



Revision of *Oenothera* sect. *Oenothera* subsect. *Emersonia* (Onagraceae)

Werner Dietrich; Peter H. Raven; Warren L. Wagner

Systematic Botany, Vol. 10, No. 1 (Jan. - Mar., 1985), 29-48.

Stable URL:

<http://links.jstor.org/sici?sici=0363-6445%28198501%2F03%2910%3A1%3C29%3AR00SOS%3E2.0.CO%3B2-I>

Systematic Botany is currently published by American Society of Plant Taxonomists.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/aspt.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

Revision of *Oenothera* sect. *Oenothera* subsect. *Emersonia* (Onagraceae)

WERNER DIETRICH

Botanisches Institut der Universität, Universitätsstrasse 1,
D-4000, Düsseldorf 1, Germany

PETER H. RAVEN

Missouri Botanical Garden, P.O. Box 299,
St. Louis, Missouri 63166

WARREN L. WAGNER

Bernice P. Bishop Museum, P.O. Box 19000-A,
Honolulu, Hawaii 96817

ABSTRACT. *Oenothera* sect. *Oenothera* subsect. *Emersonia* consists of four species, *O. stubbei* sp. nov., *O. maysillesii*, *O. macrosceles*, and *O. organensis*, which have scattered relictual distributions in central and northern Mexico and the Organ Mountains, New Mexico, United States. Diagnostic features of subsect. *Emersonia* include: perennial habit; stems decumbent, ascending or weakly erect, rooting at the nodes in *O. maysillesii* and *O. stubbei*; dentate to subentire leaves, erect buds; yellow vesperine hawkmoth-pollinated flowers; cylindrical to narrowly lanceoloid capsules; and seeds with the testa thickened distally, this thickened area with an internal cavity. Fully fertile hybrids can be made in most combinations between these four species, and it is in part because of this result that these somewhat heterogeneous species are grouped together. Based on morphology, distribution, and ability to form fertile hybrids, especially in the case of *O. maysillesii*, with members of the other four subsections of sect. *Oenothera*, the species of subsect. *Emersonia* appear to represent a lineage that diverged relatively early in the evolution of the section. All four species of subsect. *Emersonia* are diploid, $n = 7$, but some of the plants of each species that we examined are heterozygous for usually one or two reciprocal translocations and up to four translocations in some populations of *O. maysillesii*. *Oenothera macrosceles* is self-compatible, but modally outcrossing; the other three species are self-incompatible. Among the species in subsect. *Emersonia*, features of the seeds are heterogeneous, more so than in most other sections of *Oenothera*. Certain seed characters suggest relationships between species of subsect. *Emersonia* and those of other subsections of sect. *Oenothera*.

DEDICATION. This work is dedicated to Professor Dr. Wilfried Stubbe of the Botanisches Institut der Universität Düsseldorf, on the occasion of his 65th birthday on January 21, 1985. This dedication honors the pioneering research of Professor Stubbe on *Oenothera*, especially concerning the evolution of plastids and the interactions of plastome and genome in sect. *Oenothera*.

Oenothera sect. *Oenothera* subsect. *Emersonia* is here considered to consist of four species that were first grouped together by Stubbe and Raven (1979). These species occur in northern and central Mexico and southern New Mexico. Subsect. *Emersonia* was established by Munz in 1965 as a section of subg. *Raimannia*; he included only *O. organensis* in it. At that time, Munz included *O. maysillesii* and *O. macrosceles* in sect. *Raimannia*. The fourth species that we include in subsect. *Emersonia* is here described as new; it is closely related to *O. macrosceles*.

Cleland (1968) only once obtained hybrids between *Oenothera macrosceles* and any member

of subg. *Raimannia* (sensu Munz 1935, 1965). In contrast, the other species of subg. *Raimannia* were demonstrated to form fertile hybrids readily with one another. Stubbe and Raven (1979) greatly extended Cleland's experiments, and established that hybrids between *O. maysillesii*, *O. organensis*, and *O. macrosceles*, when obtained, are fully fertile. Recently crosses between the other three species and *O. stubbei* by Stubbe and independently by Wagner resulted in fertile hybrids, although one involving *O. organensis* was chlorophyll-deficient. The details of these latter crossing experiments are summarized below. These crossing experi-

ments indicate unambiguously that the genomes and plastomes of *O. maysillesii*, *O. stubbei*, *O. organensis*, and *O. macrosceles* are more similar to one another than they are to other species of *Oenothera*. This, together with their morphological similarities, constitutes our reason for grouping them together in subsect. *Emersonia* (Stubbe and Raven 1979).

The species of subsect. *Emersonia* can be distinguished from the other four subsections of sect. *Oenothera* only by a combination of characters. Among them, the following are notable: perennial habit; long decumbent, ascending, or weakly erect stems (rooting at the nodes in *O. maysillesii* and *O. stubbei*); dentate to subentire leaves; erect buds; floral tubes usually 5.5–15 cm long; seeds with the testa thickened distally, this thickened area with an internal cavity; and self-incompatibility in all except *O. macrosceles*.

All four species of subsect. *Emersonia* are very localized or uncommon, and they have been collected in the field only infrequently. Despite this *Oenothera organensis* is well known in the scientific literature. It is perhaps best known for the detailed studies of the genetics and physiology of self-incompatibility (Crowe 1955; Emerson 1938, 1939, 1940, 1941; Dickinson and Lawson 1975; Hecht 1950, 1961, 1964; Heslop-Harrison and Raven in press; Lewis 1948, 1949, 1951, 1952, 1960, 1979; Mäkinen and Lewis 1962). Up to 45 self-incompatibility alleles have been found in this species composed of perhaps as many as 5000 individuals. A number of attempts have been made to explain the existence of such a large number of alleles, each maintained at a low frequency (Wright 1939, 1965; Fisher 1958, 1961; Crosby 1966). Recently, Levin et al. (1979) have shown that in contrast to the rich diversity of S-alleles *O. organensis* is monomorphic at 14 of 15 allozyme loci studied. Only malic dehydrogenase was polymorphic and it displayed only two alleles.

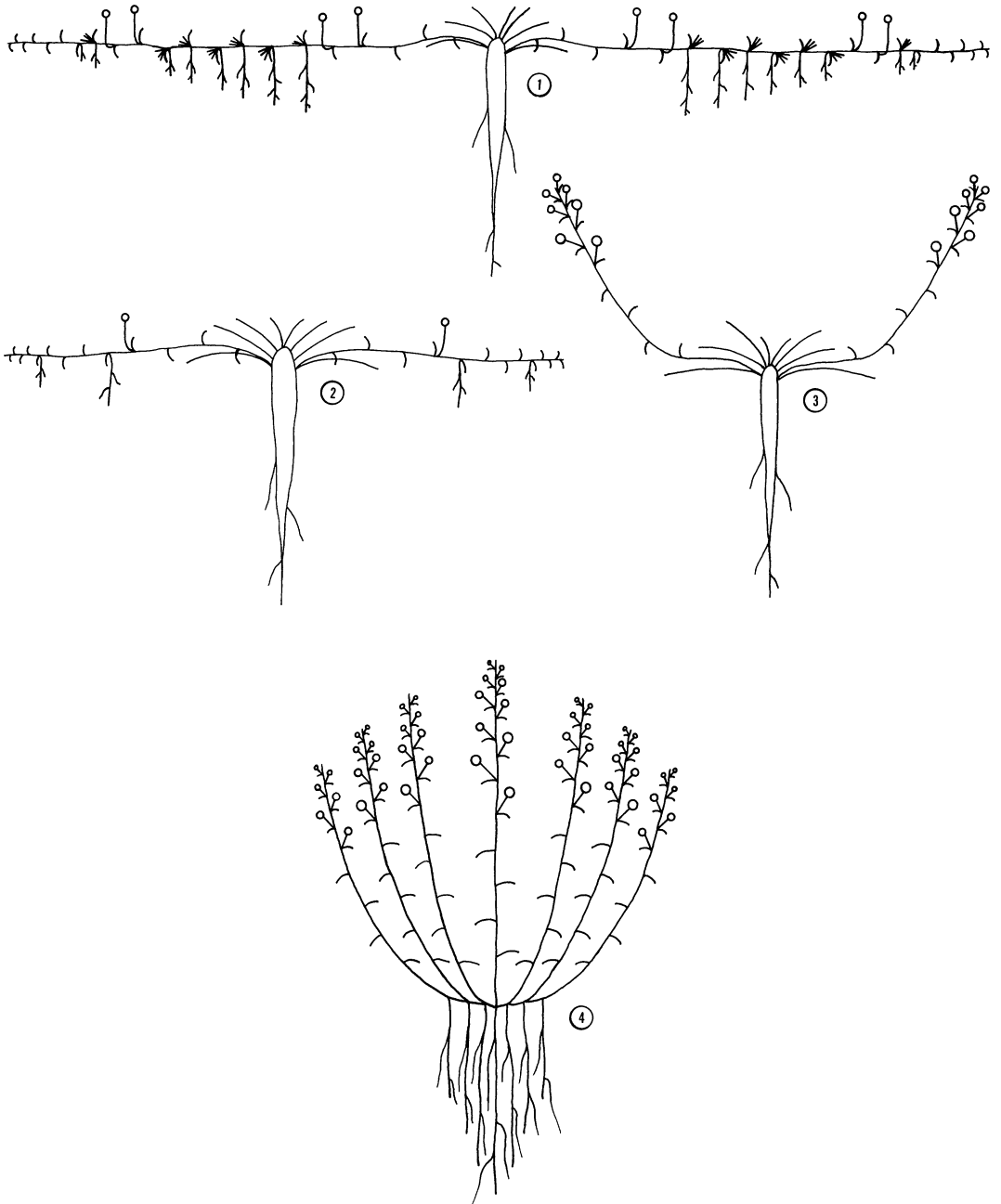
DISCUSSION OF CHARACTERS

The characters of sect. *Oenothera* subsect. *Emersonia* useful in the delimitation of the species or in the evaluation of relationships are discussed in the following pages. Morphology and internal features of seeds were examined by scanning electron microscopy (SEM). The methods used in the SEM study have been discussed elsewhere (Wagner et al. 1985).

Habit (figs. 1–4). As usual in *Oenothera* all species of subsect. *Emersonia* begin growth as a rosette. Sometimes several rosettes may be formed. Each rosette produces one to several stems. Some of the most striking differences between the species of subsect. *Emersonia* are found in characters of the stem. Two species, *Oenothera maysillesii* and *O. stubbei*, are collectively unique in the genus in the production of long decumbent stems that root at the nodes. Extensive colonies are formed in this manner from only a few individuals, and seed set in *O. maysillesii* appears to be sporadic in nature. In contrast, *O. macrosceles* reproduces vegetatively only by basal rosettes from a fleshy taproot. Its stems are ascending but become procumbent as they lengthen and never root at the nodes. In *O. organensis*, mature plants are very bushy. Short ascending to procumbent stems are produced from the rosettes, and secondary rosettes are formed at their tips. One to several weakly erect stems are produced from the leaf axils of each secondary rosette. All of the species form secondary branches; *O. organensis* is many-branched while *O. macrosceles* only occasionally forms a few ascending secondary branches.

Roots. A sparsely branched rather fleshy taproot is characteristic of the species of subsect. *Emersonia* (especially *Oenothera macrosceles*). Three of the four species, *O. stubbei*, *O. maysillesii*, and *O. organensis*, produce adventitious shoots from slender lateral roots. *Oenothera organensis* is especially vigorous in the formation of new shoots, a feature that results in a densely bushy habit. The production of shoots from lateral roots is known in at least some members of the following sections of the genus: sects. *Pachylophus* sensu stricto, *Megapterium*, *Lavauxia*, *Anogra*, *Gauropsis*, and two new sections (one for *O. muelleri* Munz and *O. tubifera* Séringe, and one for *O. havardii* S. Wats.).

Leaves. Each of the species has distinctive leaf characters. *Oenothera organensis* and *O. maysillesii* have rather thick and somewhat leathery leaves, with dentate margins and usually a strongly convex upper surface, although occasionally it is concave. *Oenothera organensis* has yellowish green, narrowly elliptic leaves with crisped margins, whereas *O. maysillesii* has dark green oblanceolate, broadly elliptic or ovate leaves. In contrast, *O. macrosceles* has thick and conspicuously fleshy subentire leaves, perhaps an adaptation to the strongly gypsiferous or al-



FIGS. 1-4. Schematic diagram of habits of *Oenothera* sect. *Oenothera* subsect. *Emersonia*. 1. *O. stubbei*. 2. *O. maysillesii*. 3. *O. macrosceles*. 4. *O. organensis*.

kaline soils that it inhabits. *Oenothera stubbei* has yellowish green, very narrowly elliptic to narrowly lanceolate leaves with remotely dentate margins. The rosette leaves in all of the species

tend to be considerably larger than the cauline ones, and in *O. macrosceles* they usually have conspicuous irregular reddish purple splotches scattered over the surface.

Pubescence. Hair types provide excellent diagnostic characters for *Oenothera* that have not been utilized fully in earlier treatments. The species of subsect. *Emersonia* can be readily distinguished on the basis of hair types, although there is some overlap between types. The types can be characterized as follows:

1) *Glandular*—Erect, transparent, blunt-tipped or clavate hairs 0.1–0.2 mm long that exude a drop of fluid. Glandular hairs occur in three species of subsect. *Emersonia*: *Oenothera stubbei*, *O. macrosceles*, and *O. organensis*. In these species they occur on the ovary and floral tube, but on the leaves only in *O. organensis*.

2) *Hirsute*—Pubescence usually consisting of long erect or spreading unicellular or, in *Oenothera organensis*, bicellular hairs, with a distinctly broadened base and attenuate apex. Hairs of this type range from 0.8–1.5 mm long (to 0.4 mm in *O. organensis*, and to 2.9 mm in *O. maysillesii*), are sometimes appressed, as in *O. maysillesii*, or on leaves of *O. organensis*, and may arise from reddish purple pustulate bases. The occurrence of hirsute pubescence in some other sections of *Oenothera* as well as in other genera of Onagreae suggests that this may be a primitive hair type.

3) *Villous*—Similar to hirsute pubescence but the hairs more slender and not perceptibly broadened at the base. This pubescence type is found only in *Oenothera stubbei*.

4) *Strigillose*—Appressed or occasionally spreading pubescence, the hairs coarse, translucent, unicellular, and 0.2–0.7 mm long. Longer hairs of this type are not always sharply distinct from shorter, spreading hirsute pubescence, although this overlap is not common. *Oenothera organensis* has unusually fine strigillose pubescence; the hairs are slender and very short, only 0.1–0.18(–0.25) mm long.

Flowers. Flowers are borne singly in the axils of the leaves. *Oenothera maysillesii* and *O. stubbei*, which reproduce vigorously vegetatively, produce relatively few flowers, typically only one to two per stem during an entire season. These flowers are usually located near the main rosette. In contrast, *O. organensis* and *O. macrosceles* produce many more flowers, often up to 10 per stem. Moreover, the flowers in these two species are produced at the tips of the stems.

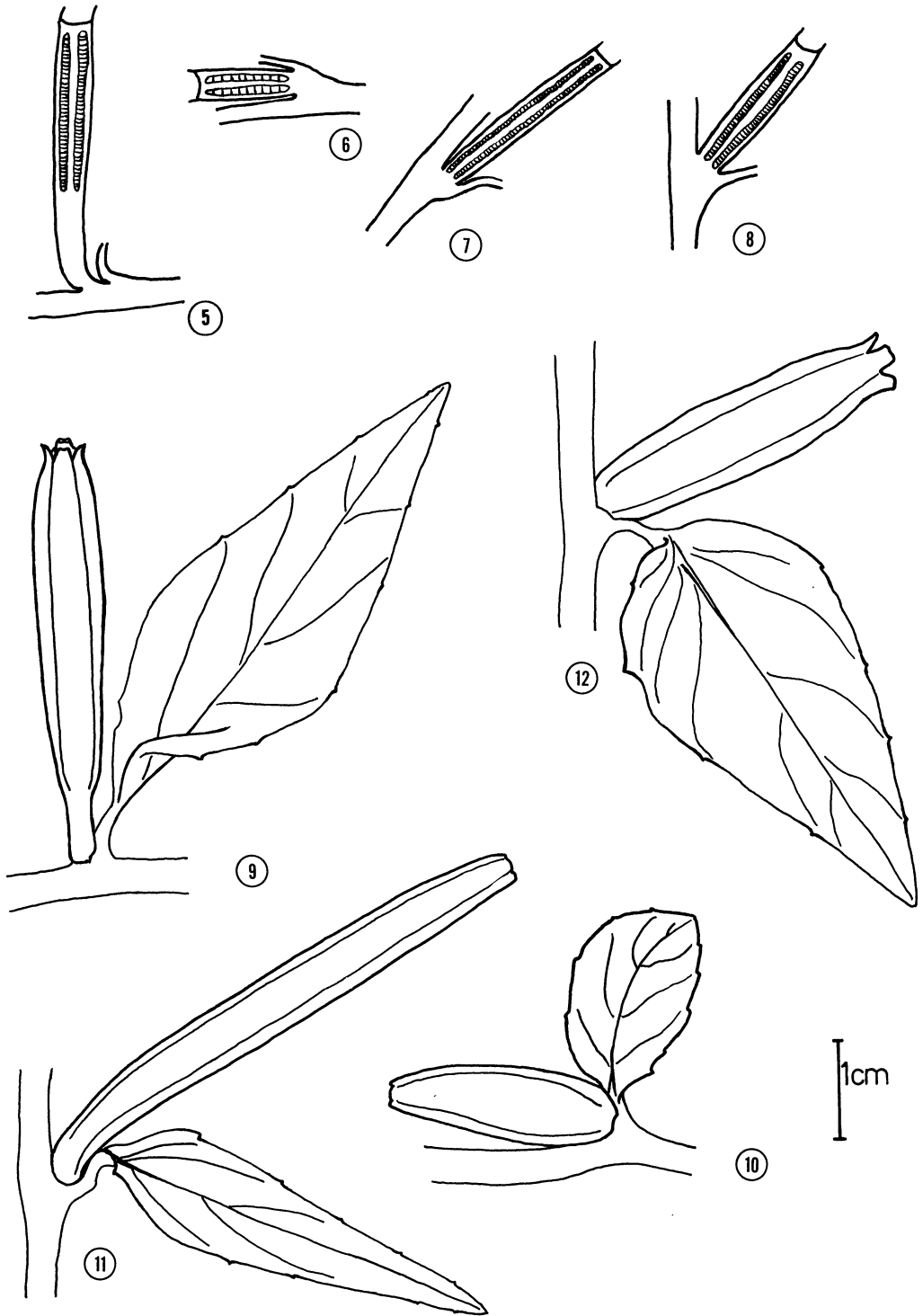
The length of the floral tube is quite variable, ranging from 5.5–9 cm in *Oenothera maysillesii* to 9–15 cm in the other species (up to 19 cm in

O. organensis). The species with longer tubes may have diverged in relation to pollination by hawkmoths with longer proboscides, such as *Manduca*, *Agrius*, and *Cocytius* (Gregory 1963, 1964), however, the pollination biology of these plants has not been studied in detail. Almost all of the other montane species of *Oenothera* in several sections from this region have floral tubes well over 12 cm long and probably represent parallel evolution in response to pollination by these long-tongued hawkmoths (Gregory 1963, 1964).

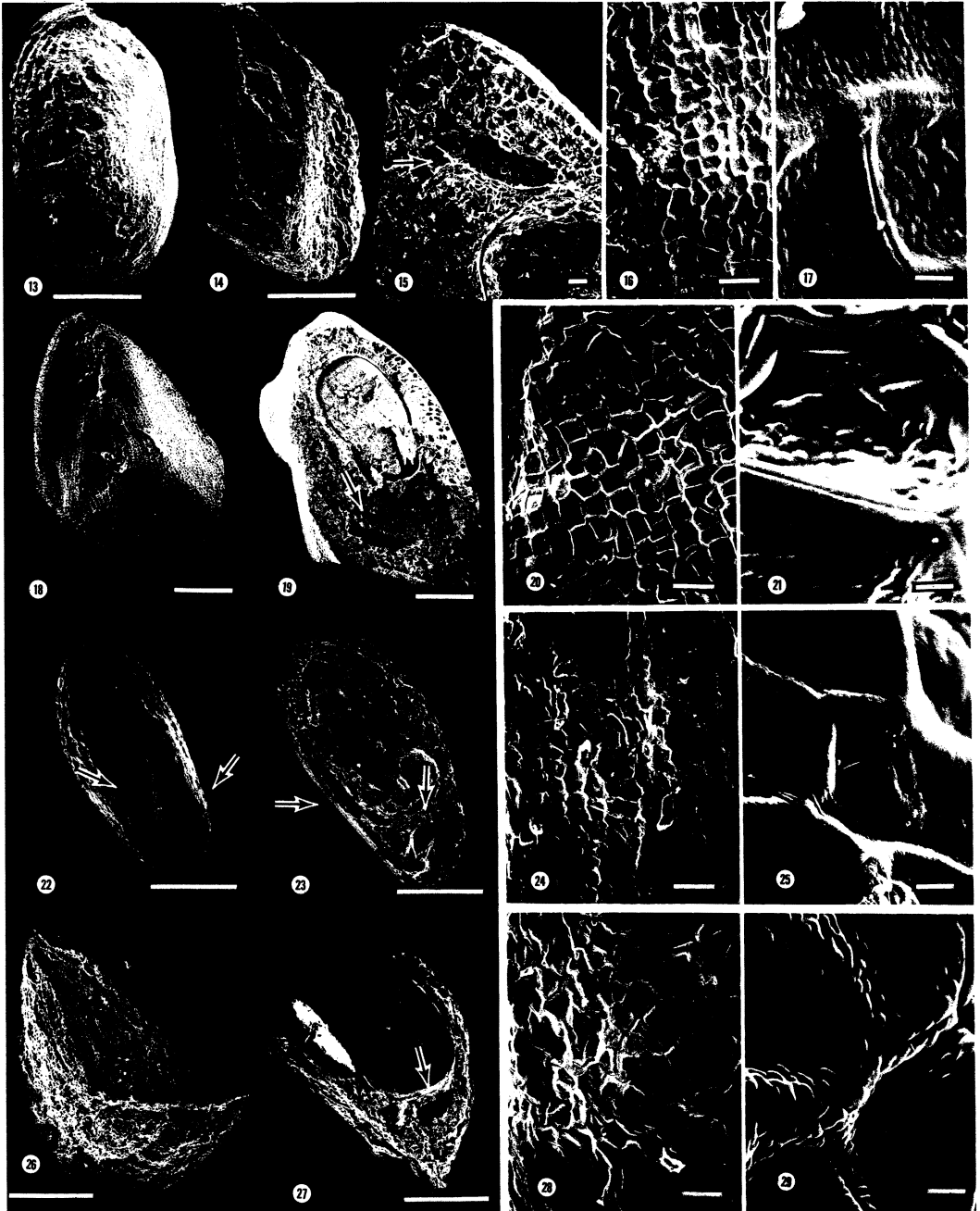
Capsules (figs. 5–12). The capsules of subsect. *Emersonia* are relatively unspecialized. They are cylindrical, except for those of *Oenothera maysillesii*, which have a lanceoloid shape. The capsules dehisce nearly their full length, except in *O. macrosceles*, in which they dehisce only one-half to three-quarters of the length. The ovaries and the arrangement of the ovules are given in figures 5–8. Capsules vary in size, from 1.8–2.6 cm long in *O. maysillesii*, to 2.5–3.5 cm in *O. organensis* and *O. stubbei*; *O. macrosceles* is more variable, with capsules 2–6 cm long. The smaller capsules of *O. maysillesii* also contain markedly fewer seeds (30–50) than do those of the other three species (100–250 seeds; see table 1). The capsules of *O. stubbei* have a unique sterile, pedicel-like basal portion (fig. 5).

Seeds (figs. 13–29). Seed features have long been employed as a major character in the segregation of infrageneric groupings in *Oenothera* (cf. Spach 1835; Raimann 1893; Munz 1965). More recently, the study of *Oenothera* seeds by SEM and light microscopy (LM) is providing new insight into the infrageneric relationships of *Oenothera* (Wagner et al. 1985; Tobe, Chin, and Wagner in prep.; Wagner in prep.).

Features of the seeds of subsect. *Emersonia* (summarized in table 1) are more heterogeneous than in any other group of closely related species in the genus. The seeds of *Oenothera macrosceles* and *O. stubbei*, however, are more similar to one another than are any other pair of species. They are similar in size, shape (figs. 13, 22), type of pitted surface topography (figs. 13, 14, 22), reticulate sculpturing (figs. 16, 24), and inconspicuous micropapillae on the exposed periclinal wall of the epidermal cells (figs. 17, 25). They differ in that the seeds of *O. macrosceles* have no angles or only obtuse angles, are pitted over the entire surface (fig. 22), never



FIGS. 5-12. Ovaries and capsules of *Oenothera* sect. *Oenothera* subsect. *Emersonia*. 5-8. Ovaries in longitudinal section showing arrangement, position and relative number of ovules in two locules. 5. *O. stubbei*. 6. *O. maysillesii*. 7. *O. macrosceles*. 8. *O. organensis*. 9-12. Lateral view of mature capsules in leaf axils. 9. *O. stubbei*. 10. *O. maysillesii*. 11. *O. macrosceles*. 12. *O. organensis*.



FIGS. 13–29. Scanning electron micrographs of seeds of *Oenothera* sect. *Oenothera* subsect. *Emersonia*. 13–17. *O. stubbei*. 18–21. *O. maysillesii*. 22–25. *O. macrosceles*. 26–29. *O. organensis*. The views are, left to right, whole seed, longitudinal section to show distal and/or raphial cavities, pattern of surface sculpturing at 250 \times , and microsculpturing of epidermal cells at 2500 \times . The white bars in each figure indicate: 500 μ m in Figs. 13, 14, 18, 19, 22, 23, 26, 27; 50 μ m in Figs. 15, 16, 20, 24, 28; and 5 μ m in Figs. 17, 21, 25, 29. The arrows indicate the seed cavities.

TABLE 1. Comparison of seed characters of *Oenothera* sect. *Oenothera* subsect. *Emersonia*.

Character	Species		
	<i>O. stubbei</i>	<i>O. mayrillei</i>	<i>O. macrosclera</i>
Number of rows per locule	2	1-2 (2 rows of ovules)	2
Number per capsule	150-180	30-50 from twice as many ovules	160-250
Shape	Oblong-obovoid to oblong-ellipsoid, straight or curved, slightly asymmetrical, angled, often somewhat laterally compressed	Obovoid, straight, asymmetrical, obtusely angled	Oblong-ellipsoid, slightly asymmetrical, straight or slightly curved, not angled or only slightly
Size in mm (length × thickness)	1.2-2.1 × 0.8-1.2	2-2.9 × 1-1.8	(1.2-)1.5-1.8 × 0.7-0.9 1.5-2.1 × 1-1.2
Color	Dark brown flecked with dark reddish purple spots or lighter straw-colored areas	Light brown with darker reddish purple splotches or stripes	Light brown flecked with dark reddish purple spots sometimes mottled with light straw-colored areas
Surface topography	Pitted on abaxial surface toward the distal end, sometimes slightly wrinkled	Flat, no relief	Pitted Irregularly pitted
Sculpturing	Reticulate, junctures of epidermal cells raised, raised area distinctly differentiated from rest of cell, the surface smooth	Conspicuously reticulate, junctures of epidermal cells raised, raised area thick and distinctly differentiated from rest of cell, the surface smooth	Reticulate, junctures of epidermal cells raised, raised area distinctly differentiated from rest of cell, the surface smooth Reticulate, irregularly so on ridges, junctures of epidermal cells raised only slightly, raised area not at all differentiated from rest of cell
Microsculpturing	Inconspicuous micropapillae	Conspicuous micropapillae, micropapillae do not extend to edge of cells	Inconspicuous micropapillae, appearing smooth Conspicuous micropapillae, micropapillae extend to edge of cells
Testa thickened	Yes	Yes	Yes, slightly
Distal end	No	Yes	No
Along raphe	None, slight depression or laterally compressed seed area	None or dark area above micropyle	None or a rapheal ridge
Superficial features of thickened area	Small ridge		Irregular ridge with a central shallow depression darker in color

have a wrinkled surface, and have a larger thickened area above the raphe with a conspicuous irregular shallow depression along the raphe (fig. 22 at left arrow), whereas those of *O. stubbei* are always angled, pitted over only a portion of the seed surface (fig. 13), often wrinkled or ridged (fig. 14), not especially thickened above the raphe and without a raphial depression (fig. 14).

Oenothera maysillesii has fewer and larger seeds than do the other species. The lack of surface topography and large seed size (fig. 18) result in part from a greatly thickened testa (fig. 19). The adaptive significance of this feature is not readily apparent. Species in other presumably related sections, such as *O. brachycarpa* A. Gray (sect. *Megapterium*) of the Chihuahuan Desert and xeric grasslands and *O. primiveris* A. Gray (which will be placed in a new section) of the deserts of the southwestern United States and northern Mexico, also have a greatly thickened mesotesta. The thick testa appears to function to increase the ability of the seeds of these species to absorb water for germination or to dissipate heat in a xeric environment (Wagner et al. 1985). It may also serve to protect the embryo from desiccation (Tobe et al. in prep.). Adaptations to a xeric environment seem less likely for the seeds of *O. maysillesii*, since this species grows in relatively cool and moist places in the pine-oak forests of the Sierra Madre Occidental. It would be necessary to understand the details of its life history better to evaluate the possible adaptive significance of this feature. It is also possible that its ancestor may have occurred in a more xeric environment than does *O. maysillesii* at present.

The seeds of *Oenothera maysillesii* are also unique in their conspicuous reticulate surface (fig. 20), produced by raised junctures between contiguous epidermal cells. The junctures are raised to a greater degree in this species (figs. 20, 21) than those of *O. stubbei* or *O. macrosceles* (e.g., fig. 16). Raised junctures of the epidermal cells similar to those of *O. stubbei* and *O. macrosceles* also occur in all species of sect. *Oenothera* subsections. *Raimannia* and *Munzia* thus far examined (Wagner in prep.). In addition, the basic shape of the seeds of many species in these two subsections is closely similar to those of *O. macrosceles* and *O. stubbei*.

The seeds of *Oenothera organensis* are unique in sect. *Emersonia* in a number of respects. The surface is irregularly pitted (fig. 26), and the

surface reticulations have only slightly raised junctures between the epidermal cells (fig. 29). In addition, the raised areas on the seeds of *O. organensis* have papillae to the edge of the epidermal cells (fig. 29) whereas the raised area in the other three species lacks these papillae (e.g., fig. 25). The pattern of *O. organensis* is closely similar to that found in sect. *Oenothera* subsection. *Oenothera* (Wagner in prep.).

CYTOLOGY

All species of *Oenothera* subsection. *Emersonia* are diploid, $n = 7$, as are most species of *Oenothera*. At least some plants of each species had 7 bivalents at meiotic metaphase I, but translocation heterozygosity was frequent. A plant with one reciprocal translocation ($5_{II} + \odot 4$) was found in each of the only two populations of *O. stubbei* studied. *Oenothera macrosceles* and *O. organensis* had one to two translocations and *O. maysillesii*, the most studied species, was most variable with one to four translocations sometimes in a single population. The widespread occurrence of reciprocal translocations in natural populations is a characteristic feature of all genera of the tribe Onagreae (Raven 1979). Details of the meiotic determinations are given under the respective species.

CROSSING RELATIONSHIPS

The species of subsection. *Emersonia* have been hybridized extensively both among themselves and with species of the other subsections of sect. *Oenothera*, as well as with species of other sections. The results of crosses made with *O. maysillesii*, *O. organensis*, and *O. macrosceles* within sect. *Oenothera* are summarized by Stubbe and Raven (1979). Subsequently, *O. stubbei* has been brought into cultivation and hybridized with the other members of subsection. *Emersonia* by Stubbe at Düsseldorf and Wagner at the Missouri Botanical Garden. The results of these crosses as well as those previously reported by Stubbe and Raven (1979) are summarized in table 2, and as follows:

1) Viable F_1 hybrids can be obtained in all combinations of the species and their reciprocals except for crosses between *Oenothera organensis* and *O. macrosceles*. They could only be hybridized successfully by using plants of the *O. organensis* parent into which the plastids of *O. maysillesii* had been introduced.

2) Hybrids between certain species combinations of subsection. *Emersonia* were sometimes

TABLE 2. Summary of interspecific artificial hybridizations of *Oenothera* species of subsect. *Emersonia*.

Hybrid combination	Pollen stainability (based on 200 grains) % filled grains	Meiotic configuration	Notes	Source
<i>O. maysillesii</i> × <i>O. stubbei</i>	35–45% with <i>O. maysillesii</i> as ♀; by Wagner	—	Hybrids are green and vigorous in both directions, slightly less so when <i>O. stubbei</i> is ♀ parent	Stubbe pers. comm. (Düsseldorf); Wagner (St. Louis)
<i>O. maysillesii</i> × <i>O. macroseces</i>	22%	7 _{II}	Hybrids with <i>O. maysillesii</i> as ♀ parent are green to light green and the reciprocals are pale when young and mottled later; normal seed set	Stubbe and Raven 1979
<i>O. maysillesii</i> × <i>O. organensis</i>	50%	5 _{II} + ⊙4	Hybrids are green when <i>O. maysillesii</i> is parent and the reciprocals are difficult to obtain because pollen from short floral-tubed <i>O. maysillesii</i> cannot traverse the very long floral tubes of <i>O. organensis</i> ; seed set in hybrids normal	Stubbe and Raven 1979
<i>O. macroseces</i> × <i>O. stubbei</i>	47–60% with <i>O. stubbei</i> as ♀, 66% with <i>O. macroseces</i> as ♀; by Wagner	—	Hybrids pale green in both directions; they sometimes died due to increasing chlorophyll deficiency when <i>O. macroseces</i> is ♀ parent	Stubbe pers. comm. (Düsseldorf); Wagner (St. Louis)
<i>O. macroseces</i> × <i>O. organensis</i>	—	—	Crosses with <i>O. organensis</i> as ♀ parent produced empty seed; the reciprocal produced white seedlings. When an <i>O. organensis</i> × <i>O. maysillesii</i> hybrid with plastids of <i>O. maysillesii</i> was crossed to <i>O. macroseces</i> pale but viable plants resulted	Stubbe and Raven 1979
<i>O. stubbei</i> × <i>O. organensis</i>	—	—	Hybrids when <i>O. stubbei</i> is ♀ parent are nearly full green; the reciprocals are white. Hybrids in both directions are somewhat variegated; the green areas have <i>O. stubbei</i> plastids	Stubbe (Düsseldorf)

pale green or white and slow-growing. Moreover, there were often reciprocal differences noted. Many of these results are based on plastome-genome incompatibility where the plastids of one species are unable or able at a reduced efficiency to function in the presence of the genome of the other species.

3) The chromosomes paired completely in all of the F₁ hybrids examined and the chromosomal structure was closely similar.

4) Pollen stainability is reduced in the hybrids examined, ranging from 22% to 66% stainable pollen. The basis for these reductions is not known. Seed set appeared essentially

normal, however, when the hybrids were "open-pollinated" (i.e., grown outside in Düseldorf and visited by the local insects).

5) *Oenothera stubbei* is interfertile with the other three species. Full green or pale green hybrids were obtained in most combinations between it and the other species. This suggests that the plastome of *O. stubbei* is nearly as tolerant and thus as unspecialized as that of *O. maysillesii* (Stubbe pers. comm.), which is the least specialized in sect. *Oenothera*.

The species of subsect. *Emersonia* can also be hybridized with species of sect. *Oenothera* subsects. *Munzia*, *Oenothera*, and *Raimannia*, although in all cases the resulting hybrids have strongly reduced fertility (Stubbe and Raven 1979). In summary from that work:

1) *Oenothera maysillesii* hybridizes most successfully with other species of sect. *Oenothera*. It can form hybrids with the species of subsect. *Oenothera*, yet low pollen fertility (10–40%) is characteristic of these crosses. Relatively high chiasma frequency was observed in some hybrids with subsect. *Oenothera*, but univalents and chains of chromosomes were observed in some combinations involving entities with complex structural heterozygosity.

Hybrids between *Oenothera maysillesii* and species of subsect. *Munzia* were obtained but had strongly reduced fertility and poor chiasma formation. Hybrids were obtained with great difficulty between *O. maysillesii* and *O. drummondii* Hook. of subsect. *Raimannia*; they were pollen- and ovule-sterile. Crosses between *O. maysillesii* and other species of subsect. *Raimannia* consistently failed.

2) Hybrids between *Oenothera macrosceles* and species of subsect. *Munzia* were successful only with *O. longituba* Dietrich and *O. scabra* Krause (both of series *Renneria*) as pistillate parents. These hybrids had strongly reduced fertility. Hybrids between *O. macrosceles* as the pistillate parent and species of subsect. *Oenothera* could be obtained only when *O. elata* H.B.K. (*O. hookeri* Torr. & A. Gray) or *O. jamesii* Torr. & A. Gray were used; white seedlings resulted. The reciprocal hybrid with *O. elata* was green but had only 18% stainable pollen. No hybrids could be obtained between *O. macrosceles* and species of subsect. *Raimannia*.

3) *Oenothera organensis* forms hybrids with species of subsect. *Oenothera* relatively easily but the resulting hybrids had frequent failure of chiasma formation and 10% stainable pollen.

The hybrids had full seed set, however, when open-pollinated. Hybrids could be formed between *O. organensis* and *O. affinis* Camb., *O. indecora* Camb., *O. longiflora* L., *O. longituba*, and *O. sandiana* Hasskarl. In these hybrids fertility was extremely reduced, and only a few seeds per capsule were produced following open pollination.

Oenothera stubbei has not yet been involved in an extensive hybridization program with species of other subsections.

Attempts to hybridize the species of subsect. *Emersonia* with those of other sections of *Oenothera* never yield viable hybrids. Crosses between *Oenothera organensis* and *O. xylocarpa* Coville (sect. nov., ined.) and *O. macrocarpa* Nutt. (sect. *Megapterium*), however, resulted in the formation of seeds with abortive embryos or empty seed coats. With some difficulty slow-growing white seedlings that die have been obtained in crosses between *O. macrosceles* and *O. muelleri* (Raven 1970), and between *O. maysillesii* and *O. macrocarpa* Nutt. (Wagner unpubl.). Other than these cases just mentioned crosses with the species of subsect. *Emersonia* and species outside sect. *Oenothera* fail completely.

In summary, Stubbe and Raven (1979) showed that *Oenothera maysillesii*, *O. macrosceles*, and *O. organensis* form a closely related group based on the fact that viable and fertile hybrids that had normal meiosis could be obtained between them. We have summarized the results of hybridization with *O. stubbei* that have been obtained since 1979. These results agree with its close morphological similarity with *O. macrosceles* in indicating the relationships of *O. stubbei*. The plastome of *O. stubbei* appears to be nearly as generalized as that of *O. maysillesii*. The species of subsect. *Emersonia* consistently produce less fertile hybrids in intersubsectional combination than they do in hybrids with one another.

RELATIONSHIPS

Based on the extensive knowledge of the crossing relationships presented above and on shared morphological features, although few, Stubbe and Raven (1979) concluded that *Oenothera maysillesii*, *O. macrosceles*, and *O. organensis* constitute a group of species more closely related to one another than to any other species. *Oenothera stubbei* also clearly belongs to this group; in fact, it represents a connecting link

between the other species of subsect. *Emersonia*. It shares the specialized rooting stem habit with *O. maysillesii* and a number of seed features with both *O. macrosceles* and *O. organensis*. The greater ability of *O. maysillesii* to form green viable hybrids with other species suggests that it has the most generalized genome and plastome in the section (Stubbe and Raven 1979). *Oenothera stubbei* may be similar in this respect. In contrast, *O. macrosceles* and *O. organensis* are clearly specialized both morphologically and genetically.

Nearly all of the features of the seeds of *Oenothera macrosceles* and many of those of *O. stubbei* are closely similar to features of the seeds of subsects. *Raimannia* and *Munzia*, while the features of the distal and raphial cavity of *O. macrosceles* are similar to those of *O. primiveris* (see Wagner et al. 1985). The crossing data, however, do not support the suggested relationships. Likewise the seed shape, color, surface sculpturing, and microsculpturing of the seeds of *O. organensis* are closely similar to those of subsect. *Oenothera*. The crossing data in this case support this suggested relationship to some extent. Finally, the seed shape and greatly thickened testa of *O. maysillesii* are similar and apparently related to these features in such species as *O. primiveris*, *O. muelleri*, and *O. brachycarpa*. Obviously some of these shared characters among the species of subsect. *Emersonia* are shared primitive features while others are shared derived features; only the latter suggest common ancestry. A meaningful interpretation of the phylogeny of subsect. *Emersonia*, however, will be dealt with in a subsequent paper on relationships and classification of the entire genus (Wagner and Raven in prep.). A cladistic analysis of subsect. *Emersonia* would essentially be equivalent to one of the entire genus. The reason for this is that the species of subsect. *Emersonia* apparently represent a lineage that diverged early in the evolution of sect. *Oenothera* and possibly the genus (Stubbe and Raven 1979). Thus other genera of the tribe Onagreae would be the only meaningful outgroups for the polarization of characters.

TAXONOMIC HISTORY

The first species of subsect. *Emersonia* to be discovered was *Oenothera macrosceles*, found by Josiah Gregg in northern Mexico in 1847 and described by Asa Gray two years later. It has been in cultivation since 1937, when Ralph

Cleland incorporated it into his extensive experimental studies of *Oenothera*. The next species to be described was *O. organensis*, collected by G. Vasey in 1882 in New Mexico and first described as *O. macrosiphon* Wootton and Standley, based on plants collected by Wootton in 1894. Munz provided the new epithet *organensis* in 1938 because of the earlier use of *macrosiphon* by Lehmann in 1859 for the South American species now known as *O. affinis* Camb. *Oenothera organensis* has been extensively used for experimental studies since 1935 when Sterling Emerson initiated his studies of genetic self-incompatibility. *Oenothera maysillesii* was discovered in 1950 in the Sierra Madre Occidental near Durango, Mexico, by James Maysilles (1959). Munz described it in 1960 based on plants collected by Maysilles in 1955. It has been in experimental cultivation since 1970 when Dennis Breedlove sampled a wide series of populations. Dietrich first detected the entity that we describe here as *O. stubbei* during the course of his studies of herbarium material in 1978. Earlier collections, such as the first two made in 1934 by F. W. Pennell and some days later by Mueller and Mueller, were originally determined as *O. macrosceles*. In 1978 Sanders, Whalen, and Funk succeeded in locating a population of this rare and apparently very localized species, and since that time it has been in cultivation at the Botanical Institute of the University of Düsseldorf, Germany, and the Missouri Botanical Garden.

TAXONOMIC TREATMENT

Oenothera L. sect. **Oenothera** subsect. **Emersonia** (Munz) Dietrich, Raven, & W. L. Wagner, comb. et stat. nov. *Oenothera* L. subg. *Raimannia* (Rose) Munz sect. *Emersonia* Munz, N. Amer. Fl. II. 5:105. 1965.—TYPE: *Oenothera organensis* Munz (based on *Oenothera macrosiphon* Woot. & Standl., non Lehmann, 1858).

Oenothera § *Euoenothera* sensu S. Wats., Proc. Amer. Acad. Arts 8:574. 1873, pro parte.

Onagra sensu Small, Bull. Torrey Bot. Club 23:172. 1896, pro parte.

Raimannia Rose, Contr. U.S. Natl. Herb. 8:330. 1905, pro parte. *Oenothera* L. subg. *Raimannia* (Rose) Munz, Amer. J. Bot. 22:650. 1935, pro parte; Aliso 4:491. 1960. *Oenothera* L. subg. *Raimannia* (Rose) Munz sect. *Raimannia*; Munz, N. Amer. Fl. II. 5:105, 1965, pro parte.

Perennial herb from a stout taproot, some-

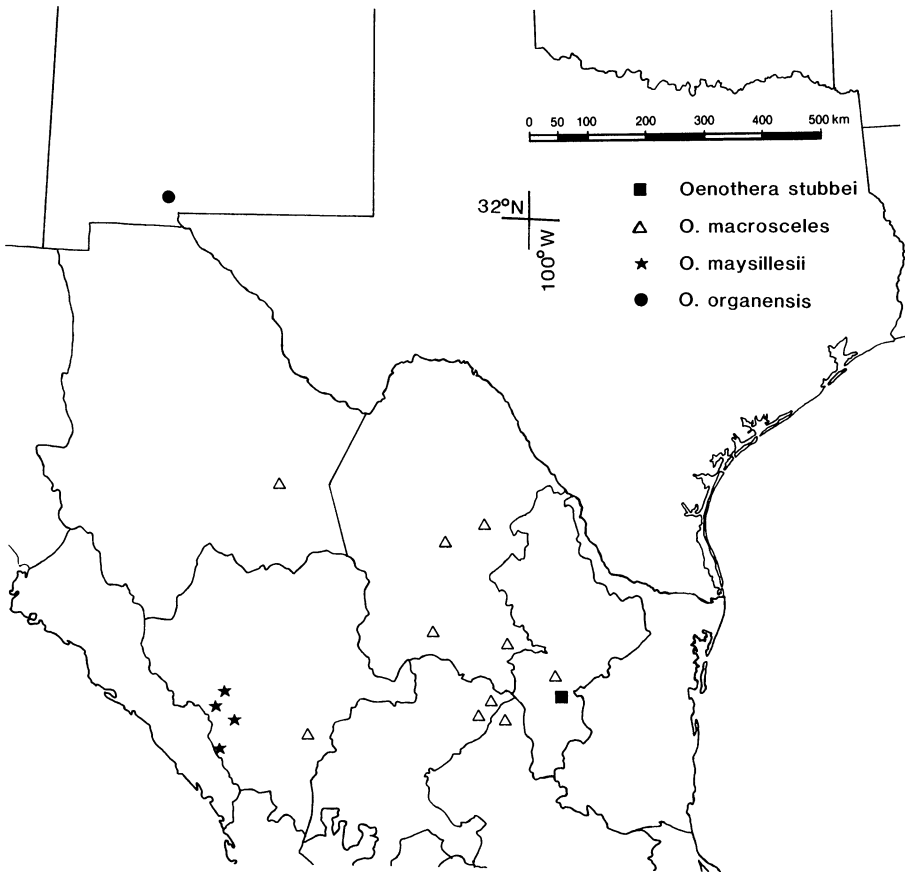


FIG. 30. Distribution of *Oenothera stubbei*, *O. maysillesii*, *O. macrosceltes*, and *O. organensis*.

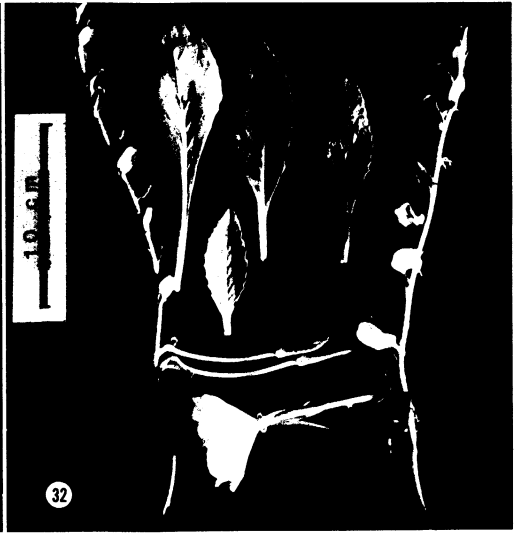
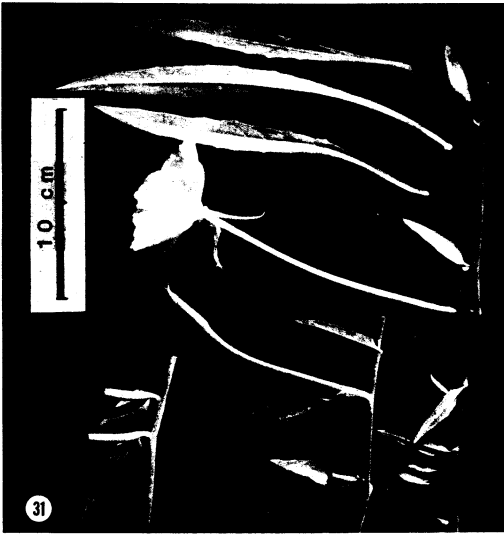
times (in 3 species) producing adventitious shoots from lateral roots, the stems decumbent to ascending, often rooting at the nodes in *Oenothera maysillesii* and *O. stubbei*. Leaves narrowly oblanceolate to broadly elliptic, dentate, flat or undulate in *O. organensis*, sometimes flecked with reddish purple spots. Buds erect with free sepal-tips. Flowers opening near sunset. Floral tube 5.5–19 cm long. Petals yellow, very broadly to broadly obovate, truncate to emarginate at the apex, 2.2–5.5 cm long, 3–5.5 cm wide. Sepals separating in pairs and reflexed or sometimes splitting along only one suture and reflexed to one side as a unit, or separate and reflexed individually. Stigma held above the anthers at anthesis or sometimes surrounded by anthers which shed pollen directly on the stigma in *O. macrosceltes*. Capsules cylindrical to narrowly lanceoloid, sessile. Seeds in 2 rows in each locule, or in 1 irregular row (from 2 rows

of ovules) in *O. maysillesii*, obovoid or oblong-ellipsoid; testa thickened at the distal end and sometimes above the raphe, the thickened area with an empty cavity. Self-incompatible, or self-compatible in *O. macrosceltes*. Basic chromosome number, $x = 7$.

Distribution (fig. 30). Mesic sites (to xeric ones in *Oenothera stubbei*), in pine-oak forests, meadows, and canyons, to boggy sites in grassland, from the Organ Mountains, New Mexico, southeastern Chihuahua, southern Coahuila and Nuevo León, northern Zacatecas and San Luis Potosí, and southern Durango, Mexico, 1100–2600 m.

KEY TO SPECIES OF *OENOTHERA*
SUBSECT. *EMERSONIA*

Plants of shrubby habit, the stems weakly erect; bracts rotund to truncate at base; stems conspicuously hirsute (the hairs with reddish purple pustulate bases), mixed with strigillose and



FIGS. 31-32. Flowering stem and leaves of *Oenothera* subsect. *Emersonia*. 31. *O. stubbei* (cult. at DUSS from: Mexico, Nuevo León, Sanders et al. 1203). 32. *O. maysillesii* (cult. at DUSS from: Mexico, Durango, Breedlove 18812).

- glandular hairs; Organ Mountains, New Mexico 4. *O. organensis*
- Plants not shrubby, growing as a rosette with long decumbent flowering stems; bracts obtuse to attenuate at base; stems more or less densely strigillose and sometimes glandular pubescent or subglabrous, but not hirsute or only sparsely so (the hairs lacking pustulate bases); Mexico.
- Leaves fleshy and succulent; plants subglabrous or sparsely strigillose and glandular pubescent; stems not rooting at nodes; Chihuahua, Coahuila, Nuevo León, Zacatecas, San Luis Potosí, and Durango, Mexico 3. *O. macroseles*
- Leaves not fleshy or succulent; plants moderately to densely pubescent; stems rooting at nodes.
- Floral tube 5.5-9 cm long; capsule lanceoloid, 1.8-2.6 cm long, appressed to stem, sessile; leaves dark green, oblanceolate to elliptic; stems 10-25(-40) cm long; Durango, Mexico 2. *O. maysillesii*
- Floral tube 10-14(-15) cm long; capsules cylindrical, 2.5-3.5 cm long, erect, with pedicel-like sterile portion 3-11 mm long; leaves pale or yellowish green, very narrowly oblanceolate to narrowly elliptic; stems 30-300 cm long; Nuevo León, Mexico 1. *O. stubbei*

1. ***Oenothera stubbei*** Dietrich, Raven, & W. L. Wagner, sp. nov. (fig. 31).—TYPE: Cultivated in the Botanical Garden of Düsseldorf, Germany, 3 Aug 1979, from seed collected along road from Galeana to Doctor Arroyo, 14 km S of Jct. of rd. to San Roberto, 2.1 km N of Pablillo (24°35'N, 100°00'W), ridge covered with open pine forest with exposed gypsum outcrops and washes, common in semishade along washes, 2100 m, 5 Aug 1978, R. Sanders, M. Whalen, and V. Funk 1203 (holotype: MO-2926846; isotypes: DUSS, M).

Caulis 3-30 dm longi, subrepentes ad nodos radicantes; rosulae folia anguste elliptica usque peranguste oblanceolata, 8-23 cm longa, 0.6-2 cm lata; folia caulina peranguste elliptica usque lanceolata, 2-7 cm longa, 0.5-1.5 cm lata; folia omnia tenuia sparsim dentata; tubus floralis 10-14 cm longus; capsulae cylindricae, 2.5-3.5 cm longae, erectae, basi tenue infertili elongata 3-11 mm longa insidentes.

Perennial herb from stout taproot up to 1.5 cm in diameter, sometimes producing adventitious shoots from slender lateral roots, forming a rosette; stems several, decumbent, 3-30 dm long, often rooting at nodes, often with secondary branches, usually flushed with red, densely to sparsely strigillose with hairs 0.2-

0.6 mm long, also moderately to densely villous especially on younger parts of stem with hairs 0.8–1.3 mm long (sometimes in cultivation an ascending main stem may arise out of the center of the rosette up to 5 dm high). Leaves pale or yellowish green, thin, remotely dentate, moderately strigillose on both surfaces and margins, also sparsely villous especially on veins and margins; stem leaves very narrowly elliptic or narrowly lanceolate to lanceolate, 2–7 cm long, 0.5–1.5 cm wide, the apex acute, the base attenuate to obtuse and oblique; petiole 0.5–5(–11) mm long; rosette leaves very narrowly elliptic to very narrowly oblanceolate, 8–23 cm long, 0.6–2 cm wide, the apex acute, gradually tapering into petiole 2–4(–7) cm long. Buds with free sepal-tips ca. 3–8(–10) mm long. Flowers held upright by curved sterile basal part of ovary, usually 1–2 (or more when cultivated) per stem near the rosette, not strongly scented. Ovary densely strigillose and villous, sometimes sparsely glandular pubescent in upper part, 1.5–2 cm long, ca. 2.5 mm in diameter, the sterile basal portion curved, this pedicel 3–11 mm long. Floral tube 10–14(–15) cm long, flaring to ca. 7 mm at mouth, sparsely strigillose, also sparsely villous or glandular pubescent, glabrous within. Sepals splitting along one suture and reflexed as a unit at anthesis or sometimes separating as pairs, usually with a reddish purple stripe along margin, sparsely strigillose, villous and glandular pubescent or only villous and glandular pubescent, 3–5 cm long, 6–8 mm wide. Petals yellow, fading orange, drying reddish purple, broadly obcordate, 3–5 cm long, 3.5–5.5 cm wide. Staminal filaments yellow, 20–26 mm long. Anthers yellow, 10–18 mm long. Style 12.5–17.5 cm long, the visible part 2.5–3.5 cm long; stigma lobes 5–9 mm long, elevated above anthers at anthesis. Capsule cylindrical, 2.5–3.5 cm long, 4–5 mm in diameter, held upright, usually curved at base, tapering at base to sterile pedicel-like portion 3–11 mm long, dehiscing nearly the full length of capsule. Seeds 150–180 per capsule arranged in 2 rows in each locule, 1.2–2.1 mm long, 0.8–1.2 mm thick, obovoid-ellipsoid to oblong-ellipsoid, curved or straight, angled and sometimes wrinkled or ridged, often somewhat laterally compressed, dark brown flecked with very dark reddish brown or reddish purple spots, pitted mostly on abaxial surface toward micropylar end, longitudinally striate,

surface reticulate, the raphe sometimes conspicuous but usually visible only as a shallow depression or flat surface; testa distally thickened, the thickened area with small internal cavity not visible externally. Self-incompatible. Gametic chromosome number $n = 7$ (7 bivalents or 5 bivalents and ring of 4 at meiotic metaphase I).

Dry, open or partially shaded sites on gypsum slopes, outcrops, or steep eroding banks of washes in open *Pinus arizonica* woodland or scrub vegetation dominated by species of *Arctostaphylos*, *Ceanothus*, *Rhus*, *Juniperus*, and *Nolina*, from the Sierra Madre Oriental near Pablillo, Nuevo León, 1900–2150 m. Known to flower Jun–Sep.

Specimens examined from cultivated plants. MEXICO. **Nuevo León:** 2.1 km N of Pablillo (24°35'N, 100°00'W), *Sanders et al.* 1203 (1 plant with 7 bivalents, 1 plant with 5 bivalents and ring of 4; DUSS, M, MO); 2.1 km N of Pablillo, *Henrickson & Lee* 17622 (1 plant with 5 bivalents and ring of 4; MO).

Additional specimens examined. MEXICO. **Nuevo León:** Sierra Madre Oriental: ca. 20 km S of rd. to Linares on rd. to Dr. Arroyo, *Cruden* 2221 (MO); 10.3 mi E of San Roberto Jct. at Hwy. 57 (ca. 74 air mi SE of Saltillo), *Henrickson & Lee* 17618 (MO); 17 road mi S of Galeana, 1.3 mi N of Pablillo (24°35'N, 100°0'W), *Henrickson & Lee* 17622 (CSLA, MO, TEX); ca. 1.5 mi SW of Galeana (24°50'N, 100°04'W), *Mueller & Mueller* 1015 (GH, MICH, POM); ca. 15 mi SW of Pablillo, *Mueller & Mueller* 1081 (GH); Pablillo S of Galeana, *Pennell* 16979 (PH, US); 1 mi N of Pablillo, *Reveal et al.* 2647 (GH, MICH, MO); 2.1 km N of Pablillo, *Sanders et al.* 1203 (LL).

This rare new species is dedicated to Wilfried Stubbe, who has made in-depth studies of *Oenothera*, especially concerning the evolution of plastids and interaction of plastome and genome in sect. *Oenothera*. It clearly differs from *O. macrosceles* by its long creeping stems that root at the nodes, thin leaves and the specialized pedicel-like sterile portion of the capsule.

2. *OENOTHERA MAYSILLESII* Munz, *Aliso* 4:490. 1960 (fig. 32).—TYPE: Mexico, Durango, growing in thick humus in oak-pine forest with mosses and mesophytic herbs, San Luis del Río, 51 road mi NW of Coyotes, 2600 m, 22 Jul 1955, *J. H. Maysilles* 7972 (holotype: RSA-117508!; isotype: MICH!).

Perennial herb from stout taproot up to 2 cm in diameter, sometimes producing adventitious shoots from slender lateral roots, forming rosette; stems several, decumbent, 2–3(–6) dm

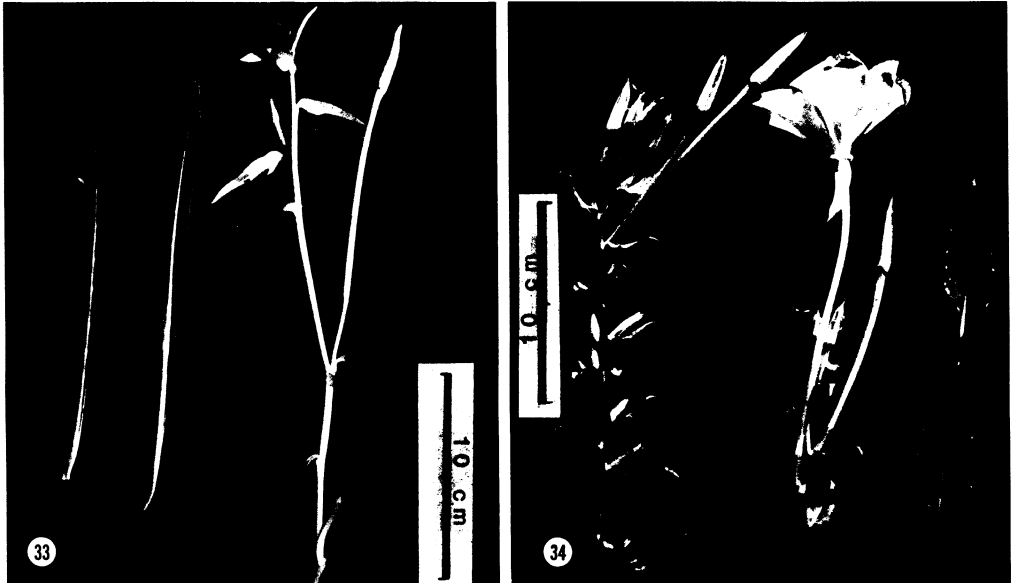
long, often rooting at nodes, often with short secondary branches, green or flushed with red, densely strigillose with hairs 0.15-0.6(-0.7) mm long (these hairs sometimes spreading on young parts and leaf margins), and sparsely hirsute with hairs (0.9-)1.2-2.9 mm long. Leaves dark green, thick and somewhat leathery, the upper surface usually distinctly convex, sometimes concave, coarsely serrate to dentate, with each tooth reddish purple at tip, densely strigillose to strigose on both surfaces on young leaves to moderately so on mature ones, the hairs often spreading rather than appressed, especially on young leaves; stem leaves narrowly ovate, elliptic or narrowly elliptic, 1-2.5 cm long, 0.4-1 cm wide, the apex acute, the base attenuate to cuneate; petiole 1.5-3 mm long; rosette leaves usually appressed close to ground, oblanceolate to broadly elliptic, 4-11 cm long, 1-3.5 cm wide, the apex acute to obtuse, attenuate or abruptly narrowed to petiole 0.3-4 cm long. Buds with free sepal-tips 2-7 mm long. Flowers held upright by curved apical portion of ovary, usually 1-2 (or more in cultivation) arising out of axil of fourth and sixth leaves of stem, with faint sweet scent. Ovary densely strigillose and ascending-hirsute, 0.7-1.2 cm long, 1.5-2 mm in diameter, somewhat curved toward apex. Floral tube 5.5-9 cm long, flaring to 3-5 mm at mouth, flecked with yellowish green spots or flushed with red, sometimes flecked with reddish purple spots or streaks, sparsely to moderately strigillose and sparsely hirsute. Sepals separating in pairs and reflexed at anthesis, with reddish purple stripe along margins, nearly always flecked with reddish purple spots, sparsely to moderately strigillose and sparsely hirsute, 2-3.5 cm long, 5-8 mm wide. Petals yellow, fading orange, drying lavender, broadly obovate, slightly retuse to truncate at apex, 2.5-3 cm long, 3.5-4.2 cm wide. Staminal filaments yellow, 12-25 mm long. Anthers yellow, 6-10 mm long. Style 7-11.5 cm long, the visible part 2-2.5 cm long; stigma lobes 5-9 mm long, elevated above anthers at anthesis. Capsule narrowly lanceoloid, 1.8-2.6 cm long, 4-7 mm in diameter at base, closely appressed to stem, sessile, dehiscent nearly full length of capsule. Seeds 30-50 per capsule from twice as many ovules arranged in one irregular row per locule or two rows (ovules always in two rows), 2-3 mm long, 1-1.8 mm thick, obovoid, straight, asymmetrical, obtusely angled, dark brown, the

surface flat and anticlinal walls of epidermal cells appearing as reticulations, the raphe inconspicuous; testa thickened at distal end and also above raphe, this thickened part with small internal cavity not visible externally. Self-incompatible. Gametic chromosome number, $n = 7$ (7 bivalents at meiotic metaphase I, or bivalents and small rings up to ring of 8 chromosomes).

Forming small to very large colonies in mesic or dry sites such as open meadows, along wooded, grassy, or rocky stream banks or in scattered clumps at forest edge or sometimes in pine-oak forest from the Sierra Madre Occidental in an area west of Cd. Durango bounded by San Luis del Río, Llano Grande, and ca. 50 mi NNW of Estación Coyotes, 2100-2600 m. Known to flower Jul-Aug but may flower at times on either end of this time period.

Specimens examined from cultivated plants (G numbers refer to Stanford Garden numbers). MEXICO. Durango: 50 mi N of Estación Coyotes, just SE of the settlement Guachilas, *Breedlove 18812* (DUSS, M, MO); 48 mi NNW of Estación Coyotes, 1970, *Breedlove s.n.* (G301; MO); 46.6 mi NNW of Estación Coyotes, 1970, *Breedlove s.n.* (G302; MO); 44.3 road mi NNW of Estación Coyotes, San Luis del Río (type locality), 1970, *Breedlove s.n.* (G303: 1 plant with 1 bivalent, ring of 8, and ring of 4; 1 plant with probable 5 bivalents and ring of 4; and 1 plant with 2 bivalents, ring of 6, and ring of 4; MO); 36.9 mi NNW of Estación Coyotes, 1970, *Breedlove s.n.* (G305: 1 plant with probable 4 bivalents and ring of 6; MO); 30 mi NNW of Estación Coyotes, 1970, *Breedlove s.n.* (G306: 1 plant with 4 bivalents and ring of 6; MO); 28.2 mi NNW of Estación Coyotes, 1970, *Breedlove s.n.* (G307: 1 plant with 3 bivalents and two rings of 4; MO); 26.6 mi NNW of Estación Coyotes, 1970, *Breedlove s.n.* (G308: 1 plant with 3 bivalents and ring of 8; MO); 24.3 mi NNW of Estación Coyotes, 1970, *Breedlove s.n.* (G309: 1 plant with 3 bivalents and ring of 8; MO); 22.4 mi NNW of Estación Coyotes, 1970, *Breedlove s.n.* (G310: 1 plant with probable 3 bivalents and ring of 8; MO); 17.8 mi NNW of Estación Coyotes, 1970, *Breedlove s.n.* (G311: 1 plant with 2 bivalents, ring of 6, and ring of 4; MO); 35 km N of Coyotes, *Breedlove 44288* (cult. no. at DUSS 80-195: 1 plant with 4 bivalents and ring of 6; 1 plant with 3 bivalents and ring of 8; DUSS).

Additional specimens examined. MEXICO. Durango: Santo Domingo, 20 mi N of rail station of Coyotes, *Breedlove 15763* (1 plant with 4 bivalents and ring of 6 by R. Cleland; MO), *Breedlove 16426* (CAS); Guachichilas, 50 mi N of Estación Coyotes, *Breedlove 18812* (MO); 35 km N of Estación Coyotes, *Breedlove 44288* (MO); San Luis, 51 road mi NW of Coyotes, *Maysilles 7219* (MICH, RSA); Laguna del Progreso, 34 road mi



FIGS. 33–34. Flowering stem and leaves of *Oenothera* subsect. *Emersonia*. 33. *O. macroscelces* (cult. at DUSS from: Mexico, Coahuila, Munz 15043). 34. *O. organensis* (cult. at DUSS from: U.S.A., New Mexico, “probably Munz 13268 via Emerson via Straub”).

N of railroad at Coyotes, *Maysilles* 8330 (MICH); Llano Grande, 42 mi WSW of Cd. Durango, *Maysilles* 8483 (MICH).

Oenothera maysillesii has, like *O. stubbei*, a remarkable ability for vegetative reproduction by the stems rooting at the nodes and by adventitious shoots from roots. It is most closely related to *O. stubbei* but differs in its shorter stems, thick, dark green leathery leaves, short floral tubes, closely appressed, short lanceoloid capsules, and larger seeds with prominent reticulations. *Oenothera maysillesii* is geographically disjunct from the other species of subsect. *Emersonia* as well as ecologically differentiated. It occurs at higher elevations and in a more mesic environment than the other species.

3. *OENOTHERA MACROSCELES* A. Gray, Mem. Amer. Acad. Arts s.n. 4:43. 1849 (fig. 33).—TYPE: “Vara de San José [Durango]—marshy borders of Springs, Ojo de San Bernardo [Chihuahua; 26°30'N, 104°29'W], 6 May, and Pelayo [Durango; 26°04'N, 104°15'W], 8 May, [18]47”, J. Gregg 598 (holotype: GH!; isotypes: MO!, NY!). Based on Gregg’s handwritten label it is not possible to determine at which of the three localities or combination of localities he collected the

type material. Correct interpretation of Gregg’s handwritten label was aided by his diary (Gregg 1944, pp. 112–116). *Onagra macroscelces* (A. Gray) Small, Bull. Torrey Bot. Club 23:172. 1896. *Raimannia macroscelces* (A. Gray) Rose, Contr. U.S. Natl. Herb. 8:331. 1905.

Fleshy perennial herb from stout taproot 2–4 cm in diameter, forming rosette; stems several, woody and wiry, ascending but becoming procumbent as they grow, 3–15 dm long, young parts green flushed with red, sometimes with ascending secondary branches, subglabrous or sparsely strigillose with hairs 0.2–0.4(–0.6) mm long, sometimes mixed with glandular hairs 0.1–0.2 mm long, and sparsely hirsute with hairs 0.8–1.5 mm long. Leaves yellowish green, thick and fleshy, usually sparsely strigillose along margins especially on young leaves, also rarely very sparsely hirsute toward base of leaf, subentire to indistinctly lobed; stem leaves very narrowly elliptic to oblong-oblancheolate to narrowly oblancheolate or rarely ovate, 4–8 cm long, 0.3–2 cm wide, the apex acute, gradually narrowed into petiole or the base truncate and slightly oblique; petiole 0–10 mm long; rosette leaves often flecked with reddish purple spots, oblancheolate to narrowly oblancheolate, 7–

25(-30) cm long, 1.5-4 cm wide, gradually narrowed to petiole 1-9 cm long. Buds quadrangular in cross-section; sepal junction strongly concave, with free sepal-tips 0.5-1.2 mm long. Flowers held upright, 1-2 opening per day, up to ca. 10 total per stem, slightly pungent. Ovary glabrous or sparsely glandular pubescent especially toward apex, 1.5-2.5 cm long, 1.5-1.8 mm in diameter, sometimes somewhat curved toward apex. Floral tube (6.5-)9-15.5 cm long, flaring to 3-5 mm at mouth, turning deep orange-red after anthesis, glabrous or sparsely glandular pubescent. Sepals separating in pairs or singly and reflexed at anthesis, usually with reddish purple stripe along margin, glabrous to sparsely glandular pubescent, 2.5-4 cm long, 5-7 mm wide. Petals yellow, fading reddish orange, drying lavender, broadly obovate, 3.5-4.5 cm long, 3.5-4.5 cm wide. Staminal filaments yellow, 15-25 mm long. Anthers yellow, 10-15 mm long. Style 10.2-18 cm long, the visible part 2.5-3.7 cm long; stigma lobes 4-12 mm long, surrounded by anthers to somewhat elevated above anthers at anthesis. Capsule cylindrical, quadrangular, 2-6 cm long, 3-5 mm in diameter, standing at acute angle from stem, sessile, the basal 3-5 mm of capsule sterile, dehiscent $\frac{1}{2}$ - $\frac{3}{4}$ the length of capsule. Seeds 160-250 per capsule arranged in two distinct rows in each locule, (1.2-)1.5-1.8 mm long, 0.7-0.9 mm thick, slightly asymmetrical, oblong-ellipsoid, straight or slightly curved, light brown and often flecked with darker, reddish purple spots or mottled with lighter straw-colored areas, the surface pitted throughout and finely reticulate, the raphe inconspicuous; testa thickened at distal end and slightly along raphe, the thickened part with small internal cavity not visible externally. Self-compatible, but modally outcrossing. Gametic chromosome number, $n = 7$ (7 bivalents and small rings up to ring of 6 chromosomes at meiotic metaphase I).

Locally common in wet or seasonally wet sites such as margins of boggy areas, springs, seasonally wet flats, or ditches in alkaline clays or gypsum soils with plants like *Distichlis*, *Flaveria*, *Suaeda*, and *Sporobolus airoides* (Torr.) Torr. Endemic to the Chihuahuan Desert Region from southeastern Chihuahua, southern Coahuila, Nuevo León, and southeastern Durango to northeastern Zacatecas and adjacent San Luis Potosí, 1100-2000 m. Flowering Apr-Oct.

Specimens examined from cultivated plants.

MEXICO. **Coahuila:** Ojo Caliente near Ramos Arizpe, *Marroquín & Valdes Rayna* 3700 (cult. no. DUSS 81-781: 4 plants with 5 bivalents and ring of 4, 1 plant with 2 bivalents and ring of 6, and ring of 4; DUSS, MO); Ramos Arizpe, 5 mi E of Saltillo, seeds from *Munz* 15043 (DUSS, M, MO); Ojo Caliente, 26 km E of Saltillo, *Wagner et al.* 4096 (cult. no. DUSS 80-197: 4 plants with 7 bivalents, 9 plants with 4 bivalents and ring of 6; DUSS, MO). **Durango:** 17 mi SW F. I. Madero, *Wagner & Solomon* 4316 (cult. no. DUSS 80-196: 5 plants with 7 bivalents, 3 plants with 5 bivalents and ring of 4, 1 plant with 3 bivalents and 2 rings of 4; DUSS, MO). **Without exact locality:** Grown at Stanford University from seeds obtained by Cleland, *Raven* 67-432 (DS, TEX).

Additional specimens examined. MEXICO. **Chihuahua:** Mouth of Arroyo Carrizo, 20 km N of Julimes downstream Río Conchos at Rancho Laborcita, *Johnston et al.* 11371 (MO); 5 km S end of Sierra del Roque, 20 km N of Julimes, *Johnston et al.* 11380 (MO); San Tiburcio (29°16'N, 105°01'W), *Purpus* 5565 (GH, NY, UC, US). **Coahuila:** Saltillo, *Arsene* 3461 (ILL, MO, NY, US); Parque El Chorro near Saltillo, 1965, *Christman s.n.* (MU); 3 mi W of Cuatro Ciénegas de Carranza near Ciénega Anteojo, *Henrickson* 14291 (MO); 7 mi S of Anteojo, *Kenoyer & Crom* 2855 (A, MICH); Sierra de San Marcos, 1968, *J. Lewis s.n.* (MO); Morillo near Saltillo, *Lyonnet* 3486 (US); Hermanas, *Marsh* 1644 (F, NY, SMU, SRSC); El Chorro, 13 mi E of Saltillo, *McVaugh* 12293 (MEXU, MICH, RSA, US); Ramos Arizpe, 5 mi E of Saltillo, *Munz* 15043 (BH, CAS, DS, GH, MO, UC); Saltillo, *Palmer* 211 (C, F, G, GH, K, MO, NY, POM, UC, US); Parras, 112 mi W of Saltillo, *Palmer* 338 (GH, K, MASS, NA, NY, PH, US, VT, YU); W of Poso de la Becerra (10 mi SW of Cuatro Ciénegas), *Pinkava et al.* 3850 (MO); Poso de Anteojo, *Pinkava et al.* 5509 (ARIZ); Ojo Caliente (26 mi E of Saltillo), *Wagner et al.* 4096 (MO). **Durango:** Near cd. Durango, *Palmer* 115 (GH, MO, NY, UC, UMO, US); 17.7 mi SW of F. I. Madero on Hwy. 40, *Wagner & Solomon* 4316 (MO). **Nuevo León:** Near Galeana, *Chase* 7634 (ARIZ, F, GH, ILL, MICH, MO, NA, NY); W of Linares near hwy. marker Km 61, *Fryxell* 1345 (CAS); along Mex. Hwy. 60, 11 mi W of Iturbide, 40 mi W of Linares, *Ward* 7716 (FLAS, MICH). **San Luis Potosí:** 16.1 km WSW of Cedral, on road to Catorce, *Chiang et al.* 8257 (MO). **Zacatecas:** Cedros, *Kirkwood* 3 (F, MO). **Without exact locality:** *Gregg* 129 (MO); "New Mexico," *Gregg s.n.* (NY).

Oenothera macrosceles, a very distinctive species, has the widest distribution of any of the four species of subsect. *Emersonia*. It is the only self-compatible member of the subsection, and has the highest seed production. It is also apparently the most specialized species in subsect. *Emersonia*, with its fleshy and nearly glabrous leaves; these features may be adaptations to its specialized habitat.

4. *OENOTHERA ORGANENSIS* Munz, in Emerson, Genetics 23:190. 1938 (fig. 34).—Based on *Oenothera macrosiphon* Woot. & Standl., Contr. U.S. Natl. Herb. 16:155. 1913, non Lehmann, 1858.—TYPE: New Mexico, Doña Ana Co., Organ Mountains, 29 Aug 1894, E. O. Wooton s.n. (holotype: US-241243!; isotypes: NY!, UNM!, US!).

Bushy perennial herb, initially from slender taproot with single rosette, but later numerous adventitious shoots arise from taproot and lateral roots, the root system then appearing fibrous; stems numerous, many-branched, weakly erect to sprawling, 3–6 dm tall, forming clumps 10–15 dm in diameter, green and also usually flushed with red, moderately hirsute with hairs (0.4–)0.8–1.5 mm long with reddish purple pustulate bases, the pustules often elongate, also moderately finely strigillose with hairs 0.1–0.18(–0.25) mm long, the epidermis exfoliating near base. Leaves yellowish green, moderately thick, the upper surface usually convex, irregularly and remotely dentate, moderately hirsute with erect to somewhat appressed hairs 0.2–1 mm long, the larger hairs usually with reddish purple pustulate bases confined to larger veins and midrib, the shorter hairs usually without pustulate bases on secondary veins, the young leaves nearly always also glandular pubescent; stem leaves narrowly elliptic, strongly crisped, 5–11 cm long, 1.5–3.5 cm wide, with a broadly acute apex and a narrowly cuneate base; petiole 0.5–1 cm long; bracts narrowly lanceolate to ovate or sometimes narrowly elliptic, strongly crisped, 2.5–10 cm long, 1–3 cm wide, the apex acute to apiculate, the base narrowly cuneate to rounded or truncate and usually somewhat oblique, subsessile; rosette leaves very narrowly oblanceolate, undulate, remotely and bluntly dentate, 9–23 cm long, 1–2.5 cm wide, the apex broadly acute, gradually tapering into petiole 0.8–1.5 cm long. Buds with free sepal-tips 3–10 mm long. Flowers 1–2 opening per day per stem from apex, not strongly scented. Ovary densely to moderately pustulate-hirsute, finely strigillose, and glandular pubescent, 1.3–1.7 cm long, 2–2.5 mm in diameter. Floral tube 10–16.5(–19) cm long, flaring to 5–8 mm at mouth, green or reddish turning deep orange-red after anthesis, moderately pustulate-hirsute and glandular pubescent. Sepals separating in pairs and reflexed at anthesis, with reddish purple stripe along the

margin, moderately pustulate-hirsute and glandular pubescent, 2.5–5 cm long, 5–9 mm wide. Petals yellow, fading deep orange-red, drying lavender, broadly obovate, with a re-tuse to truncate apex, 3–5.5 cm long, 3–5 cm wide. Staminal filaments yellow, 18–35 mm long. Anthers yellow, 10–19 mm long. Style 14–23.5 cm long, the visible part 2.5–4.5 cm long; stigma lobes 3–8 mm long, elevated above anthers at anthesis. Capsule 3–10 per stem, cylindrical, 2.5–3.5 cm long, 4–5.5 mm in diameter, standing at acute angle from stem, sessile, dehiscing at least $\frac{3}{4}$ length of capsule. Seeds 100–160 per capsule arranged in two distinct rows per locule, 1.5–2.1 mm long, 1–1.2 mm thick, obovoid, asymmetrical, irregularly angled, often slightly curved distally, dark reddish brown sometimes with darker flecks, the surface irregularly pitted and with collapsed papillae, the raphe visible as distinct ridge or flat surface; testa somewhat thickened distally, the thickened area with small internal cavity not visible externally. Self-incompatible. Gametic chromosome number, $n = 7$ (7 bivalents, 5 bivalents and ring of 4, or 4 bivalents and ring of 6 at meiotic metaphase I [Emerson 1938]).

Locally common in the larger rhyolite canyons of the Organ Mountains, Doña Ana County, New Mexico, especially on the east side, along water courses and in eroded basins filled with gravel and rocks, 1800–2300 m (Emerson 1939; Munz 1965; Levin et al. 1979). Flowering Jun–Sep.

Specimens examined from cultivated plants. U.S.A. NEW MEXICO. **Doña Ana Co.:** Organ Mountains, grown at Michigan State University from root cuttings obtained by Emerson in 1959, *Bandurski s.n.* (MICH); grown at California Institute of Technology, Pasadena, from seeds collected at type locality, 1942, *Emerson s.n.* (CAN, CAS, CS, DAO, DUKE, DS, F, GA, GH, ILL, ISC, KSC, MICH, MIN, MO, MT, NA, NCU, NDA, NY, OKL, OKLA, PENN, POM, SMU, UC, UMO, US); grown at Claremont from Munz 13268: *Munz 13461* (POM), *13918* (POM), *14033* (POM), *14046* (POM), *14599* (BH, CAS, G, GH, NY, POM, US); grown at Stanford University, *Raven 65-117* (TEX); from seeds received in the sixties from J. Straub (Cologne), who obtained seeds from S. Emerson in 1955, exact source unknown (probably from *Munz 13268*) (DUSS, M, MO).

Additional specimens examined. U.S.A. NEW MEXICO. **Doña Ana Co.:** Organ Mountains, Dripping Spring, 1898, *Cockerell s.n.* (NMC); *Dunn 8400* (RSA); *Munz 13268* (BH, CAS, F, G, GH, NY, POM, US); *Ice Canyon, Ritter 38-46* (MO, UC); *Van Pattens, 1906,*

Standley s.n. (MO, US); E face of North Organ Needle, 1977, *Todsen s.n.* (NMC); 1882, *Vasey s.n.* (US); *Wooton 114* (ARIZ, BH, CS, MASS, MIN, MO, NMC, NY, US); Van Patten, 1899, *Wooton s.n.* (US); 1902, *Wooton s.n.* (NMC); Ice Canyon (T23S, R4E, sec. 7), *Worthington 7677* (COLO); Indian Hollow Canyon (T22S, R4E, sec. 28), *Worthington 7488* (COLO).

Oenothera organensis is the most distinctive species of subsect. *Emersonia*. Not only does it differ from the other species in its habitat, but also in other characters of pubescence and many details of seed morphology. To some extent, *O. stubbei*, with its angled and somewhat compressed seeds, provides a connecting link between *O. organensis* and the other species of subsect. *Emersonia*. Likewise, the crossing results indicate that *O. organensis*, although distinctive, should be grouped with the other species of subsect. *Emersonia*.

Oenothera organensis is currently listed in the lists of endangered and threatened wildlife and plants by the U.S. Fish and Wildlife Service (1980, p. 82524). This species has been studied recently by R. Spellenberg for the Bureau of Land Management, Las Cruces, New Mexico, and R. Worthington for the Fish and Wildlife Service, Albuquerque, New Mexico (these unpublished reports are available from individual agencies). These reports estimate the current populations of *O. organensis* to total somewhere between 2000 to 5000 individuals. The latter number was estimated by K. Ritter (Ph.D. student, University of California, Berkeley, California) who studied this species for several years. Worthington pointed out that the population size probably fluctuates greatly due to periodic drought. The reports conclude that although human activity has increased over the years in the Organ Mountains there is no clear and present threat to populations of *O. organensis*. R. Fletcher (U.S. Forest Service, Albuquerque, New Mexico, pers. comm.) suggests, however, that extensive water development in the area could influence the seasonally mesic habitats of *O. organensis*.

ACKNOWLEDGMENTS. This work was supported by grants from the U.S. National Science Foundation to Peter H. Raven, and a grant to Prof. W. Stubbe and W. Dietrich from the "Deutsche Forschungsgemeinschaft". Werner Dietrich would like to thank Prof. Wilfried Stubbe for helpful discussions and for providing facilities to work at the Botanical Institute of the University of Düsseldorf; Mrs. L. Mencke for laboratory assistance and in the cultivation of plants. We

would like to thank S. Mill and G. Hoch for careful preparation of the manuscript, A. Cronquist, M. Denton, P. Hoch, and an anonymous reviewer for useful comments on an earlier draft, and M. Veith for assistance in the SEM Lab at Washington University, Biology Department. We are grateful to those individuals who contributed seeds and to those who provided personal communications, especially R. Fletcher, A. Hecht, J. Henricksen, K. Ritter, and R. Spellenberg. We would also like to thank the staffs of the following herbaria for the loan of material for this study: A, ARIZ, BH, C, CAN, CAS, CS, CSLA, CU, DAO, DS, DUKE, F, FLAS, G, GA, GH, ILL, ISC, K, KSC, LL, M, MASS, MEXU, MICH, MIN, MO, MU, NA, NCU, NDA, NMC, NY, OKL, OKLA, OSH, PENN, PH, POM, RSA, SD, SMU, SRSC, TEX, UC, UMO, US, VT, YU.

LITERATURE CITED

- CLELAND, R. E. 1968. Cytogenetic studies on *Oenothera* subgenus *Raimannia*. *Jap. J. Genet.* 43:329-334.
- CROSBY, J. L. 1966. Self-incompatibility alleles in the population of *Oenothera organensis*. *Evolution* 20:567-579.
- CROWE, L. K. 1955. The evolution of incompatibility in species of *Oenothera*. *Heredity* 9:293-322.
- DICKINSON, H. G. and J. LAWSON. 1975. Pollen tube growth in the stigma of *Oenothera organensis* following compatible and incompatible intraspecific pollinations. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 188:327-344.
- EMERSON, S. H. 1938. The genetics of self-incompatibility in *Oenothera organensis*. *Genetics* 23:190-202.
- . 1939. A preliminary survey of the *Oenothera organensis* population. *Genetics* 24:524-537.
- . 1940. Growth of incompatible pollen tubes in *Oenothera organensis*. *Bot. Gaz. (Crawfordsville)* 101:890-911.
- . 1941. Linkage relations of two gametophyte characters in *Oenothera organensis*. *Genetics* 26:469-473.
- FISHER, R. A. 1958. *The genetical theory of natural selection*, 2nd ed. New York: Dover Publications.
- . 1961. Possible differentiation in the wild population of *Oenothera organensis*. *Austral. J. Biol. Sci.* 14:76-78.
- GREGG, J. 1944. *Diary and letters of Josiah Gregg: Excursions in Mexico and California*. Norman: University of Oklahoma Pr.
- GREGORY, D. P. 1963. Hawkmoth pollination in the genus *Oenothera*. *Aliso* 5:357-384.
- . 1964. Hawkmoth pollination in the genus *Oenothera*. *Aliso* 5:385-419.
- HECHT, A. 1950. Growth of pollen tubes of *Oenothera organensis* through otherwise incompatible styles. *Amer. J. Bot.* 47:32-36.

- . 1961. Partial reduction of an incompatibility substance in the styles of *Oenothera organensis*. *Genetics* 46:869.
- . 1964. Partial inactivation of an incompatibility substance in the stigmas and styles of *Oenothera*. Pp. 237–243 in *Pollen physiology and fertilization*, ed. H. F. Linskens. Amsterdam: North Holland Publishing Co.
- HESLOP-HARRISON, Y. and P. H. RAVEN. In prep. Stigma form and surface in relation to self-incompatibility in Onagraceae (Myrtales).
- LEVIN, D. A., K. RITTER, and N. C. ELLSTRAND. 1979. Protein polymorphism in the narrow endemic *Oenothera organensis*. *Evolution* 33:534–542.
- LEWIS, D. 1948. Structure of the incompatibility gene. I. Spontaneous mutation rate. *Heredity* 2:219–236.
- . 1949. Structure of the incompatibility gene. II. Induced mutation rate. *Heredity* 3:339–355.
- . 1951. Structure of the incompatibility gene. III. Types of spontaneous and induced mutation. *Heredity* 5:399–414.
- . 1952. Serological reactions of pollen incompatibility substances. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 140:127–135.
- . 1960. Genetic control of specificity and activity of the S antigen in plants. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 151:468–477.
- . 1979. Genetic versatility of incompatibility in plants. *New Zealand J. Bot.* 17:637–644.
- MÄKINEN, Y. L. A. and D. LEWIS. 1962. Immunological analysis of incompatibility (S) proteins, and of cross reacting material in a self-compatible mutant of *Oenothera organensis*. *Genet. Res. Camb.* 3:352–363.
- MAYSILLES, J. H. 1959. Floral relationships of the pine forest of western Durango, Mexico. Ph.D. dissertation, Univ. of Michigan, Ann Arbor.
- MUNZ, P. A. 1935. Studies of Onagraceae. IX. The subgenus *Raimannia*. *Amer. J. Bot.* 22:645–663.
- . 1965. Onagraceae. N. Amer. Fl. II. 5:1–278.
- RAIMANN, R. 1893. Onagraceae in Engler and Prantl, *Die Natürlichen Pflanzenfamilien* III. 7:199–223.
- RAVEN, P. H. 1970. *Oenothera brandegeei* from Baja California, Mexico, and a review of subgenus *Pachylophus* (Onagraceae). *Madroño* 20:350–354.
- . 1979. A survey of reproductive biology in Onagraceae. *New Zealand J. Bot.* 17:575–593.
- SPACH, E. 1835. *Monographia Onagrearum*. *Nouv. Ann. Mus. Hist. Nat.* III. 4:321–408.
- STUBBE, W. and P. H. RAVEN. 1979. A genetic contribution to the taxonomy of *Oenothera* sect. *Oenothera* (including subsects. *Euoenothera*, *Emersonia*, *Raimannia*, and *Munzia*). *Pl. Syst. Evol.* 133: 39–59.
- UNITED STATES FISH AND WILDLIFE SERVICE. 1980. Endangered and threatened wildlife and plants: Review of plant taxa for listing as endangered or threatened species. *Federal Register* 45 (242, IV):82480–82569.
- WAGNER, W. L., R. STOCKHOUSE, and W. KLEIN. 1985. The systematics and evolution of the *Oenothera caespitosa* species complex (Onagraceae). *Monogr. Syst. Bot. Missouri Bot. Gard.* 12:(in press).
- WRIGHT, S. 1939. The distribution of self-sterility alleles in populations. *Genetics* 24:538–552.
- . 1965. The distribution of self-incompatibility alleles in populations. *Evolution* 18:609–619.

Note added in proof: We have recently learned that *Oenothera stubbei* is being cultivated on the campus of the University of Arizona (G. Starr, pers. comm.; to be mounted at MO) and at the Tree of Life Nursery in San Juan Capistrano, California (1984, *Evans s. n.*; MO). It is being propagated at Tree of Life in preparation for introduction into the horticultural trade. Both introductions are based on a single collection, probably from Coahuila but incorrectly attributed from a source in Baja California (G. Starr, pers. comm.).