-like odor, weakly scented in autogamous populations. Floral tube 2—7 cm in length, flaring somewhat at the mouth. Sepals separating in pairs or individually, reflexed at anthesis. Petals deep yellow, fading reddish orange to purple, drying purple. Capsule lanceoloid to ovoid, falcate or curved to nearly straight, quadrangular in cross-section, the angle acute, asymmetrical at the base, sessile. Seeds 3–3.5 mm long, in two rows in each locule, obovoid to oblanceoloid; the testa much thickened above the raphe and at the distal end into a U-shaped structure, the thickened area with a central cavity that externally appears as a pore at the distal end and a groove along the raphial face; the surface coarsely rugose on the distal half of the abaxial side, the surface papillose, the papillae apically depressed. Self-compatible, rarely self-incompatible, outcrossing to autogamous. Basic chromosome number, $x = 7$.

Section *Eremia* consists of a single species occurring in sandy soils on flats, low hills, margins of sand dunes, and along arroyos in low desert to mountain foothills of all three North America warm deserts (Chihuahuan, Mojave, and Sonoran).

6. OENOTHERA PRIMIVERIS A. Gray, Pl. Wright. 2: 58. 1853. *Lavauxia primiveris* (A. Gray) Small, Bull. Torrey Bot. Club 23: 182. 1896. *Oenothera cespitosa* Nutt. var. *primiveris* (A. Gray) H. Lév., Monogr. Onoth. 71. 1902.—TYPE: MEXICO. Dry hills near ''El Paso'' [actually Cd. Juarez, Chihuahua], 1140 m, February–April 1852, *C. Wright 1376* (holotype: GH!; isotypes: G!, GH! [2], MO!, PH!). According to Standley (Contr. U.S. Natl. Herb. 13: 143–146), Wright collected this specimen on the south side of the Rio Grande. Figs. 4d, e, f; 5.

*Oenothera johnsonii* Parry, Amer. Naturalist 9: 270. 1875. *Oenothera cespitosa* Nutt. race *johnsonii* (Parry) H. Lév., Monogr. Onoth. 70. 1902. *Pachylophus johnsonii* (Parry) Rydb., Fl. Rocky Mts. 598 & 1064. 1917.—TYPE: U.S.A. Utah: Washington Co., dry hills near St. George, 900 m, early May 1874, *C. C. Parry 64* (holotype: GH!; isotypes: BM!, G! [2], MO! [3], NA!, NY!, P, PH!, YU!).

*Oenothera bufonis* M. E. Jones, Contr. W. Bot. 8: 28. 1898. *Oenothera primiveris* A. Gray subsp. *bufonis* (M. E. Jones) Munz, N. Amer. Fl. II. 5: 103. 1965. *Oenothera primiveris* A. Gray var. *bufonis* (M. E. Jones) Cronquist in Welsh, Great Basin Naturalist 46: 259. 1986.—TYPE: U.S.A. California: Inyo Co., upper edge of *Larrea* belt, sand, Darwin Mesa, Argus Mountains, 1500 m, 8 May 1897, *M. E. Jones s.n.* (lectotype: POM-38614!; isolectotypes: photo MO!; DS! [2], NY!, POM!; Munz, Amer. J. Bot. 18: 736. 1931).

*Lavauxia lobata* A. Nelson, Bot. Gaz. (Crawfordsville) 47: 429. 1909.—TYPE: U.S.A. Nevada: Lincoln Co., sandy washes, Meadow Valley Wash, 7 April 1905, *L. N. Goodding 2172* (lectotype: GH; isolectotypes:

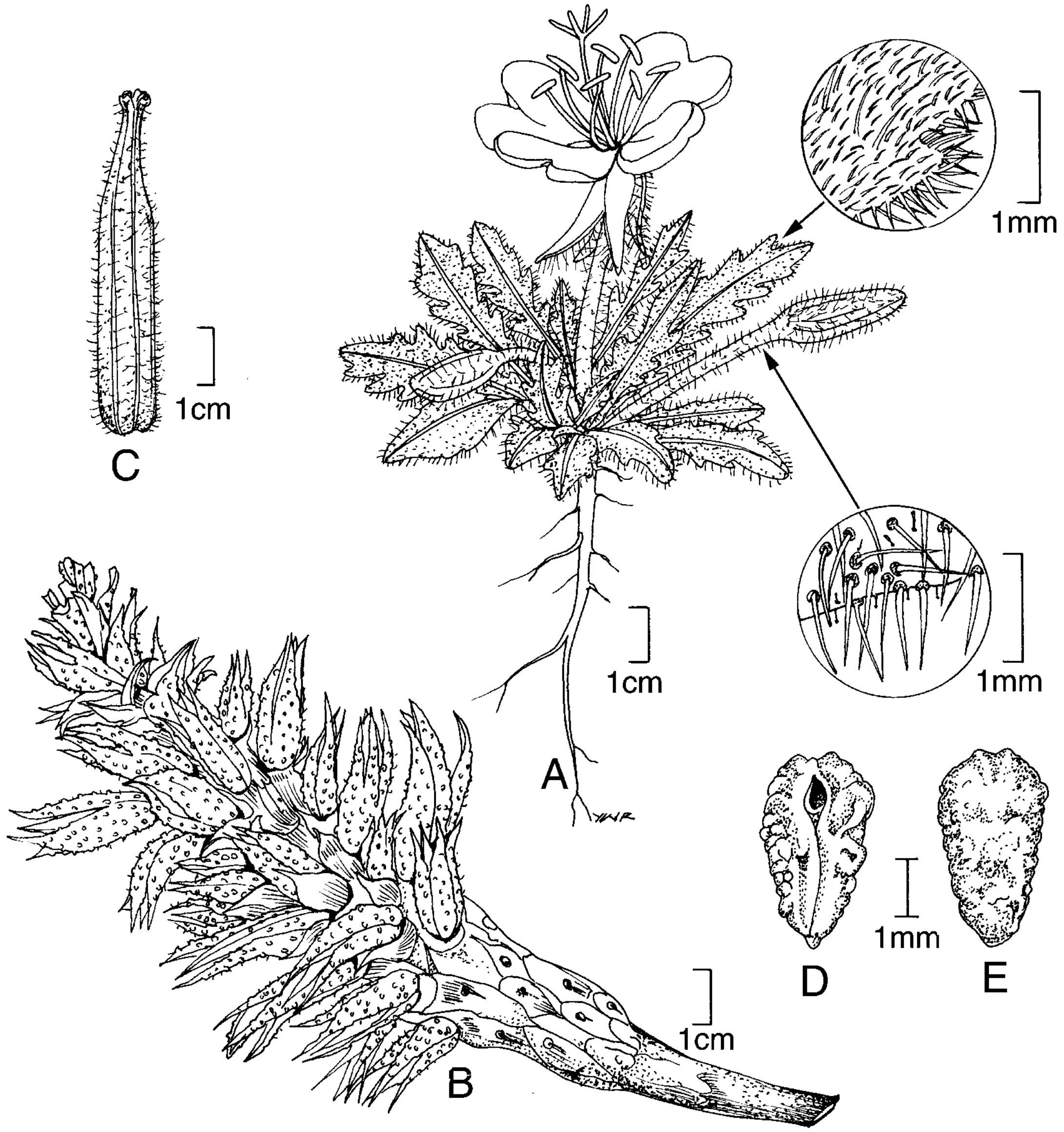

FIG. 5. A–E. *Oenothera primiveris*. A. Habit with telescoped views of four trichome types (*Wagner & Mill 4556,* MO and 35 mm slides). B. Dead fruiting plant (*Pavlik s.n.* in 1978, MO). C. Predehiscence capsule (*Wagner & Mill 4564,* MO). D–E. Seed (*Pavlik s.n.* in 1978, MO). D. Adaxial view. E. Abaxial view.

E!, MIN!, MO!, UC!; Munz, Amer. J. Bot. 18: 736. 1931.). In the original publication Nelson mentions *Goodding 37* and *47* not *Goodding 2162* and *2172.* A note by Nelson in the front of Goodding's field notes says to add 2125 to each of the numbers, thus *Goodding 37* and *47* become *2162* and *2172* (R. Hartman, pers. comm.).

*Oenothera primiveris* A. Gray var. *caulescens* Munz, Leafl. W. Bot. 4: 239. 1946. *Oenothera primiveris* A. Gray subsp. *caulescens* (Munz) Munz, N. Amer. Fl. II. 5: 103. 1965.—TYPE: U.S.A. Arizona: Yuma Co., open flats, 7 mi S of Wellton, 30 March 1941, *P. A. Munz 16606* (holotype: CAS-325178!; isotypes: photo MO!; BH! [2], POM!).

Acaulescent to short caulescent winter annual herbs from a somewhat fleshy taproot; when present stems 0.5–3.5 dm long, 1–2.5 cm in diameter, densely leafy, simple and erect or sometimes with several ascending secondary branches arising from near the base, in robust plants stems and caudex hollow and greatly enlarged especially toward the base, hirsute, the hairs 0.3–2.3 mm long, usually with reddish purple pustulate bases, moderately strigillose, the hairs 0.2–0.6 mm long, closely appressed to the surface or somewhat spreading. Leaves (1.4–)6–15(–28) × (0.2–)1–3.5(–5.6) cm, green to grayish green, usually flecked with reddish purple splotches, the blade oblanceolate to linear-oblanceolate, pinnatifid or bipinnatifid to shallowly pinnately lobed, sinuate-dentate or subentire (young or small leaves), the apex of the lobes obtuse to occasionally acute, hirsute, the hairs mostly lacking pustulate bases, and often also strigillose, rarely only strigillose, occasionally also sparsely glandular puberulent, the hairs 0.1–0.2 mm long, these hairs inconspicuous, the pubescence usually more dense on or occasionally confined to the margins and major veins, apex obtuse, gradually tapering to the petiole (0.9–)3.5–8(–14) cm long. Flowers 1–4 rarely more per plant opening per day, 1–2 hours before sunset, rapidly fading the following morning, strongly scented with a sweet lemony fragrance or a pungent semen-like odor to weakly scented in autogamous populations. Ovary 5–15(–20) mm long, moderately to densely hirsute, the reddish purple pustulate bases of the hairs very prominent, also densely to moderately strigillose and usually sparsely glandular puberulent. Floral tube (2–)2.6–6 (–7.2) cm long, flaring (3–)4–7 mm at the mouth, usually flecked with reddish purple streaks of spots and/or tinged with red, moderately hirsute and strigillose, also usually glandular puberulent, glabrous within. Sepals (0.7–)1.2–2.5(–3) × 0.2–0.6 cm, usually separating and reflexed in pairs at anthesis or occasionally separating individually, usually flecked with reddish purple splotches and reddish tinged, pubescence the same as on floral tube. Petals (0.6–)1.3–3.5(–4) × (0.8–)1.6–4(–4.6) cm, deep yellow, fading reddish orange to purple, drying purple, very broadly obcordate. Staminal filaments 6–16 mm long, yellow. Anthers 3–10 mm long, yellow. Style (3.2–)4–9(–10) cm long; stigma lobes 2–8 mm long, elevated above the anthers in chasmogamous plants to surrounded by them in autogamous plants. Capsule1.0–4.5(–6.0) × 0.4–0.8 cm, lanceoloid to ovoid, quadrangular in cross-section, hard and woody at maturity, sigmoid or curved, occasionally straight, the apex gradually tapering to a sterile beak 4–15 mm long, the free tips 3–5 mm long, dehiscing 1/4–2/3 the length of the capsule, sessile. Seeds ca. (4–)30–140(–160) per capsule, 3–3.5 mm long, 1–1.4 mm wide, 1.4–1.6 mm high, arranged in two adjacent rows in each locule, obovoid to oblanceoloid, somewhat irregularly shaped; the testa much thickened above the raphe and at the distal end, the distal thickened area with a cavity visible externally with a conspicuous groove surrounded by a U-shaped thickened area terminating at a pore at the distal end, the surface a dull dusty brown, papillose, the papillae depressed apically, coarsely rugose on the distal half of the abaxial side. Self-compatible, rarely self-incompatible, outcrossing to modally autogamous. Gametic chromosome number, $n = 7$.

***Phenology.*** Flowering from mid-February to May, after rains, rarely as late as June.

***Distribution and Habitat (Fig. 1).*** Occurring in the Chihuahuan, Mohave, and Sonoran deserts in sandy soils on flats, low hills and margins of sand dunes or along arroyos and roadsides, 30–1600 m or rarely slightly higher, from southeastern California across southern Nevada to southern Utah counties of Emery, Kane and Washington, northwestern Mohave Co, Arizona, and south of the Mogollon Plateau to southern New Mexico, western Texas, Chihuahua, Sonora, and Baja California Norte, Mexico, in desert scrub dominated by some combination of *Larrea*, *Ambrosia*, *Lycium*, *Atriplex*, *Yucca*, *Dasylirion*, *Nolina*, cacti or *Prosopis*, or in Utah, vegetation dominated by *Ericameria*, *Artemisia*, *Juniperus*, and *Forestiera* to openings in grasslands dominated by *Bouteloua* and *Hilaria* or oak-grassland in southeastern Arizona and southern New Mexico.

***Representative Specimens Examined.*** MEXICO. Baja California Norte: Valley of San Juan (near 28° 44′ N, 113° 37′ W), *Moran 8079* (RSA, UC, US); Cuesta la Ney (near 28° 19′ N, 113° 07′ W), *Moran 12644* (SD, RSA); Arroyo de la Purification (28° 20′ N, 113° 34′ W), *Moran & Reveal 20219* (US); San Quintin Bay (30° 22′ N, 115° 55′ W), *Palmer 663* (MICH, NY, US); Calmalli (28° 14′ N, 113° 33′ W), *Purpus 224* (F, US); 9 mi S of Higuera, *Wiggins 16725* (DS). Chihuahua: 42 mi S of Ahumada on Hwy. 45, *Harmon & Denver 5357* (UMO). Sonora: 7 mi W of Hwy. 15 along southern rd. to Bahia Kino, Municipio of Hermosillo, *Breedlove 15891* (DS); ca. 1 km S of Km 71 on Hwy. 2, 6 mi W of Los Vidrios (ca. 32° 03′ N, 113° 33′ W), 1 km N of Pinacata lava shield, *Drees et al. 20589* (ARIZ); 2.8 mi by rd. S of Papago Tanks, Pinacate region (ca. 31.8° N, 113.6° W), *Felger 18731* (ARIZ); ca. 1 mi NE of Sierra del Rosario, Gran Desierto (ca. 32° 06½′ N, 114° 10′ W), *Felger et al. 20801* (ARIZ); 47 km S of Nogales, on rd. to Hermosillo, *Frye et al. 2268* (DS, GH, NY, RSA, UC, UTC); less than 2 km from Cucurpe (near 30° 20′ N, 110° 43′ W), *Nabhan & Sheridan 323* (ARIZ); Penasco, *Raven 11679* (RSA, UC); 4 km S of Capilla de San Francisco, midway between Hermosillo & Guaymas, *Ripley 14308* (CAS, NY); Magdalena, *Rose 15132* (US); 64 mi NE of Ures toward Moctezuma, *Straw 2121* (RSA); Cienega ca. 1 mi E of Rancho Agua Fria on Rio Saracachi (E of Cucurpe), 1977, *Van Devender et al. s.n.* (ARIZ); fork of rd. leading from hwy. to San Miguel, 6 mi S of Carbo, *Wiggins 6234* (DS); Cedros, W side of Rio Cedros (27° 43′ N, 109° 15′ W), *Wiggins 6428* (DS); 7 mi S of Sasabe, *Wiggins 8180* (DS).

U.S.A. Arizona: Cochise Co., Benson, *Demaree 42053* (ASC, RSA [2]); E of Wilcox, 1919, *Goodding s.n.* (UC); N of Pomerene 10–20 mi, *Goodding 21–62* (ARIZ); W slope of the Dragoons, SW Cochise stronghold, *Good-*

*ding 58–62* (ARIZ); Miller Canyon 1/2 mi from hwy., Huachuca Mt. Range, 1944, *Lefebure s.n.* (POM); near Chiricahua Natl. Mon., Ed Rigg's Ranch, *Reeves R2555* (ASU, WTS); Bowie, *Thornber 2423* (ARIZ); Portal, entrance to Coronado Natl. Forest, *Wagner 12* (UNM). Gila Co. Gila River, 2 mi below Coolidge Dam, *Maguire 10412* (BRY, NY, UTC); Globe, *Nelson & Nelson 1810* (GH, MICH, NDA, RM, US). Graham Co., Ft. Grant, 1889, *Cairns s.n.* (WIS [2]); ca. 7 mi E of Solomon along Hwy. 78, *Higgins 2888* (BRY, WTS). Greenlee Co., Clifton, *Davidson 241* (DS [2], UC); Duncan, 1920, *Durant s.n.* (POM). Maricopa Co., ca. 7 mi NE of Mesa, *Crosswhite 75* (WIS [2]); Aguila, *Jones 25882* (CAS, CU, DS, MONT, ND, POM); NW corner of White Tank Mts. Park, *Keil 6282* (ASU); 21 mi W of Gila Bend, *Shreve 10148* (COLO, MICH, UC, US); 5.6 mi N of Pima Co. line along Hwy. 85, *Wagner & Mill 4565* (MO); Gila River 3 mi N of Gila Bend, *Wiggins 8410A* (DS). Mohave Co., Squaw Mts., *Braem 67* (DS); E of Big Sandy River, ca. 40 mi SE of Kingman, *Cronquist 10579* (NY); Hackberry, *Demaree 40115* (CAS, RSA); 15 mi W of Kingman, *Maguire s.n.* (BRY, NY, UTC); U.S. Hwy. 66, 13.6 mi SW of Kingman, *Raven 11774* (RSA); 6.8 mi S of jct. Hwy. 93 & I-40 along I-40 at Kingman, *Wagner & Mill 4580* (MO); 57.8 mi SE of Hoover Dam along Hwy. 93, *Wagner & Mill 4584* (MO). Navajo Co., 20 mi N of Holbrook on Hwy. 66, *Provencio 57* (ASC). Pima Co., 16 mi NW of Tucson Mt. Sofferd, *Abrams 13081* (DS); 5 mi W of Sells, *Fosberg 7739* 9LA, NO, PH, POM); 1 mi S of Why along Hwy. 86, ca. 10 mi S of Ajo, *Hitchcock 25501* (ID, UC); ca. 4 mi S of Continental, along hwy. to Amado, *Hitchcock 25554* (COLO, DS, NY, RM, UC, WS); Juan Jose Tank in Cabeza Prieta Game Refuge, *Manthey 1567* (UNM); Mt. Lemmon, *Morrison 65* (ASC); W side of Baboquivari Mts., *Nelson & Nelson 1176* (GH, NDA, NY, RM, UC, US); Tres Alamos Canyon, Ajo Mts., 1939, *Nichol s.n.* (ARIZ); near Vail, *Peebles 11364* (ARIZ, CAS, US); Sierrita Bajada, 15 mi S of Tucson, *Shreve 10094* (ARIZ); Fresnal, *Thackery 89* (ARIZ, US); Tucson, *Thornber 510* (ARIZ, DS, MIN [2], NMC, UC); Hwy. 85, 0.5 mi S of jct. Hwy. near Why, *Wagner & Mill 4566* (MO); 6 mi S of Tucson–Ajo rd. on Baboquivari foothill trail, *Wiggins 8707* (DS, MICH, NY, POM, UC, US). Pinal Co., lower San Pedro Basin, *Bingham 296* (ARIZ); Casa Grande Natl. Mon., *Elmore 12* (ARIZ); Maricopa, *Parish 63* (F, GH, NY); Sacaton, *Peebles 6534* (ARIZ [2], CAS, NA); 10 mi W of Casa Grande, *Peebles & Smith 10705* (ARIZ, GH); Oracle, *Thornber 4557* (ARIZ); Pacific Canyon, 3.5 mi S of Superior on Hwy. 177, 1973, *Wood s.n.* (ASU). Santa Cruz Co., Tumacacori Mts., *Fosberg 7743* (LA); 15–17 mi from Nogales on rd. to Arivaca, *Peebles & Loomis 6997* (NA). Yavapai Co., W Clear Creek, 10 mi E of Camp Verde, 1978, *Keller s.n.* (MNA); Hwy. 93, 2.9 mi NW of Congress Jct. rd., *Pinkava et al. 11455a* (ASU); Montezuma Well, *Stockert 2384* (MNA); Jct. Hwys. 89 & 93, *Wagner & Mill 4571* (MO [2]). Yuma Co., Mesa Citrus Farm of the Univ. of Ariz., 8.5 mi S of Yuma, 1939, *Hendrickson s.n.* (BH, POM); King Valley, 2.2 mi N of Tyson, *Holmgren & Holmgren 6625* (ASU, BRY [2], MONTU [2], NY [2], UTC [2], WTS [2]); 18 mi NW of Hope on rd. to Parker, *Munz et al. 22969* (RSA); 0.4 mi W of Ligurta along Rte. 80, *Pinkava 10080* (ASU); 3.2 mi N of Dateland, *Raven 11716* (RSA, UC); 13 mi E of Tule Well, *Shreve 6222* (ARIZ); 20 mi E of Wellton on Hwy. 80, *Wagner & Mill 4564* (MO). California: Imperial Co., 0.5 mi N along rd. to Blythe from U.S. Hwy. 80, *Balls & Everett 22892* (RSA). Inyo Co., Panamint Mts., *Coville & Funston 535* (MIN); upper end of Deep Springs Valley near Gilbert Pass, *Ferris & Bacigalupi 8053* (CAS, DS, MICH [3], MONT, POM [2], UC, US); Owens Valley, 1 mi S of Olancha, *Wolf 6689* (ARIZ, BH, DS, RSA). Kern Co., 3–5 mi N of Rosamond, *Abrams 11187* (DS); U.S. Hwy. 6 ca. 10 mi N of Mohave, 1940, *Copeland s.n.* (UC); Boron, *Linsley & MacSwain 59–65* (RSA, UC); 36.5 mi N of Mohave along Hwy. 14, *Wagner & Mill 4554* (MO). Riverside Co., Rice Valley, 9.5 mi S of Rice, *Holmgren & Holmgren 6493* (BRY, MONTU, NY); along Hwy. 60–70 W of Blythe, *Klein & Gregory 146* (RSA); Hopkins Well, *Linsley & MacSwain 60–3* (RSA, UC). San Bernardino Co., 10 mi N of Hinkley, *Clokey & Anderson 6771* (BH, MIN, NY, RM, RSA, UC, US, UTC); between Barstow & Mohave, 5 mi E of Kramer, *Ferris 9725* (DS, GH, LA, MICH, POM, UC); 6 mi SE of Kelso, *Henrickson 9397* (ARIZ, LL, NY); E edge of Twenty-Nine Palms, *Hitchcock & Muhlick 23271* (G, RM, UT, UTC); along U.S. Hwy. 91–466 ca. 13 mi NE of Yermo, *Klein 846* (RSA); 4 mi W of Ludlow, *Munz & Hardwood 3420* (POM, RM, US); Fenner, *Munz 16559* (POM, UC); 1 mi S of Windmill Station, 25 mi NE of Baker, *Munz & Everett 17414* (RSA); 20.7 mi N of Adelanto on Hwy. 395 (jct. with rd. to George Air Force Base), *Wagner & Mill 4556* (MO); 1 mi N of I-15 on rd. to Calico Ghost Town, *Wagner & Mill 4557* (MO). Nevada: Clark Co., Arrow Canyon, NE end of Arrow Canyon Range, *Fisher 492* (UNLV); on rd. into the Valley of Fire, 4 mi E of Hwy. 93, *Gregory 380* (RSA); 18 mi NE of Las Vegas, *Munz et al. 22990* (DAO, RSA, UC); 1.5 mi S of Jct. I-15 & Jean exit, ca. 1/4 mi E of I-15, *Wagner & Mill 4592* (MO). Esmeralda Co., between Beatty and Goldfield, *Milner 9332* (UT). Lincoln Co., 1.5 mi S of Leith, *Holmgren & Holmgren 7840* (NY, UNLV). Nye Co., Amargosa Desert, along Hwy. 95, 4.5 mi WNW of Lathrop Wells, *Holmgren & Holmgren 6356* (ASU, ID, NY, WTS); 20 mi S of Goldfield, 1907, *Jones s.n.*(POM). New Mexico: Dona Ana Co., Valley of Rio Grande below Dona Ana, *Parry et al. s.n.* (PH); Rincon, 1881, *Vasey s.n.* (US); Organ Mts., 1900, *Wooton s.n.* (COLO, DS, KSC [2], MIN, NMC [2], NY, RM). Grant Co., City of Rocks State Park, 3 mi E of Faywood and ca. 15 mi S of Hurley, *Hess & Stickney 3414* (ARIZ); Howell's Ridge, Little Hatchet Mts., 1973, *Van Devender*

*& Spaulding s.n.* (ARIZ). Hidalgo Co., ca. 1/2 mi inside border on U.S. Hwy. 80, W of Sterns, *Dunn et al. 14132* (DS); 22 km S of Animas on Co. Rd. 338, *Garton 16971* (CAN [2]); Guadalupe Canyon, 25 mi E of Douglas, *Hess & Stickney 3441* (ARIZ, NY); E of San Luis Pass, *Jackson 2417* (UNM); Lordsburg, 1930, *Jones s.n.* (BM, DS, ND, POM); San Simon Valley between Rodeo and Arizona–New Mexico line (31° 50′ N, 109° 02′ W), 1978, *Moir s.n.* (NMC); Animas Mts., Lower Indian Creek, *Wagner 557* (UNM). Luna Co., Florida Mts., 1919, *Alraues s.n.* (DS); Rock Hound State Park, 10 mi SE of Deming, *Bird 547* (UMO); 4 mi E of Gage, *Glowenke 10715* (PENN); Hermanas, *Herrick 336* (NMC [2], US). Socorro Co., San Antonio, Bosque del Apache Natl. Wildlife Refuge, *Fleetwood 644* (US). Texas: Brewster Co., Terlingua Creek, N of Agua Fria Mt., *Cory 31565* (POM); Tornillo Creek bed at Hot Springs, *Sperry 1642* (SRSC); Burro Mesa, Big Bend Natl. Park, *Warnock 18283* (SRSC). El Paso Co., El Paso, *Hanson 543* (MO), *Hanson 544* (NY, US); McKelligan Canyon, Franklin Mts., *Warnock 7672* (SRSC); ca. 20 mi E of El Paso, *Warnock & Johnston 16213* (SRSC). Hudspeth Co., Van Horn Mts., *Tharp & Havard 49299* (TEX); along Rio Grande River, 2 mi E of Indian Hot Springs, *Turner et al. 409* (GH, SRSC). Jeff Davis Co., Valentine–Van Horn, *Whitehouse 8283* (TEX). Presidio Co., along Alamito Creek, 26 mi S of Marfa, *Correll & Rollins 23656* (LL, NY); Rio Grande near mouth of Alamito Cr., *Hinckley 1419* (NY); ca. 2 mi N of Shafter, *Hinckley 2881* (BH, NY, SRSC); ca. 1 mi NE of Harper ranchhouse, 35 mi S of Marfa, *Hinckley 2889* (BH, NY). Ward Co., 5 mi N of Barstow, *Moore et al. 17* (NY, UC, WS). Utah: Emery Co., without further locality, *Cottam 5169* (UT). Kane Co., 40 mi S of Boulder, 1937, *Maguire s.n.* (NY). Washington Co., ca. 5 mi N of St. George, Pine Valley Mts., *Atwood 4680* (BRY); Warner Valley, ca. 7 mi SW of Hurricane, *Atwood & Higgins 4435* (BRY, COLO, WTS); 1 mi NW of Bloomington, *Christian 780* (ARIZ, POM, MNA, UNLV, UT, UTC); La Verkin, *Cottam 4749* (BRY [2]); 5 mi W of Leeds, *Maguire & Blood 4448* (CU, UTC); 4.8 mi S of Gunlock, *Wagner 4597* (MO).

*Oenothera primiveris* is polymorphic, as is often the case with desert annual species. Much of the variation appears to be ecological, depending on moisture regime. However, there is a geographical basis for some of the variation, and two (Wagner 1993, 2002) or three (Munz 1965) subspecies have been recognized. Earlier (Wagner 1993), I treated *O. primiveris* subsp. *caulescens* as a synonym of *O. primiveris* subsp. *primiveris* because caulescent plants are not as geographically limited as Munz (1965) thought, and they grow sympatrically with acaulescent plants (e.g., Yuma Co., Arizona, *Wagner & Mill 4564*). Moreover, they differ only in this one characteristic from acaulescent plants. Throughout the range of *O. primiveris*, populations are very variable, including variation in all of the diagnostic characters used to distinguish the other two subspecies. There is extensive intergradation of the two previously recognized species (large and small flowered in Fig. 1) across a broad zone of sympatry in northern Mexico, California, Nevada, and western Arizona. In the western part of the overall range of *O. primiveris* plants with larger flowers and usually elevated stigmas, grayish green leaves, and occasionally self-incompatibility were assigned to *Oenothera primiveris* subsp. *bufonis*, while plants from the eastern part of the range represented the other end of the spectrum (*Oenothera primiveris* subsp. *primiveris*) with smaller to much smaller flowers, stigmas completely surrounded by the anthers at anthesis, and generally greener leaves. Field studies across this wide geographical range revealed extensive sympatry and mixing of the differentiating characters (e.g., Yuma Co., Arizona, *Wagner & Mill 4571*; Yavapai Co., Arizona, *Wagner & Mill 4573,* and Sonora, R. Felger, pers. comm.). Because of the widespread occurrence of populations that are not possible to assign to one or the other subspecies it does not seem possible to artificially subdivide this variable species. Rather the variation in flower size is a reflection of a high degree of autogamy in the eastern part of the range of *O. primiveris* and extensive variation in amount of autogamy in the western part of the range. The situation is comparable to that seen in the widespread *Oenothera flava* (A. Nelson) Garrett (sect. *Lavauxia*). The smaller-flowered populations of *O. primiveris* from southeastern Arizona to Texas and Chihuahua, Mexico, may occasionally be outcrossed by hawkmoths but, judging from the reduced amounts of nectar in the floral tube and weak scent, presumably are usually autogamous.

Petals fade with first direct sun and thus are not visited by morning-active bees that collect pollen; Linsley et al. (1964) found no native bees visiting *Oenothera primiveris*.

III. OENOTHERA L. sect. CONTORTAE W. L. Wagner, Ann. Missouri Bot. Gard. 73: 478. 1986.—TYPE: *Oenothera xylocarpa* Coville.

*Oenothera* subg. *Pachylophus* sensu Munz, Amer. J. Bot. 18: 728. 1931, pro parte; N. Amer. Fl. II. 5: 98. 1965, pro parte.

Acaulescent perennial herbs from a thick fleshy taproot. Pubescence of two types: short-hirsute, the hairs erect to curved and somewhat appressed, 0.2–0.3 mm long, occasionally also sparsely hirsute especially on floral parts, the hairs 0.5–1.2 mm long. Leaves forming a simple rosette, the blade usually oblanceolate to obovate in outline, occasionally suborbicular, pinnately lobed, the lateral lobes often greatly reduced, abruptly tapering to a long petiole. Buds erect, quadrangular in cross-section, without free sepal-tips. Flowers opening near sunset, fading the following morning, borne directly from the rosette, fragrance strong sweet. Floral tube 2.7–5.5 cm long, flaring at the mouth. Sepals separating individually or in pairs, reflexed at anthesis. Petals bright yellow, fading salmon red. Capsule lanceoloid, flexible, falcate, tapering gradually to a long slender sterile apex, quadrangular in cross-section, the angles acute, conspicuously asymmetrical at the base, often contorted and twisted, the surface conspicuously wrinkled, sessile. Seeds in one row in each locule, often becoming two rows toward the base of the capsule, obovoid, coarsely rugose, the surface with turgid and collapsed papillae, the raphial face with two small longitudinal ridges nearly the length of the seed. Self-compatible, outcrossing. Basic chromosome number, $x = 7$.

*Oenothera* sect. *Contortae* comprises only a single species, *O. xylocarpa*, which occurs in three disjunct areas in California and Nevada: 1) Mount Rose, Washoe Co., Nevada, 2) southern Sierra Nevada in southwestern Mono Co., California, from the vicinity of Crestview south to Casa Diablo, and 3) southern Sierra Nevada in Inyo and Tulare cos., California, 2250–3050 m.

7. OENOTHERA XYLOCARPA Coville, Contr. U.S. Natl. Herb. 4: 105. 1893. *Anogra xylocarpa* (Coville) Small, Bull. Torrey Bot. Club 23: 174. 1896.—TYPE: U.S.A. California: Tulare Co., west side of Whitney Meadows (now known as Big Whitney Meadows, Upper Kern River Basin), 2875 m, 19 August 1891, *B. H. Dutcher 1627* (holotype:US-48881!, photos MO!, UC!; isotypes: CU!, DS!, GH!, NY!). Figs. 4g, h; 6. The collector of this specimen, B. H. Dutcher, is hand-written on the label of the holotype of the standard label of the expedition, which has Coville and Funston printed as collectors.

Acaulescent perennial herb from a thick fleshy taproot, rosette simple. Leaves 2.6–4.2(–6.2) × 1.4–4.2 cm, usually oblanceolate to obovate in outline, occasionally suborbicular, pinnately lobed, the lateral lobes oblong to lanceolate, often absent or reduced to only a few lobes toward the terminal lobe, canescent with short erect to curved and somewhat appressed hairs, 0.2–0.3 mm long, usually with reddish purple spots scattered over the surface, the margin dentate, the base rounded to cordate, abruptly tapering to the petiole 2.5–9(–11.5) cm long. Flowers 1 to 3 or rarely more per day opening near sunset, with a strong sweet fragrance. Ovary 12–18 mm long, curved at the base, densely short-hirsute, pedicel ca. 1 mm long. Floral tube 2.7–4.5(–5.5) cm long, flaring to 4–5 mm at the mouth, densely short-hirsute and also sometimes sparsely long-hirsute, glabrous within. Sepals 2.5–3 × 0.35–0.5 cm, separate and reflexed at anthesis, occasionally reflexed in pairs, infused with deep red often very intensely, moderately to densely short-hirsute. Petals 2.5–3.8 × 3–4 cm, intensely yellow, fading deep salmon red, broadly obcordate, the notch shallow. Staminal filaments 17–23 mm long, yellow. Anthers 7–10 mm long, yellow. Style 4.4–6.5(–8) cm long; stigma lobes 3–4 mm long, somewhat elevated above the anthers at anthesis. Capsule 3.5–9.0 × 0.7–1.1 cm, lanceoloid, strongly asymmetrical at the base, falcate, often contorted and twisted, flexible at maturity, the surface conspicuously wrinkled, quadrangular in cross-section, tapering to a conspicuous sterile apex 10–30(–40) mm long, dehiscing 2/3–3/4 the length of the capsule. Seeds 2.4–3.2 × 1.3–1.7 mm, arranged in one row in each locule, often becoming two rows toward the base, obovoid, often truncate at the apex, coarsely rugose, the surface papillose, the raphial face with two longitudinal ridges nearly the length of the seed, dark purplish brown appearing nearly black. Self-compatible, but modally outcrossing. Gametic chromosome number, $n = 7$.

***Phenology.*** Flowering June and July, rarely later.

***Distribution and Habitat (Fig. 1).*** Locally abundant in open meadows, flats or slopes on loose granitic gravel, sand or pumice, 2250–3050 m, in *Pinus jefferyi* forest with *Artemisia tridentata* or in *Pinus contorta* subsp. *murrayana* to *Abies magnifica* forest from three disjunct areas in California and adjacent Nevada: 1) Mount Rose, Washoe Co., Nevada, 2) southern Sierra Nevada, southwestern Mono Co., California, from the vicinity of Crestview south to Casa Diablo, and 3) area in the southern Sierra Nevada bounded by Horseshoe and Big Whitney Meadows to the east and north, and Casa Vieja and Volcano Meadows to the south and west, west-central Inyo and eastern Tulare Cos., California.

***Representative Specimens Examined.*** U.S.A.: California: Inyo Co., Sierra Nevada, upper end of Horseshoe Meadows, 1947, *Cox s.n.* (DS). Mono Co., Smokey Bear Flat, 1979, *DeDecker s.n.* (MO); S of Lee Vining, *Moldenke et al. 25838* (TEX); along U.S. Hwy. 395, 4.6 mi S of Crestview, *Raven 14263* (GH, RSA, UC). Tulare Co., Tunnel Ranger Station, *Ferris 3753* (DS); N side of Toowa Range, *Hall et al. 8402* (UC); basin of Upper Kern River at Volcano Meadows (originally called Whitney Meadows), *Hall & Babcock 5489* (ARIZ, DS, PH, RM, UC); tunnel to Ramshaw Meadow, *Howell 25907* (CAN, G, US); S fork of Kern River, *Jepson 962* (JEPS); Golden Trout Creek, Kern River, Groundhog Meadow, *Jepson 4948* (JEPS); S end of Bakeoven Meadows, near S fork of Kern River, *Munz 15092* (COLO, RSA); Volcano Creek, *Peirson 783* (RSA); W end of Casa Vieja Meadow, *Twisselmann et al. 18089* (CAS); Sierra Nevada, without further locality, 1875, *Muir s. n.* (MO). Nevada: Washoe Co., Mt. Rose, *Heller 9894* (DS, GH, MONT, NT, PH); 3 mi S of Mt. Rose, *Hitchcock & Martin 5544* (DS, NA, NY, POM, UC, UTC); Mt. Rose Summit, *Ornduff 4337* (LA).

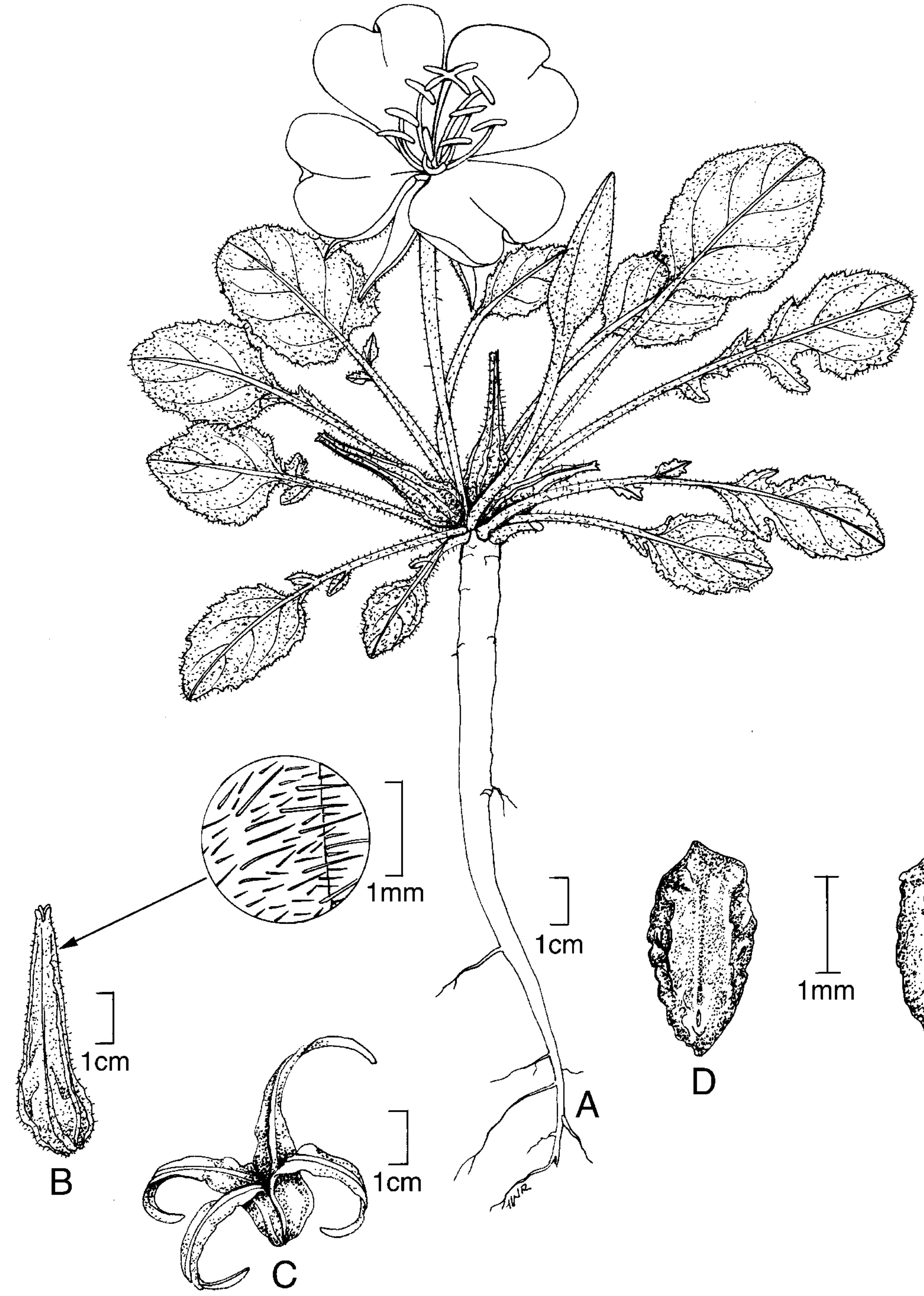

FIG. 6. A–E. *Oenothera xylocarpa*. A. Habit (*Howell 25907*, US) with root (*Munz 11084*, US). B. Predehiscence capsule (*Tiehm 7551*, MO) with telescoped view of trichomes. C–E. *DeDecker s.n.* in 1979, MO. C. Dehisced capsule. D. Adaxial view of seed. E. Abaxial view of seed.

IV. OENOTHERA L. sect. RAVENIA W. L. Wagner, Ann. Missouri Bot. Gard. 73: 477. 1986.—TYPE: *Oenothera muelleri* Munz.

*Oenothera* subg. *Pachylophus* sensu Munz, Amer. J. Bot. 18: 728. 1931, pro parte; N. Amer. Fl. II. 5: 98. 1965, pro parte.

*Oenothera* subg. *Raimannia* sensu Munz, N. Amer. Fl. II. 5: 104. 1965, pro parte.

Fleshy-leaved perennial herbs from a large fleshy taproot, stems several, 5–70 cm long, arising from the rosette, unbranched or with short lateral branches, decumbent to ascending, lateral roots occasionally producing new shoots. Pubescence of two types: hirsute, the hairs usually with a purple pustulate base, and strigillose; the leaves sometimes glabrous. Leaves forming a basal rosette and also cauline, oblanceolate to lanceolate or linear-lanceolate, pinnately lobed to sinuate-dentate or subentire, gradually tapering to the base, sessile or with a winged petiole. Buds curved downward by the recurved floral tube, becoming erect before anthesis, sharply quadrangular in cross-section, the angles acute, without free sepal-tips. Flowers opening near sunset and fading the following morning, borne singly in the leaf axils, fragrance sweet with a peppery background odor, less prominent in autogamous taxa. Floral tube 6.5–20 cm in length. Sepals separate and reflexed at anthesis. Petals white, fading pink to rose, drying purple. Capsules oblong-lanceoloid, somewhat curved, quadrangular in cross-section, the angles acute to rounded, the base symmetrical to slightly asymmetrical, sessile. Seeds 3–7 mm long, in one or two rows per locule, obovoid to oblong or oblanceoloid, often somewhat irregular; the testa much thickened above the raphe and at the distal end, the thickened area with a cavity not visible externally or rarely appearing as a distal pore and/or a raphial groove, the abaxial surface with longitudinal ribs. Self-incompatible or self-compatible, outcrossing to autogamous. Basic chromosome number, $x = 7$.

***Distribution (Fig. 1).*** The three species of section *Ravenia* have relatively narrow ranges in montane habitats in four disjunct areas of Mexico: 1) northern Coahuila (*O. riskindii*); 2) southern Coahuila, Nuevo León and Tamaulipas (*O. muelleri* and *O. tubifera* subsp. *tubifera*); 3) southern Durango (*O. tubifera* subsp. *macrocarpa*); and 4) southern Hidalgo, east to central Puebla, and south to extreme northern Guerrero (*O. tubifera* subsp. *tubifera*).

### KEY TO THE SPECIES OF *OENOTHERA* sect. *RAVENIA*

1. Leaves (0.7—)1.7—4.5 cm wide; sepals 3.2—5 cm long; seeds 3—7 mm long; stigma elevated above anthers; anthers 12—26 mm long.
    2. Stems suberect to sprawling, become decumbent as they lengthen; cauline leaves 4–6 cm long, margins entire or with a few lobes toward the base; seeds with a visible raphial groove . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8. *O. riskindii*
    2. Stems decumbent; cauline leaves oblanceolate to lanceolate, 5–18 cm long, pinnately lobed or sinuate-dentate throughout; seeds with a cryptic cavity and no raphial groove . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 9. *O. muelleri*
1. Leaves 0.5—1.2 cm wide; sepals 1.3—2.5 cm long; seeds 3—4 mm long; stigma surrounded by anthers; anthers 7—11 mm long . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 10. *O. tubifera*

**8. Oenothera riskindii** W. L. Wagner, sp. nov.—TYPE: MEXICO. Coahuila: Mcpo. de Muzquiz, Rincón de María (28° 27′ 30″ N, 102° 44′ W), common perennial in oak woodland, in mesic, sheltered, northern exposed portion saddle at summit of rincon, associated with *Quercus gravesii*, *Prunus*, *Rhamnus betulaefolia*, *Salvia regla*, and *Tilia*, ca. 2320 m, 23 Aug 1975, *T. Wendt, E. Lott, & D. H. Riskind 1289* (holotype: TEX!; isotype MO!). Figs. 4i, j; 7.

Species haec ab *O. muelleri* differt caulibus suberectis ad porrectis decumbentibus, foliis 4–6 cm longis, marginis integeris vel paucilobis versus basem, semine sulco raphe visibili.

Stems several, up to 40–70 cm long, arising from a rosette, green with purple stripes, primary stems ascending, becoming more decumbent as they elongate, each node usually with shorter lateral branches, upper portion of stem sparsely hirsute, the hairs 0.8–2 mm long, usually with purple pustulate bases, also sparsely strigillose, the hairs 0.3–0.4 mm long, the older portion of stem glabrate with epidermis becoming chartaceous, tan and splitting with age. Leaves thick and fleshy, green and usually with purple splotches scattered over the surface, midrib pale green, strigillose and often very sparsely hirsute, the hairs denser on the margins and veins. Rosette leaves 17–38 × 2.6–4.5 cm, oblanceolate, subentire to irregularly pinnately lobed, apex acute to short-acuminate, gradually attenuate to the base, petioles 0.8–8 cm, narrowly winged pale green. Cauline leaves and bracts 4–12 × 1.8–3.2 cm wide, broadly lanceolate, ovate or occasionally oblanceolate, subentire and the upper 2/3 to 3/4 remotely denticulate, the lower part with an asymetrical pair of lance-oblong lobes, or irregularly pinnately lobed throughout, apex acute to short-acuminate, sessile or sometimes lower leaves tapering to a winged petiole 1–5 cm long. Flowers few, only one or two per plant opening per day, fragrance sweet with a peppery background odor. Ovary 26–33 mm long, nearly straight throughout, sessile, strigillose and hirsute, the longer hairs with purple pustulate bases. Floral tube 9.5–15.2 cm long, flaring to 5–7 mm at the mouth, very sparsely hirsute and sparsely strigillose, glabrous within. Sepals 3.3–4.7 × 0.5–0.8 cm, tinged reddish purple, sparsely hirsute and strigillose, the hairs confined to the margins. Petals 2.9–4.8 × 3.8–6 cm, white, fading pink, drying lavender, broadly obcordate. Sta-

FIG. 7. A–G. *Oenothera riskindii* (A–D from cultivated plant of *Wagner 6933,* E–G from *Villarreal et al. 8709*). A, B. Stem with telescoped view of trichomes. C. Stem showing nodding buds. D. Flower. E. Dehisced capsule. F. Adaxial view of seed. G. Abaxial view of seed.

minal filaments 15–32 mm long, cream-colored. Anthers 16–26 mm long, yellow. Style 13.5–19 cm long; stigma lobes 6–9 mm long, elevated well above the anthers or surrounded by them at anthesis. Capsule 5.0–7.6 × 0.6–0.8 cm, oblong-lanceoloid, quadrangular in cross-section, straight or falcate throughout, becoming somewhat narrower, tapering to a sterile apex ca. 11–15 mm long, the free tips 4–7 mm long, dehiscent ½ to nearly the full length of the capsule. Seeds (4–)6–7 mm long, (1.8–)2.2–2.8 mm thick, arranged in one row per locule, reddish brown, irregular in shape due to compression in the capsule during development, but basically obovoid to nearly oblong or irregularly fusiform, usually angled, often flattened or with a narrow wing on the raphial face toward the distal end; the testa much thickened above the raphe and in distal half, the thickened area with an internal cavity, this cavity open and visible as a longitudinal groove on the raphial face, sometimes a thin membranous layer sealing the cavity, which when present often splits, the abaxial surface with several longitudinal ribs, the surface dull, somewhat roughened and wrinkled. Self-incompatible. Somatic chromosome number, $2n = 14$.

***Phenology.*** Known to flower in August, but in cultivation the lower elevation population flowered as early as June and as late as October in cultivation Washington, DC and Falls Church, VA.

***Distribution and Habitat (Fig. 1).*** *Oenothera riskindii* is known only from open oak woodland, from 1690 to 2000 m, Rincón de María and Rancho el Rincón on the SW margin of Serranias del Burro, Coahuila, Mexico.

***Specimens from Cultivated Plants.*** MEXICO. Coahuila: Rincón de María of the limestone Sierra de la Encantada (Sa. De Santa Rosa), 84 air km NW of Músquiz (ca. 28° 27′ 11″ N, 102° 04′ 50″ W), at 1980 m on scree slopes, cult. from *Villarreal et al. 8715, Wagner 6937* (K, MO, RSA, US), same locality at 1690 m (ca. 28° 27′ 26″ N, 102° 04′ 44″ W), cult. from *Villarreal et al. 8709, Wagner 6933* (US, ARIZ, CIIDIR, GH, IEB, IBUG, K, MEXU, MICH, MO, NMC, RSA, TEX).

***Additional Specimens Examined.*** MEXICO. Coahuila: Rincón de María of the limestone Sierra de la Encantada (Sa. De Santa Rosa), 84 air km NW of Músquiz (ca. 28° 27′ 11″ N, 102° 04′ 50″ W), at 1980 m on scree slopes, *Hendrickson et al. 22536* (TEX), *Villarreal et al. 8715* (TEX, US), same locality at 1690 m (ca. 28° 27′ 26″ N, 102° 04′ 44″ W), *Villarreal et al. 8709* (TEX, US); Municipio Villa Acuña, Rancho El Rincón, on SW margin of Serranias del Burro (part of Sierra del Carmen, ca. 80 km SE of Big Bend National Park, TX (ca. 28° 40′ N, 102° 15′ W), *Ruiz & Doan-Crider 172* (TEX).

I take great pleasure to honor David H. Riskind of the Texas Parks and Wildlife Department, Austin, Texas with this species. He pioneered the exploration of the Rincón de María area with Tom Wendt, from which a number of number of interesting regional endemics have been discovered. The narrowly endemic *Oenothera riskindii*, from the rarely collected Rincón de María and adjacent Serranias del Burro, Coahuila, was first collected in 1978 by Tom Wendt and David H. Riskind. The northernmost of the three species of sect. *Ravenia*, *O. riskindii* has several unique of features, including suberect stems that become more decumbent as they lengthen, ovate stem leaves that are 4–6 cm long, their margins entire or with a few lobes toward the base, and seeds with a visible raphial groove. The closely related *O. muelleri*, which occurs to the south in Nuevo León and Tamaulipias, has decumbent stems, stem leaves that are 5–18 cm long oblanceolate to lanceolate with pinnately lobed or sinuate-dentate margins, and seeds with a cryptic cavity and no raphial groove. Self-incompatibility was determined by 30 self-pollinations resulting in no seed-set on cultivated collections (*Wagner 6933* and *6937*).

9. OENOTHERA MUELLERI Munz, Bull. Torrey Bot. Club 64: 304. 1937.—TYPE: MEXICO. Nuevo León: Sierra Infiernillo, ca. 15 mi SW of Galeana, rare in open woods bordering the fields and scattered in the pine savannah, 2450 m, *C. H. & M. T. Mueller 804* (holotype: POM-210702!, photo MO; isotypes: F!, GH!, MICH!). Figs. 4k, l; 8.

Stems several, 5–30 cm long, arising from basal rosette, simple, decumbent, sparsely to moderately hirsute, the hairs 0.8–2 mm long, usually with purple pustulate bases, also sparsely strigillose especially on upper portion of the stem, the hairs 0.3–0.4 mm long. Leaves thick and fleshy, dark green, usually with large purple splotches scattered over the surface, strigillose and often also very sparsely hirsute, the hairs usually confined to the margins and major veins, sometimes glabrous. Rosette leaves (6.5–)12–24 × (0.7–)1.7–3 cm, oblanceolate, sinuate to pinnately-lobed, persistent, apex acute to obtuse, petiole 0–4 cm long. Cauline leaves 3.5–18 cm × 1.1–3.3 cm wide, broadly oblanceolate to lanceolate or ovate, pinnately-lobed to sinuate-dentate, the lobes lance-oblong, apex rounded, usually sessile, sometimes lower leaves tapering to a winged petiole 1–5 cm long. Flowers usually one or two per plant opening per day, fragrance sweet with a peppery background odor. Ovary (11–)16–25 mm long, somewhat curved at the base, sessile, strigillose and hirsute, the hairs with purple pustulate bases. Floral tube (12–)14–20 cm long, flaring to ca. 7 mm at the mouth, tinged reddish purple, glabrous to sparsely hirsute externally, glabrous within. Sepals 3.2–4.9 × 0.35–0.6 cm, often with a broad purple stripe or reddish purple throughout, sparsely hirsute and strigillose along the margins. Petals 4.2–6.2 × 3.8–6.3 cm, white, fading pink to rose, drying purple, broadly obcordate, the notch shallow with a deltoid tooth 2–3 mm long. Staminal filaments 20–22(–25) mm long, cream-col-

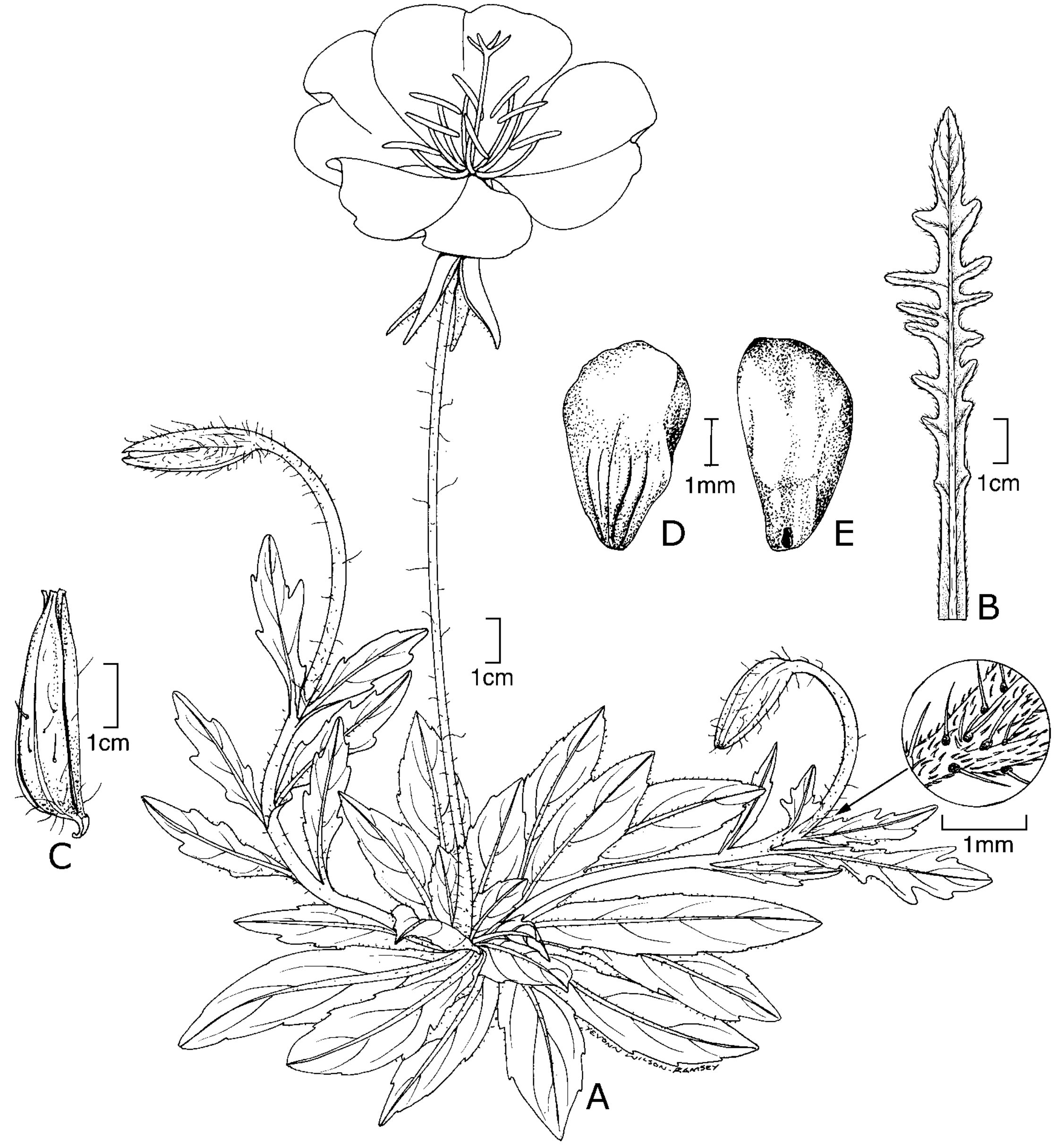

FIG. 8. A–D. *Oenothera muelleri* (*Pennell 17142,* US; flower and telescoped view of trichomes per *Lloyd 4081,* MO). A. Habit, telescoped view of trichomes on upper stem. B. Capsule just prior to dehiscence. C. Abaxial view of seed. D. Adaxial view of seed.

ored. Anthers (12–)14–17 mm long, yellow. Style 16–21 cm long; stigma lobes 7–13 mm long, somewhat elevated above the anthers at anthesis. Capsule 3.0–4.5 × 0.4–0.9 cm, oblong-lanceoloid, quadrangular in cross-section, becoming somewhat narrower and curved towards the base, tapering to a sterile apex ca. 4–8 mm long, the free tips ca. 3 mm long, dehiscing nearly the full length of the capsule. Seeds ca. 40–60 per capsule, 3–5(–6) mm long, (1.5–)2–3.5 mm thick, arranged in one row per locule, brown to reddish brown, irregularly obovoid to nearly oblong, usually angled, often flattened on the raphial face toward the distal end or sometimes flattened parallel to the abaxial-adaxial axis; the testa much thickened above the raphe and at the distal end, the thickened area with an internal cavity, this cavity not visible externally, the abaxial surface with several longitudinal ribs, the surface dull, appearing smooth. Self-incompatible. Gametic chromosome number, $n = 7$.

***Phenology.*** Flowering from June to September.

***Distribution and Habitat (Fig. 1).*** *Oenothera muelleri* occurs in open, often rocky sites, along arroyos, on slopes, in pine forests or grass- or scrub-dominated habitats, 2400–3100 m, from three disjunct areas in northeastern Mexico: 1) Cerro Potosi, Nuevo León, 2) near Pablillo and Cieneguillas, Nuevo León, 3) Pena Nevada, Tamaulipas.

***Additional Specimens Examined.*** MEXICO. Nuevo León: Mt. Infiernillo, 19.5 mi S of Hwy. 60, 9.5 mi S of Pablillo (ca. 24° 36′ N, 99° 159′ W), *Bell & Rice 17854* (LL [2], MICH, NCU); Cerro Potosi (24° 52′ N, 100° 14′ W), *Chiang et al. 8059* (LL, MO); Cerro Potosi, *Hinton 17147* (ENCB, MO); 3.2 mi below microwave stat., Cerro Potosi, *Lewis 174* (LL, TEX); E slope of Cerro Potosi, *McGregor et al. 358* (KANU); Cieneguillas, Pablillo SE of Galeana (ca. 24° 31′ N, 99° 58′ W), 1934, *Pennell s.n.* (PH [2], US); E slope of Cerro Potosi near Galeana, *Sharp 45735* (RSA); Puerto Pino, La Joya, Zaragoza, *Hinton 17553* (TEX), *Hinton 27225* (TEX). Tamaulipas: 2 mi S of Marcella, base of Pena Nevada (23° 46′ N, 99° 52′ W), *Stanford et al. 2559* (DS, NY, RM, RSA, US, WS).

***Specimens from Cultivated Plants.*** MEXICO. Nuevo León: cult. at MO from on rd. from Diez y Ocho de Marzoto Microwave Station, Cerro Potosi, *Lloyd 4081* (MO)

10. OENOTHERA TUBIFERA Sér. in DC., Prodr. 3: 50. 1828. *Lavauxia tubifera* (Sér.) Rose, Contr. U.S. Natl. Herb. 8: 329. 1905.—TYPE: Séringe's description was based on a duplication of *Plate 377* of the Sessé and Mocino collection, citing ''fl. mex. ined. t. 377'' (G holotype not seen, photo F, tracings POM, US). The original plates were loaned to A. P. de Candolle who had them duplicated before Mocino took them away to Barcelona in 1817. Séringe did not see the original, now at The Hunt Institute, since he did not arrive at Geneve until 1820 (Briquet 1940) three years after the originals were taken away. McVaugh (2000) added that this type is represented by 0858 in the Toner Collection and in Calques des Dessins (Field Museum neg. 30670). Fig. 9.

Stems several, 3–35 cm long, arising from basal rosette, simple, decumbent, sparsely to densely strigillose, the hairs 0.3–0.5 mm long, also sparsely hirsute, the hairs 1–2 mm long, and usually with purple pustulate bases. Leaves thick and fleshy, linear-lanceolate to lanceolate, denticulate to subentire, rarely dentate or with a few small lobes, strigillose and often sparsely hirsute, the hairs usually confined to the margins and major veins, sometimes more evenly distributed. Rosette leaves (6–)10.5–18(–22) × 0.5–1.0 cm, tapering gradually to a winged petiole 8–65 mm long. Cauline leaves 4.5–10(–11) × 0.6–1.2 cm wide, tapering gradually to a winged petiole 7–23 mm long. Flowers usually one or two per plant, not noticeably scented. Ovary (13–)16–25(–38) mm long, moderately to densely strigillose and sparsely to moderately hirsute, the longer hairs with pustulate bases, somewhat curved toward the base, sessile. Floral tube 6.5–12(–15) cm long, flaring only slightly to ca. 4–6 mm at the mouth, moderately or rarely sparsely strigillose and also usually sparsely hirsute, glabrous within. Sepals (1.3–)1.6–2.5 × 0.25–0.4 cm, usually infused with reddish purple, separate and reflexed at anthesis, strigillose and hirsute, often sparsely so or the hairs confined mostly to the margins. Petals 1.7–2.6 × 1.5–2.7 cm, white, fading pink, drying purple, obcordate. Staminal filaments 9–14 mm long, cream-colored. Anthers 7–11 mm long, yellow. Style 8.5–15.5(–16.3) cm long; stigma lobes 3–6 mm long, surrounded by the anthers at anthesis. Capsule 2.6–4.3(–5.6) × 0.7–0.9 cm, oblong-lanceoloid, quadrangular in cross-section, curved throughout but more strongly so toward the asymmetrical base, tapering slightly to a sterile apex ca. 4 mm long, the free tips 1–2.5 mm long, dehiscing nearly the full length of the capsule. Seeds ca. 100 per capsule, 3–4 mm long, 1.8–2.3 mm wide, arranged in two partially overlapping rows in each locule, oblanceoloid, sometimes slightly flattened; the testa much thickened above the raphe and at the distal end, the thickened area with an internal cavity, this cavity visible as a narrow, superficial longitudinal groove, sometimes the distal end broader and sealed by a thin membrane, light brown to reddish brown, the surface dull, appearing smooth, the adaxial surface with several longitudinal ribs. Self-compatible and probably mostly autogamous. Gametic chromosome number, $n = 7$.

***Phenology.*** Flowering from July to September.

***Distribution and Habitat (Fig. 1).*** *Oenothera tubifera* occurs in open, often rocky or sandy sites, meadows, slopes or along watercourses, pine or pine-oak woodland or forests to subalpine fir forests, 2300–3250 m, from three disjunct areas in Mexico: 1) southern Hidalgo, México, east to Llano Grande in Central Puebla and south to extreme northern Guerrero, 2) Sierra de la Marta, Coahuila, and 3) the Sierra Madre Occidental east of cd. Durango.

The plants from Durango differ in a number of primarily quantitative characters from those from the other two disjunct areas and thus are here recognized as a distinct subspecies.

## KEY TO THE SUBSPECIES OF *OENOTHERA TUBIFERA*

1. Capsules 3.6—5.6 cm long; stems 20–35 cm long; sepals 2.2—2.5 cm long; floral tube 10.8—15 cm long . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 10a. *O. tubifera* subsp. *macrocarpa*

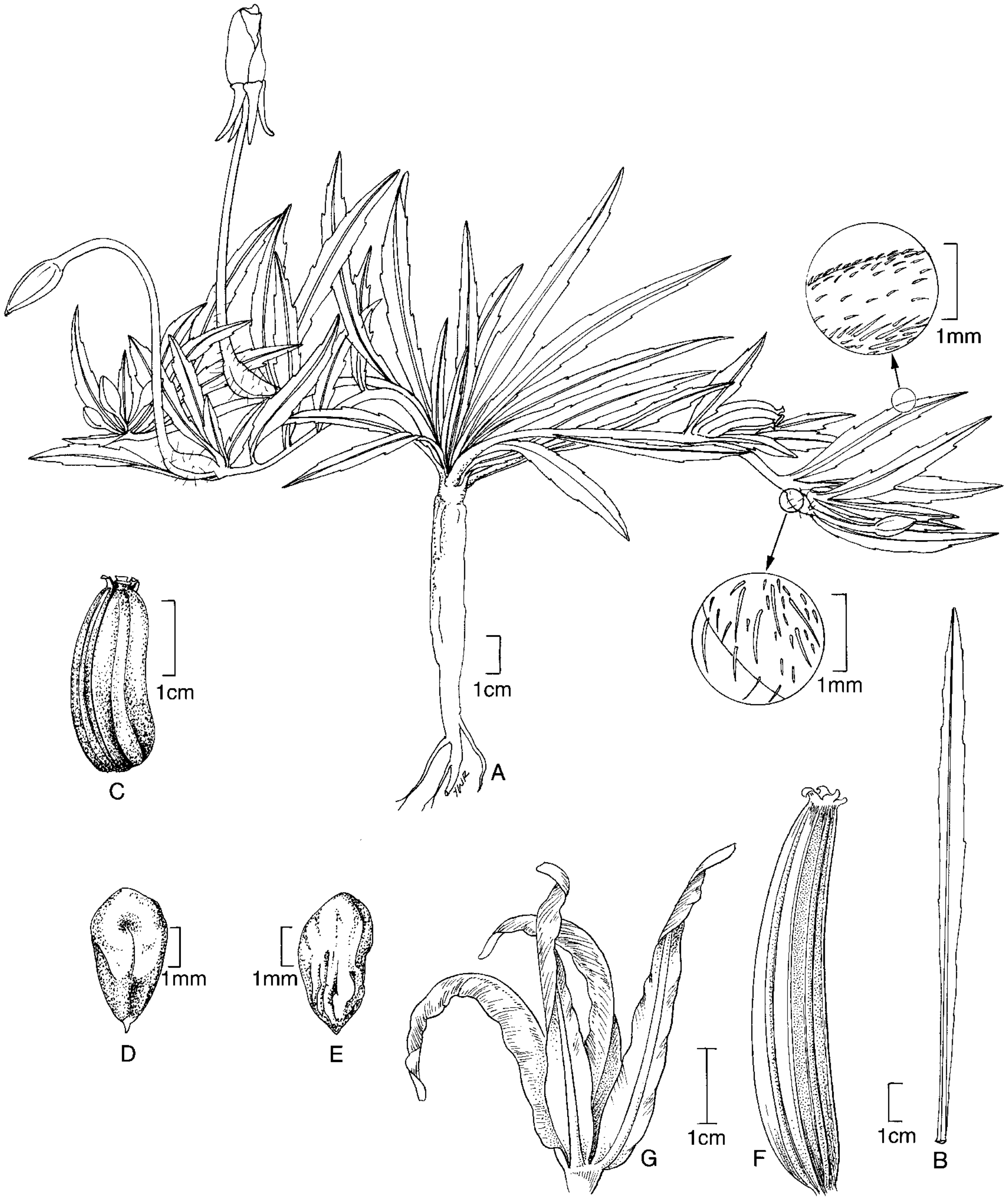

FIG. 9. A–G. *Oenothera tubifera* (A–E subsp. *tubifera*; F–G subsp. *macrocarpa*). A. Habit (*Lyonnet 690,* US; unopened flower from *Rose & Hay 5622,* US) with telescoped views of trichomes of ovary and leaf. B. Basal leaf (*Rzedowski 35709,* MO). C–E. *Rzedowski 36789,* MO. C. Mature capsule. D. Adaxial view of seed. E. Abaxial view of seed. F. Predehiscence mature capsule (*Wagner & Brown 3958,* MO). G. Dehisced capsule (*Breedlove 14321,* MO).

1. Capsules 2.6—3.4 mm long; stems 3–15 cm long; sepals 1.5—2.2 cm long; floral tube 6.5—12.5 cm long . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *O. tubifera* subsp. *tubifera*

**10a. Oenothera tubifera** Sér. subsp. **macrocarpa** W. L. Wagner, subsp. nov.—TYPE: MEXICO. Durango: 51 mi W of Durango along Hwy. 40, plateau area, *Pinus*, *Quercus*, and *Arbutus*, moist depression, rocky loam, 16 Aug 1978, *W. L. Wagner & L. Brown 3958* (Holotype: MO-2725059!). Fig. 9.

Differt a subsp. *tubifera* capsulis 3.6–5.6 cm longis.

Stems 20–35 cm long. Cauline leaves 6—11 cm long. Floral tube 10.8—15 cm long. Sepals 2.2—2.5 cm long. Capsules 3.6—5.6 cm long.

***Phenology.*** Flowering in July and August; with more collecting this range will most likely increase.

***Distribution and Habitat (Fig. 1).*** *Oenothera tubifera* subsp. *macrocarpa* is known from in open, often rocky or sandy sites, meadows, slopes, in pine-oak forests, 2200–2450 m, from the Sierra Madre Occidental east of cd. Durango.

***Additional Specimens Examined.*** MEXICO. Durango: 13 mi E of El Salto along Hwy. 40, *Breedlove 14321* (MO).

### 10b. OENOTHERA TUBIFERA Sér. subsp.TUBIFERA Fig. 9.

Stems 3–15 cm long. Cauline leaves 3—8(–11) cm long. Floral tube 6.5—12.5 cm long. Sepals 1.5—2.2 cm long. Capsules 2.6—3.4 cm long.

***Phenology.*** Flowering from July to September.

***Distribution and Habitat (Fig. 1).*** *Oenothera tubifera* subsp. *tubifera* occurs in open, often rocky or sandy sites, meadows, slopes or along watercourses, pine woodland and forests to subalpine fir forests, 2300–3250 m, from two disjunct areas in Mexico: 1) southern Hidalgo, México, east to Llano Grande in Central Puebla and south to extreme northern Guerrero, and 2) Sierra de la Marta, Coahuila.

***Additional Specimens Examined.*** MEXICO. Coahuila: La Siberia, Sierra de la Marta, cerca del Ejido Santa Rita, ca. 6 km SE de San Antonio de las Alazanas (25° 12′N, 100° 30′ W), *1x semester de Biología UANE s.n.* (TEX). D. F.: SSW of La Cima, *Iltis et al. 964* (WIS); Parres (El Guarda) (19° 09′ N, 99° 11′ W), *Miranda 492* (MEXU); La Cima, *Pringle 13507* (GH, MICH, US, VT [2]); La Cima, *Rzedowski 20455a* (MO); Naucalpan, *Rzedowski 35709* (MO). Guerrero: Km 48 on hwy. to Federal Acapulco, *Sanchez 838* (MEXU). Hidalgo: El Chico (near Pachuca) (20° 13′ N, 98° 44′ W), *Lyonnet 2206* (US); near Zerezo and below Parque Nacional El Chico, *Moore 3132* (BH, GH); above Pueblo Nuevo and below Parque Nacional El Chico on rd. from Real Del Monte to El Chico, *Moore & Wood 3714* (A, BH [2], MICH); Sierra de Pachuca, *Rose & Hay 5622* (US); between Somorriel & Las Lajas (19° 59′ N, 98° 32′ W), *Rose et al. 9240* (US). México: W of Rio Frio, 40 mi E of Mexico City, *Manning & Manning 536566* (GH); La Gavia River, 35 km from Toluca, Km 105 on Toluca-Morelia Hwy., *Sharp 44285* (NY, RSA); 55 km SE of Mexico City, *Weaver 714* (POM, US); 26 mi SE of tollgate near Queretaro, turnpike, Hwy. 57, *Wieder et al. 53* (UMO). Puebla: Llano Grande, Camino Mexico-Puebla, *Lyonnet 690* (US).

The single collection of *Oenothera tubifera* subsp. *tubifera* from Coahuila is somewhat atypical in that the leaves are dentate or have a few small lobes toward the base. Field studies are necessary to determine if it represents another taxon, especially since it occurs hundreds of km disjunct from other populations of this subspecies.

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