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The Oenothera Hookeri Group

Philip A. Munz
THE OENOThERA HOOKERI GROUP
PHILIP A. MUNZ

In the southwestern part of North America, ranging from southern Washington to central Mexico, is a large-flowered group of species of the genus *Oenothera*, subgenus *Euoenothera*, which differs from the other members that have been studied in the subgenus, by tending to have normal chromosome-pairing at meiosis. If circles of chromosomes are formed they are usually small, and balanced lethals are lacking. Thus, normal inheritance and Mendelian segregation can take place as in most groups of plants. Furthermore, these species are open-pollinated. For many years they have been studied cytologically and genetically by Dr. Ralph E. Cleland, first at Baltimore, Maryland, and later at Indiana University. During this same period I have collected them pretty much throughout their range and have then grown them, mostly at Claremont, California. I have furnished seed to Dr. Cleland and he has likewise sent me such cultures as he secured from other collectors, so that we have both cultivated and studied the same lots of material. It is from such studies, which began on my part about 1934, that the present paper has come.

EUOENOTHERA VERSUS ONAGRA

Linnaeus (Sp. Pl. 346, 1753) originally listed three species of *Oenothera*: *Oe. biennis*, *Oe. mollissima*, and *Oe. fruticosa*. Spach (Nouv. Ann. Mus. Paris, ser. III, 4: 323-324, 1835) divided *Oenothera* into many genera and was followed in this by Raimann (Engler and Prantl, Nat. Pflanzenfam. III, Abt. 7: 214-217, 1893) and by Small (Bull. Torrey Club 23: 168-194, 1896). Spach used the name *Oenothera* for the group to which *Oe. mollissima* belongs and *Onagra* for that containing *Oe. biennis*. Unfortunately for such an arrangement, *Oe. biennis* is the species selected by rule and published in a Supplement (Species Lectotypicae Generum Linnaei) to the International Rules of Botanical Nomenclature as the Standard or Type Species of the Genus *Oenothera*. Since Spach and Raimann had not acted in accordance with modern rules, Rose (Contr. U. S. Nat. Herb. 8: 330, 1905) proposed the name Raimannia for the "genus" including *Oe. mollissima* and allied species, and restored *Oenothera* to the group containing *Oe. biennis*. Thus the name *Onagra* is thrown into synonymy under *Oenothera*, sensu stricto.

If these groups are not maintained as separate genera, but as subgenera, what subgeneric names should be used? To follow the spirit of the International Rules, I see in line with Recommendations XI and XXXIV of the Rules two possibilities: either to use the name *Oenothera* as a subgenus in the genus *Oenothera* or to employ a name such as *Euoenothera* for the subgeneric category. Of course, Article 58 of the Rules calls for the use of the earliest name employed in the rank in which a given entity is being placed, so
that ordinarily the oldest subgeneric name would be the correct one. Here, however, two other problems arise: first, the Rules do not make it clear that an exception to the general procedure would be expected for the type group, so that in this case, for instance, the name Onagra would not be employed for the subgenus including the type species of the genus Oenothera, but a name like Euoenothera or Oenothera would be needed to avoid confusion. Secondly, the Rules do not say definitely whether a name used for any subdivision of the genus should be acceptable, namely that a section name used in 1840 would have validity over a subgenus name dating from 1925, or whether the subgeneric name only enters into consideration. There seems to be a difference of opinion, and procedure both for subdivisions of genera and of species should be clarified in the Rules.

The synonymy of the group in question, so far as I know, is as follows:

(1) For the group of species in which Oe. biennis falls, and which according to rule has to be considered that of the true oenotheras:

Oenothera, as genus, L. Sp. Pl. 346, 1753.


Onagra, as subgenus, Jepson, Man. Fl. Pis. Calif. 679, 1925.

Euoenothera, as sect.,

Torrey & Gray, Fl. No. Amer. 1: 492, 1840, in part.


Munz & Johnston, Contr. Gray Herb. 75: 17, 1925.

Euoenothera, as subgenus,


Munz in Kearney & Peebles, Fl. Pis. & Ferns Ariz. 625, 1942.


(2) For the group to which Oe. mollissima belongs:

Oenothera, as genus, Spach, op. cit. 323, 341.

Raimann, in Engler & Prantl, l.c.

Small, op. cit., 172.


From the above list it is obvious that strict application of priority, as of subgeneric rank, would necessitate employing Onagra as a subgeneric name; but, if any category below the rank of genus may be taken, whether section or subgenus, and also, if, since this subgenus is the type group for the genus, introduction of a different name introduces confusion, it would seem logical and correct to discard Onagra altogether and keep Euoenothera for the biennis group. Mr. C. A. Weatherby, expert on nomenclature, in a letter dated June 6, 1945 agreed with me. There is no confusion botanically in so doing, since
the name *Euoenothera* has been used only in this way for many years and *Raimannia* has been applied to the other subgenus. Unfortunately, in genetic literature such is not the case and Dr. Adolph Hecht of Washington State College has called my attention to the employment of *Euoenothera* in a series of papers by Schwemmle for the concept I would term *Raimannia*.

**Comparison of Wild and Garden Material**

Many of the characters which have been used for taxonomic purposes in the treatments of species of *Euoenothera* are exceedingly superficial, yet they are the obvious ones and naturally those that suggest themselves when herbarium material is examined. I refer to such things as color of sepals, whether red or green; color of stems, whether red or green; pubescence, whether it consists of both spreading hairs and appressed hairs, or appressed hairs only, or whether hairs are gland-tipped or not; whether marginal hairs are appressed or spreading; whether hairs are papillate or not at the base; whether sepal-tips are long or short; length of capsules; and size of seeds. Such characters are useful and are employed in this paper, but they may in many cases be governed by only single or few genic differences. More fundamental characters might be expected in the stature of the plant as a whole, in its size and method of branching, in the shape and proportion of the leaves, in the shape and position of the bracts, shape of the buds and insertion of the subulate tips of the sepals, and size of flowers. Actual height of the plant as it grows in nature, the formation of the basal rosette and final elongation of its axis into a stem, and normal branching into flowering stems,—all these features seem in nature to be definite geographical characters, varying with ecotypes or other subspecific categories, but unfortunately physiological enough to be affected easily by environment as seen by garden culture.

It has been interesting, therefore, to compare such wild plants in their original habitat with their offspring grown at Baltimore on the one hand, and at Claremont, on the other. Pubescence, color, shape of buds, shape of leaves and bracts, glandulosity, papillae, and shape of fruits were fairly constant, heritable characters, transferred from one generation to the next regardless of environment. Height of plant, however, varied greatly, from the original height in nature to smaller stature in Baltimore plants, especially in a dry season, to greater size in Claremont plants, where since they were summer growers they had to be irrigated regularly. Yet in nature, the height seems to have quite definite correlation with other characters and marks certain ecotypes. Response to an unwonted environment was perhaps most marked in rosette formation. Plants from the highlands of central Mexico, for example, regularly form rosettes and these young rosette stages can be found growing among the older flowering plants, just as can be done in this country. But in Claremont these more southern plants did not form definite rosettes at all, the axis beginning to elongate shortly after the seedling stage, so that rosette formation was prevented. That this was not due to length of day was demonstrated by the fact that the same thing was true of some of the plants from Texas and Coahuila with about the same latitude as Claremont. On the other hand, plants from the mountains of Colorado tended in Claremont to keep on forming rosettes beyond normal conditions and, when they finally
branched, perhaps the central axis continued to bear a terminal rosette for an extra year or until it rotted, while some of the branches would grow into sprawling flowering stems and others would also maintain a terminal rosette. Yet the plants from which the seed had been taken in Colorado were erect and normal. Dr. Cleland wrote me that in his cultures such behavior is correlated with length of day and that if shoots begin when day is long, habit is erect; if they fail to emerge until shorter days are at hand, the sprawling habit is adopted.

In the same way, plants grown by Cleland at Baltimore from California seed, failed to form central stem, and the branches were low and spreading in a fashion not at all normal, as for _Oenothera Hookeri_ ssp. _venusta_ (see fig. 1 and page 405 in Cleland, Proc. Amer. Philos. Soc. 75: 339-429, 1935).

On the whole, however, the characters that have been used in the past from herbarium work on the species of _Euoenothera_ showed very little variability under the different environmental conditions. They should be supplemented, however, by the habit, basal leaves, middle stem leaves and other features usually not available on the ordinary herbarium sheet. The complete picture for a taxonomic entity calls also for tips of flowering branches while in bud, to show the position and length of the bracts; for old fruiting branches, to reveal the persistence and position of the bracts in age; for specimens prepared in such a way as to indicate whether the leaf surface is crinkled along the midrib or is plane; for basal leaves, to reveal whether they are deeply toothed or entire; and for information as to the method of branching of the plant. It is obvious that acquaintance with the plant at all stages from seedling to maturity is therefore desirable.

**CYTOGENETICS**

Cleland has pointed out (Am. Nat. 78: 5-28, 1944) that in the subgenus _Euoenothera_ the problem of species is a special one, in that, many of the forms have rings of chromosomes so that at meiosis alternate chromosomes go to opposite poles of the spindle. In other words, if the ring is complete and contains all 14 chromosomes, it breaks into two sets and two sets only, one consisting of chromosomes 1, 3, 5, 7, etc. and the other of 2, 4, 6, 8, etc. Therefore, there are two genomes, hence two possible kinds of pollen grains and two possible kinds of eggs so far as inheritance goes. This situation combined with balanced lethals means the death of all homozygous zygotes and the persistence of only the heterozygous ones. Every student of genetics is familiar with the pattern as that of the so-called _Oenothera Lamarckiana_, with its _gaudens_ and _velans_ gametes. This seems to be the usual situation in the _Oenothera biennis_ group from central and eastern North America.

But in _Oenothera Hookeri_ from the more southwestern part of the continent Cleland has found a more normal type of chromosome behavior (Proc. Am. Philos. Soc. 75: 339-429, 1935 and Am. Nat. 1.c.). In California and Mexico most plants have 7 pairs of chromosomes in meiosis and the usual crossover and segregation can occur. In Arizona, New Mexico and Utah there is a tendency toward circle formation involving two pairs or three pairs of the seven, or sometimes more than one small circle. In most such cases there is
little evidence of lethals, balanced or unbalanced, and in contrast to the close-pollination of the eastern forms the southwestern have open-pollination. Hence, there is little to prevent the normal interchange of genes between different types and their Mendelian segregation afterward. In other words, the species problem is such as might be faced in any group in which mutation occurs so that there is variation, and in which gene interchange happens readily.

After many years of field and garden and herbarium work on the group and with the results of Cleland's exhaustive cytogenetic investigation, I present the present treatment. Since my earlier papers on Oenothera have used the rank of variety for the major categories below the rank of species and since I had proposed using all these papers for the treatment of the Onagraceae in The North American Flora, I at first continued its use here. However, I must admit that after working on cultivated plants for two years at the Bailey Hortorium and seeing how trivial as well as how inclusive may be the entities parading as varieties, I have become increasingly dissatisfied with the term. Therefore, I am joining those who use the category subspecies, since the entities I present are geographical entities or ecotypes with a number of distinctive characters in each case.

Cleland's interpretation of course is that the species with paired chromosomes are the primitive ones and that the rings which have come about by the process of segmental interchange give a clew to the evolution of the eastern species. He has moreover shown by innumerable crosses between species with rings and those with pairs how the former differ from the more primitive California plants. One cannot help wondering, since the plants from the highlands of central Mexico also have 7 pairs of chromosomes, whether the origin of the California forms may not have been Mexican and they may not have been part of the Tertiary flora that took its beginning there and worked its way into the western United States, the primitive chromosome condition persisting in California and Mexico. Axelrod has supported the old view of Gray and others concerning this Mexican element (Alexrod, D. L., Jour. Wash. Acad. Sci. 28: 314-322, 1938; Bull. Torrey Club 67: 477-478, 1940. Chaney, R. W. et al., Carnegie Inst. Wash. Pub. 553. 1944), which was an arid flora. It may be argued that these oenotheras are not members of an arid flora and it is true that they do grow in springy places, along streams and in wet meadows, so that the origin may have been farther north and the Mexican forms may be a conservative group that have migrated southward and have retained primitive conditions. At any rate, they are very near the California plants in their paired chromosomes and the two groups retain an ancestral condition.

In the accompanying table is presented an outline of the various races falling in the scope of the present paper, which Dr. Cleland has studied. For more information as to source of each, see the discussion under each species and subspecies.
### TABLE I

**FORMS STUDIED BY CLELAND**

<table>
<thead>
<tr>
<th>Botanical Name</th>
<th>Source of Material</th>
<th>Name used by Cleland</th>
<th>Chromosome configurations</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>I. Oe. Hookeri</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>a. ssp. eu-Hookeri</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wolf 1435, Calif.</td>
<td>Johansen</td>
<td>7 pairs</td>
<td></td>
</tr>
<tr>
<td>Near Berkeley, Calif.</td>
<td>Hookeri de Vries</td>
<td>7 pairs</td>
<td></td>
</tr>
<tr>
<td>C. Piper Smith, Calif.</td>
<td>Franciscana</td>
<td>circle 4, 5 pairs</td>
<td></td>
</tr>
<tr>
<td>Hall 13277, Calif.</td>
<td>Hall 27</td>
<td>7 pairs</td>
<td></td>
</tr>
<tr>
<td><strong>b. ssp. montereyensis,</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Johansen, Calif.</td>
<td>Mateo</td>
<td>7 pairs,</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>circle 4, 5 pairs</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>circle 8, 3 pairs</td>
<td></td>
</tr>
<tr>
<td><strong>c. ssp. Wolfii</strong></td>
<td></td>
<td></td>
<td>none studied</td>
</tr>
<tr>
<td><strong>d. ssp. hirsutissima</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Munz 13000a, Ariz.</td>
<td>Hirsutissima</td>
<td>7 pairs,</td>
<td></td>
</tr>
<tr>
<td>Munz 13260, Ariz.</td>
<td>Ramsey</td>
<td>circle 4, 5 pairs</td>
<td></td>
</tr>
<tr>
<td>Munz 13281, New Mex. Embudo</td>
<td></td>
<td>circle 4, circle 4, 3 pairs</td>
<td></td>
</tr>
<tr>
<td>Munz 13279, New Mex. Taos</td>
<td></td>
<td>7 pairs</td>
<td></td>
</tr>
<tr>
<td>Munz 13277, New Mex. Raton</td>
<td></td>
<td>circle 4, 5 pairs</td>
<td></td>
</tr>
<tr>
<td>Munz 13283, New Mex. Albuquerque</td>
<td></td>
<td>circle 4, 5 pairs</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>circle 6, circle 4, 2 pairs</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>circle 8, 3 pairs</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>bal. lethal</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>7 pairs</td>
<td></td>
</tr>
<tr>
<td><strong>e. ssp. venusta</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hall, Calif.</td>
<td>A–50</td>
<td>circle 4, circle 4, 3 pairs</td>
<td></td>
</tr>
<tr>
<td>Wm. M. Hiesey, Calif.</td>
<td>Heusi</td>
<td>7 pairs</td>
<td></td>
</tr>
<tr>
<td>A. H. Sturtevant, Calif.</td>
<td>Dalton</td>
<td>circle 4, circle 4, 3 pairs</td>
<td></td>
</tr>
<tr>
<td>A. H. Sturtevant, Calif.</td>
<td>Devil’s Gate</td>
<td>7 pairs</td>
<td></td>
</tr>
<tr>
<td>Munz 13236, Calif.</td>
<td>Venusta</td>
<td>circle 4, 5 pairs</td>
<td></td>
</tr>
<tr>
<td>Hall 13030, Calif.</td>
<td>Hall 30</td>
<td>7 pairs</td>
<td></td>
</tr>
<tr>
<td>Munz, Mataguey Creek, Mataguay Calif.</td>
<td></td>
<td>circle 4, 5 pairs</td>
<td></td>
</tr>
<tr>
<td>Hall 13021, Calif.</td>
<td>Hall 21</td>
<td>7 pairs</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>circle 6, 4 pairs, dim. pair</td>
<td></td>
</tr>
<tr>
<td><strong>f. ssp. ornata</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Munz 14546</td>
<td>Ornata</td>
<td>circle 4, 5 pairs</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>7 pairs</td>
<td></td>
</tr>
<tr>
<td><strong>g. ssp. angustifolia</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Munz 14551, Idaho</td>
<td>Macbrideae</td>
<td>circle 8, 3 pairs</td>
<td></td>
</tr>
<tr>
<td>Lehenbauer, Nevada</td>
<td>Reno</td>
<td>circle 4, 5 pairs</td>
<td></td>
</tr>
<tr>
<td>Johansen, Mono Co., Calif.</td>
<td>Mono</td>
<td>circle 4, 5 pairs</td>
<td></td>
</tr>
<tr>
<td>Munz 15016, Utah</td>
<td>Jensen</td>
<td>7 pairs and dim. extras</td>
<td></td>
</tr>
<tr>
<td>Munz 13015, Colo.</td>
<td>Ouray</td>
<td>7 pairs</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>circle 4, circle 6, 2 pairs</td>
<td></td>
</tr>
<tr>
<td>Munz 13018, Colo.</td>
<td>Gunnison</td>
<td>circle 6, 4 pairs</td>
<td></td>
</tr>
<tr>
<td>------------------------</td>
<td>---------------</td>
<td>------------------</td>
<td></td>
</tr>
<tr>
<td>Munz 13019, Colo.</td>
<td>Salida 1</td>
<td>circle 4, 5 pairs</td>
<td></td>
</tr>
<tr>
<td>Munz 13021, Colo.</td>
<td>Salida 2</td>
<td>circle 4, circle 4, 3 pairs</td>
<td></td>
</tr>
<tr>
<td>Munz 13014, Colo.</td>
<td>Silverton</td>
<td>circle 4, circle 4, 3 pairs</td>
<td></td>
</tr>
</tbody>
</table>

**h. ssp. grisea**

<table>
<thead>
<tr>
<th>Munz 13239, Calif.</th>
<th>Grisea 1</th>
<th>7 pairs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Munz 13238, Calif.</td>
<td>Grisea 2</td>
<td>circle 4, 5 pairs</td>
</tr>
<tr>
<td>Munz &amp; Johnston 11276, Calif.</td>
<td>Santa Ana</td>
<td>7 pairs</td>
</tr>
<tr>
<td>Youngberg 14, Calif.</td>
<td>Flynn Springs</td>
<td>circle 4, 5 pairs</td>
</tr>
</tbody>
</table>

**i. ssp. Hewettii (irrigua)**

<table>
<thead>
<tr>
<th>Aztec, New Mex.</th>
<th>Aztec</th>
<th>circle 4, 5 pairs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Munz 13278, New Mex.</td>
<td>Cimarron</td>
<td>7 pairs</td>
</tr>
<tr>
<td>Munz 13282, New Mex.</td>
<td>Sandoval</td>
<td>circle 6, 4 pairs</td>
</tr>
<tr>
<td>Munz 13272, New Mex.</td>
<td>Linda Vista</td>
<td>circle 4, circle 4, 3 pairs</td>
</tr>
<tr>
<td>Munz 13270, New Mex.</td>
<td>Las Cruces</td>
<td>circle 4, 6, 2 pairs</td>
</tr>
<tr>
<td>Munz 15013, Colo.</td>
<td>Durango</td>
<td>circle 4, 5 pairs</td>
</tr>
<tr>
<td>Munz 15039, Coahuila</td>
<td>Irragua San Pedro</td>
<td>circle 4, 4, 3 pairs</td>
</tr>
<tr>
<td>Munz 15042, Coahuila</td>
<td>Irragua San Miguel</td>
<td>7 pairs</td>
</tr>
</tbody>
</table>

**II. Oenothera elata**

| Munz 15048, Hidalgo, Mex. | Simsiana Zimapan | 7 pairs |
| Munz 15050, Dis. Fed., Mex. | Simsiana Puerto-aereo | 7 pairs |
| Munz 15067, Puebla, Mex. | Simsiana Texmelucan | 7 pairs |
| Munz 15076, Puebla, Mex. | Simsiana Puebla | 7 pairs |
| Munz 15070, Puebla, Mex. | Simsiana Acatzingo | 7 pairs |
| Munz 15074, Puebla, Mex. | Simsiana Cholula | 7 pairs |

**III. Oe. Jamesii**

| Munz 13580, Okla. | Jamesii b. | circle 4, circle 6, 2 pairs |
| Munz 13575, Okla. | Jamesii a.  | circle 10, 2 pairs, probably unbalanced lethal |

**IV. Oe. longissima**

<table>
<thead>
<tr>
<th>a. ssp. typica</th>
</tr>
</thead>
<tbody>
<tr>
<td>Munz 13008, Utah</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>b. ssp. Clutei</th>
</tr>
</thead>
<tbody>
<tr>
<td>Munz 15009, Utah</td>
</tr>
<tr>
<td>Eastwood &amp; Howell 6991</td>
</tr>
</tbody>
</table>
Geneticists may wonder at the inclusiveness of some of my subspecies, since a number of strains which they have grown and studied and considered different may be here treated as a single entity. It is probably generally true, however, that in any variable group selection in the garden can develop strains which may look quite different in their homozygous condition, but which in the more heterozygous condition met in nature may not segregate so readily. In growing seed of the *Oenothera Hookeri* group collected in the wild, this heterozygous situation is commonly met. It is not surprising, therefore, that not only is it necessary for the taxonomist to throw together some of these strains in order to get recognizable entities in nature, but he will find many individuals in the wild which do not fall clearly into one or another of even these more inclusive categories. Then, too, in the herbarium so many specimens are inadequate, either because of lack of representative parts of the plant or because of over- or under-maturity, that they do not fall definitely into the groups I am proposing. This does not mean, however, that there do not occur in nature definite entities or gene-complexes which occupy fairly definite ecological niches, but which may rather freely exchange genes one with another. It is these so far as I can interpret and recognize them that I am making subspecific in rank. The geneticist should remember too, that he can grow at most a limited number of strains, while the student of plants in the wild sees many more and in the herbarium may have access to hundreds of different collections so that he faces a more complex picture than is met in the garden.

**Herbarium Material Available**

In the preparation of this paper herbarium material in the following institutions has been studied, for which the abbreviations given are used in citation of specimens. These abbreviations are those suggested by Landjouw in *Chron. Bot.* 5: 142-150, 1939. To those in charge of the several institutions named I am greatly indebted for their kindness and courtesy.

- Bailey Hortorium, Cornell University (BH)
- California Academy of Sciences, San Francisco (CAS)
- Cornell University Botany Department (CU)
- Dudley Herbarium at Stanford University (DS)
- Institut de Botanique Systématique, Geneva, Switzerland (G)
- University of Goettingen (GOET)
- Gray Herbarium at Harvard University (GH)
- Indiana University (IND)
- New York Botanical Garden (NY)
- Paris, Museum National d'Histoire Naturelle (P)
- Pomona College, Claremont, California (POM)
- Rancho Santa Ana Botanic Garden (RSA)
- University of California at Berkeley (UC)
- United States National Herbarium (US)
- University of Washington, Seattle (WTU)
- Willamette University, Salem, Oregon (WILLU)

It is a pleasure also to acknowledge my indebtedness to Dr. Bradley Moore.
Davis of the University of Michigan for notes, to Dr. Ralph E. Cleland of Indiana University for suggestions, seeds, notes and reprints during the years, and to various California friends like Mr. Joseph Ewan, Mr. John Thomas Howell, Dr. David Keck, and Dr. Carl B. Wolf for seeds and other material.

In citing herbarium material that I have studied, I am showing for many cases that I first made a collection in the wild, that seed of this was sent to Dr. Cleland, and in some cases on a visit to Baltimore I collected specimens in his garden. Then I grew material at the same time in Claremont and again made specimens, often under as many as 3 or 4 numbers, these being taken at different stages from seedling to mature plants. Thus for certain numbers I had wild material, Baltimore cultivated material, and Claremont cultivated material for comparison.

Illustrations

It is a pleasure to give credit for the plates to their artist Miss Florence Mekeel who made these beautiful drawings in 1945 when we were both on the staff of the Bailey Hortorium. Dr. L. H. Bailey kindly gave them to me and I express herewith my gratitude to him.

Key to Species Treated

A. Hypanthium 3.5 cm. long.
   B. Cauline leaf-blades at least one-third as wide as long and strongly crinkled; petals 3.5-5 cm. long.
      BB. Cauline leaf-blades usually less than one-fourth as wide as long, tending to be plane; petals 2.5-4 cm. long.
      C. Capsules 4.5 mm. thick near the base, the floral bracts lanceolate and not much cupped at their base; sepal-tips various but mostly 2-6 mm. long; style not shorter than petals. Western United States to northern Mexico. 1. Oe. Hookeri
      CC. Capsules 5-7 mm. thick near the base and set in the cup-like axil of the subovate bract; sepal-tips 1-2 mm. long; style usually much shorter than petals. Central Mexico. 2. Oe. elata

AA. Hypanthium 6-12 cm. long.
   B. Cauline leaves 20-35 mm. wide, sharply sinuate-serrulate; rosette lax, the axis soon elongating; capsule 6-7.5 mm. thick near base. Oklahoma to Coahuila. 4. Oe. jamaicensis
   BB. Cauline leaves 8-22 mm. wide, obscurely sinuate-serrulate; rosette compact, well-formed; capsule 4.5-5.5 mm. thick. Utah to Arizona and eastern California. 5. Oe. longissima

Treatment of Species

1. Oenothera Hookeri T. & G.


Biennial to perennial, usually erect and simple or branched, 5-25 dm. tall, sometimes decumbent and somewhat matted; stems usually rather coarse below, with some red, pubescent, the hair varying from appressed to spreading and usually of more than one kind; rosettes well formed, rather flat, the leaves mostly elliptic-oblanccolate, more or less sinuate-dentate, long-petioled; cauline leaves gradually reduced upward, rather numerous, short-petioled to subsessile, lanceolate to elliptic-lanceolate, variously pubescent; inflorescence many-flowered, simple or branched, variously hairy, the bracts lanceolate, spreading; hypanthium variously pubescent, 2-5 cm. long, rather slender below the funnelform apex; sepals narrowly lanceolate, reflexed and connivent at anthesis, 2-4 (4.5) cm. long; with slender usually terminal subulate tips; petals
pale yellow, usually aging orange or red, 2-4.5 cm. long, about as wide, frequently with broad apical notch; filaments about half as long as the petals; anthers usually 10-14 mm. long; style equaling or exceeding the petals; stigma-lobes linear, yellowish to greenish, mostly 4-7 mm. long; capsule mostly 2.5-4.5 cm. long and 4.5-5.5 mm. thick just above the base, more or less quadrangular, gradually narrowed upward, with truncate or somewhat emarginate valves, variously pubescent; seeds dark brown, sharply angled, 1-1.6 mm. long.

Map I. Distribution of Oenothera Hookeri and its subspecies.

W—subsp. Wolffi
O—“ ornata
E—“ eu-Hookeri
A—“ angustifolia
M—“ montereyensis

G—subsp. grisea
V—“ venusta
H—“ hirsutissima
h—“ Hewetttii

**KEY TO SUBSPECIES OF OENOTHERA HOOKERI**

A. Pubescence mostly appressed, not spreading or gland-tipped, so that the plant is more or less ashy in appearance; stems scarcely or not at all muricate, 1-2.5 m. tall.

B. Bracts of young inflorescence exceeding buds, of older inflorescence spreading-recurred, lanceolate, 3-5 mm. wide, not twisted; seeds 1.3-1.6 mm. long. Southern California and northern Baja California. h. ssp. grisea

BB. Bracts of young inflorescence soon exceeded by buds, of older inflorescence twisted, linear-oblong, 1-3 mm. wide; seeds 1 mm. long. Southern Nevada to Colorado and Chihuahua. i. ssp. Hewetttii

AA. Pubescence largely loose, with some spreading hairs; stems muricate, hirsute.

B. Sepals under a lens slightly or not papillose, with few longer hairs and shorter gland-tipped ones, sometimes almost glabrous.
C. Hypanthium and sepals red; plant mostly less than 1 m. tall, simple or branched only below; leaves plane. Mostly in or above Yellow Pine Belt, mountains from Washington to California and Colorado.  

CC. Hypanthium and sepals green for most part; plant usually branched throughout. Below Yellow Pine Belt.

D. Plants mostly about 1 m. tall; stem-leaves quite plane, 4-8 cm. long, usually with appressed marginal hairs; inflorescence up to 3 dm. long; hypanthium 3-3.5 cm. long. Eastern Washington and western Idaho.  

DD. Plants up to 2.5 m. high; stem-leaves crinkled, 5-15 cm. long, usually with spreading marginal hairs; inflorescence up to 8 dm. long; hypanthium 4.5 cm. long. Tuolumne Co., California to northern Baja California.

BB. Sepals under a lens and in terminal half obviously papillose at base of some of longer hairs, which are usually numerous and tend to conceal the shorter gland-tipped ones.

C. Flowers small; sepals 2-3 cm. long; petals 2-2.5 cm. long. Northwestern California.  

CC. Flowers normally larger, except in old inflorescences.

D. Bracts of older inflorescence lance-linear, tending to twist; sepals scarcely or not glandular, the tips 2-4 mm. long. Utah to western Kansas, Chihuahua and Arizona.  

DD. Bracts of older inflorescence lanceolate, not twisted; sepals usually more glandular.

E. Sepal-tips 3-6 mm. long, the buds attenuate; sepals 3.5 cm. long. Sutter County, California to Monterey County.

EE. Sepal-tips 1-2.5 mm. long, the buds blunt; sepals mostly 2-2.5 cm. long. Along the coast, San Mateo County, California to San Luis Obispo County.

*Oenothera Hookeri var. eu-Hookeri* Munz, nom. nov.

Oe. Hookeri Torr. & Gray subsp. eu-Hookeri* Munz, nom. nov.

Oe. Jepsonii Greene, Fl. Francisc., 211, 1891.  
Oe. franciscana Bartlett, Rhodora, 16: 35, 1914.

Plate I, Figs. C-G. Map I

Plant more or less branched, 4-12 dm. high, biennial; the stems stout, usually red, erect to ascending, abundantly muricate-hirsute and with fine appressed hairs; rosette-leaves with little red, elliptic-oblanceolate, sinuate-dentate, strigose, often with pilose midribs, the marginal hairs usually appressed, the blades plane to somewhat crinkled, 10-18 cm. long, 2-4 cm. wide, acute to obtuse at apex, narrowed into petioles 5-10 cm. long; stem-leaves lanceolate, rather crowded, numerous, acute at apex, with about 8 main veins on each side of midrib, generally 6-12 cm. long, 1-2 cm. wide, short-petioled or upper sessile, with same pubescence as rosette-leaves; inflorescence dense, simple or branched, 1-4 dm. long, the axes muricate-hirsute, as well as strigose and with some fine gland-tipped hairs; first bracts broadly lanceolate, exceeding young buds, slightly flaring, the later ones narrower and shorter, crinkled on margins, spreading, hairy; hypanthium 3.5-4 cm. long, usually red, with all 3 types of hair; sepals 2-4 cm. long, usually reddish, soft-hairy, also with fine gland-tipped...
ones, papillose, the tips mostly 3-6 mm. long, connivent in the bud; petals 2.5-4 cm. long, somewhat wider, pale yellow, aging orange-red, retuse; anthers 12-14 mm. long; style equaling petals; stigma-lobes 5-6 cm. long, greenish; capsule mostly 2.5-4.4 cm. long, 5-5.5 mm. thick near base, soft-hairy and red-papillose, as well as strigulose, often red-striped, the valves truncate; seeds 1.1-1.4 mm. long.

Type locality, "California, Douglas!" the type at Gray Herbarium with narrow leaves, heavy pubescence; sepal tips 4 mm. long, blunt and coarse (cf. Davis, Proc. Am. Philos. Soc. 74: 245-253. Plate I, 1934). The collection by M. E. Jones from St. Helena matches the type. Ranging in the California Coast Ranges from Lake and Sutter counties to San Luis Obispo County.

The subspecies eu-Hookeri is distinguished by: its abundant pubescence, being hirsute and mucronate on the stems; its papillose, hairy sepals that are 2-4 cm. long and with subulate tips 3-6 mm. long; petals 2.5-4 em. long; and gland-tipped as well as non-glandular hairs. Generally it is rather a coarse plant with rather broad leaves. It is quite variable, the Douglas type having narrower leaves than in such forms as that described by Bartlett as Oe. franciscana. But in general, material from the area here allotted to it, falls fairly definitely into an entity with certain limits of variation. It intergrades somewhat with the more coastal subspecies montereyensis and material from the northern inner Coast Ranges is sometimes difficult to place definitely in ssp. Wolffi or here.

Plate I.

Oe. Hookeri ssp. montereyensis, Fig. A, buds, x 1/2.
Oe. Hookeri ssp. Wolfii, Fig. B, inflorescence, x 1/2.
Oe. Hookeri ssp. eu-Hookeri, Fig. C, rosette-leaf, x 1/2. Fig. D, capsule, x 1. Fig. E, inflorescence, x 1/2. Fig. F, seeds, x 5. Fig. G, cauline leaf, x 1/2.
County by H. M. Hall 13277, was cultivated by Cleland and seed sent to Claremont, where it was grown as Munz 13967 (POM) and 13996 (POM). It seems to fit here more closely than in any other subspecies.

As to the cytological situation found in collections cited in the preceding paragraph, it can be said that Cleland (Proc. Am. Philos. Soc. 75: 339-429, 1935) reported for "Franciscana" both circle of 4 and 5 pairs, or 7 pairs; for "Johansen" 7 pairs; and for "Hookeri de Vries" 7 pairs, as occurring in his cultures. He found "Johansen" as differing from "Hookeri de Vries" in "being larger and stouter; with broader, more crinkled, more softly hairy, lighter green, less toothed and white-veined leaves; longer, more slender, less pigmented buds, with longer, more delicate sepal teeth; larger flowers and greener stems." Crosses between the two resembled the latter "in foliage characters, the leaves being narrow, flat, and dark grey-green; in color of bracts; in shape of the floral tips. They were intermediate between the parents in stem color, in cone color and in bud shape. Pigmentation of the midribs was lacking as in Johansen. In general, the appearance was that of a robust hookeri with lighter anthocyan pigment and longer, more slender buds." Plants of this cross that were examined had circle of 4 and 5 pairs of chromosomes. In the same paper he reported crosses made between "Johansen" and "franciscana" as follows, "Johansen characters which were particularly noticeable were velvety pubescence of the foliage, spreading character of the floral tip, and red stripes on the ovary. Franciscana characters included appressed marginal hairs, deep bud and bract coloration, and general habit. Plants were intermediate in leaf breadth, bud shape and stem coloration; other characters were common to both parents." The cross showed circle 4 and 5 pairs of chromosomes. These races are thus genetic in nature. Hall 13277 from Santa Barbara County had 7 pairs of chromosomes. The differences between the type specimen of Oe. Hookeri and "Hookeri de Vries" and between "franciscana" and "Hookeri de Vries" are well tabulated by Davis (Proc. Am. Philos. Soc. 74: 245-253, 1934). They illustrate the variability to be found in what I include in ssp. eu-Hookeri.

1. (b) Oenothera Hookeri Torr. & Gray subsp. montereyensis* Munz, subsp. nov.

Plate I, Fig. A. Map I

Plants tending to be bushy, branched, often with main stems and branches spreading to almost horizontal, sometimes ascending to suberect, 3-15 dm. long; stems coarse, often with some red, densely leafy, densely soft-hirsute, many of the hairs red-papillose at base, also with fine, short, white, subappressed hairs; rosette-leaves elliptic-oblanceolate, sinuate-denticulate, from somewhat strigose with veins pilose, to densely soft-hairy all over, veins not red, marginal hairs appressed to spreading, leaf-blades 10-20 cm. long, 2-4.5 cm. wide, acute at apex, gradually narrowed basally into winged petioles 3-8 cm. long; stem-leaves tending to be crowded, spreading, not much crinkled, mostly 5-12 (15) cm. long, 1.5-2.5 cm. wide, short-petioled or the upper sessile,

*Oe. Hookeri var. montereyensis Munz, var. nov.
elliptic-lanceolate, with 8 main veins on each side of the midrib, and with same pubescence as basal leaves; inflorescence from 1-8 dm. long, muricate-hirsute and strigose, with some short gland-tipped hairs; bracts lanceolate to lance-oblong, soft-hairy and strigose, spreading, crinkled on margins, mostly shorter than buds; hypanthium 2-3.5 (4) cm. long, often reddish, pilose and with some gland-tipped hairs as well as some appressed ones; sepals 2-3 cm. long, reddish, pilose to soft-hirsute, strongly muricate, the tips mostly 1-2.5 mm. long, slightly subterminal and divergent; petals pale yellow, aging orange, 2.5-3.5 cm. long; anthers 11-13 mm. long; style equaling or exceeding the petals; stigma-lobes yellow, 4-6 mm. long; capsules 3-4 cm. long, ca. 5 mm. thick at base, green or with some red, soft-hirsute and with shorter hairs, valves mostly truncate at tips; seeds ca. 1.5 mm. long.

Planta ramosa, caulibus ramisque saepe subhorizontalibus aut ascendenti­bus, 3-15 dm. longis; caulibus crassis, dense foliosis, molle-hirsutis, muricatis et cum pilis brevibus adpressis; foliis basalibus elliptico-oblanceolatis, sinuato-denticulatis, strigosis cum venis pilosis, aut dense molle-pubescentibus; laminis 10-20 cm. longis, 2-4.5 cm. latis, apice acutis, cum pilis marginalibus adpressis, base in peti­olos 3-8 cm. longos angustatis; foliis caulibus patentibus, elliptico­ lanceolatis, 5-12 (15) cm. longis, 1.5-2.5 cm. latis, breve-peti­olatis vel superioribus sessilibus, venis principalibus 8; inflorescentia 1-8 dm. longa, muricato­hirsuta et strigosa et glandulos­o-pubescente; bracteis lanceolatis vel lanceolato­oblongis, patentibus; hypanthio 2-3.5 cm. longo, saepe rubro, piloso et glandu­loso-pubescente et strigoso; sepalis 2-3 cm. longis, muricatis, cum apicibus 1-2.5 mm. longis; petalis 2.5-3.5 cm. longis; capsulis muricato-hirsutis et strigosis, 3-4 cm. longis, 5 mm. crassis; seminibus 1.5 mm. longis.

Type, from 0.2 mile south of mouth of Alder Creek, Monterey County, California, Nov. 6, 1934, C. B. Wolf 6223, Rancho Santa Ana Botanic Garden 12778; isotypes at Gray Herbarium, New York Botanical Garden and Pomona College. Seed from type collection grown at Claremont, Munz 14274 (POM), 14603 (GH,NY,POM), 14690 (GH,NY,POM). Growing in springy places mostly along sea-cliffs of central California from San Mateo County to San Luis Obispo County. The subspecies montereyensis is near to eu-Hookeri, but tends to be more sprawling in growth, more compact and densely leafy, has shorter sepals and blunt buds with the sepal-tips 1-2.5 mm. long instead of 3-6 mm. It is confined to the immediate coast.

In 1891, E. L. Greene described an Oenothera arguta (Fl. Francisc., 212, 1891; Onagra arguta Small, Bull, Torrey Club 23: 172, 1896) as coming from moist places near Monterey. It was said to be perennial, the stems decumbent, about 1 ft. high; leaves linear-lanceolate, 2-4 in. long, 3-4 lines broad, saliently dentate, the cauline broadest at the sessile somewhat clasping base. These leaf-characters are not true of my ssp. montereyensis, nor is Greene's statement that the anthers are "about equalled by the style." His description does fit a specimen at the Gray Herbarium labeled Oenothera arguta and collected at Pacific Grove, July 1891 by Michener and Bioletti, which, while possibly not the type, seems to be authentic material. A later collection of the same thing from Pacific Grove, Sept. 7, 1903 was distributed by Heller as 7208 (GH). It persisted there even longer: Seaside, Monterey Co., May, 1913, Nellie Curtis...
These specimens are all Oenothera stricta Ledeb. a South American species of the subgenus Raimannia, which seems to have been introduced and to have maintained itself for some time on the California coast. Inquiry at University of Notre Dame, California Academy of Sciences, University of California, and United States National Herbarium failed to locate the type, but it seems certain that my montereyensis is not a synonym of Greene's argula.

Material seen of ssp. montereyensis is as follows, all from CALIFORNIA: San Mateo Co.: Half Moon Bay, W. F. Schmitt in 1913 (NY); Point Pescadero, seed sent to Cleland and grown by him as "Mateo," cultivated at Claremont, Munz 13463 (POM); Pescadero, H. L. Mason in 1921 (DS), W. R. Dudley in 1894 (DS); base of cliff, south of Capitola, C. B. Wolf 6234 (GH,NY,POM, RSA), grown at Claremont, Munz 13994 (NY,POM), 14057 (POM); above Salada Beach, Mrs. E. Sutliffe in 1921 (CAS). Santa Cruz Co.: ocean cliffs, Santa Cruz, Edith Bond in 1928 (POM), M. E. Jones in 1881 (DS,NY,POM), E. E. Smith in 1893 (DS); Seabright, P. R. Hichborn 324 (DS); Swanton, W. H. Shockley in 1919 (DS); Sea Cliffs, south of Capitola, Wolf 6234 (RSA), Monterey Co.: Carmel, near Pacific Grove, Misses Patterson & Wiltz in 1907 (DS); Hot Springs, Dudley in 1903 (DS); Coal Chute Point, Point Lobos Reserve, L. C. Wheeler 4368 (POM,UC); Spreckels, I. J. Condit in 1908 (UC). San Luis Obispo Co.: sea-cliffs on Highway 1, 1 mile south of Monterey—San Luis Obispo County line, Munz 12180 (RSA); San Simeon, K. Curran in 1888 (UC); Morro Bay, Mrs. R. W. Summers 308 (UC).

Cleland has reported on the cytology of only one strain of this subspecies, his "Mateo" (Proc. Am. Philos. Soc. 75: 339-429, 1935). He found variability in the first generation, particularly in habit, some plants having the usual compactness, others longer internodes. He concluded that it was near what I call eu-Hookeri. In his first generation he got plants with 7 pairs of chromosomes, one with circle 4 and 5 pairs, and one with circle 8 and 3 pairs. Using a 7-paired plant for seed, he got subsequent generations with 7 pairs. When crossed with eu-Hookeri these gave circle 4 and 5 pairs, 7 plants being dwarfs and 10 elongate. It thus differed from most eu-Hookeri by one segmental interchange.

1 (c). Oenothera Hookeri Torr. & Gray subsp. Wolfii* Munz subsp. nov.

PLATE I, FIG. B, MAP I

Branching plants, 5-15 dm. tall, the coarse stems green to red, hirsute with red papillae and strigulose, and with some gland-tipped hairs in inflorescence; rosette-leaves broadly elliptic-oblancoolate, rounded to obtuse at apex, sinuate-serrulate, crinkled on margins, with more or less pink on midribs, strigose on both surfaces and margins, the blades mostly 10-15 cm. long, 3-5 cm. wide, gradually narrowed at base into winged petioles 5-10 cm. long; cauline leaves not much crinkled, lanceolate, 7-15 cm. long, 1.5-2.5 cm. wide, acute to sub acuminate, with 8-10 main veins on each side of midrib, pilose and somewhat strigose, green-veined, serrulate-sinuate, sometimes rather sharply so, with marginal hairs tending to spread; inflorescence 2-4 dm. long, muricate-hirsute and white-strigose and glandular-pubescent; lower bracts broadly lanceolate,

*Oe. Hookeri var. Wolfii Munz, var. nov.
ascending-divergent, at first surpassing the young buds, later bracts narrowly oblong-lanceolate to lanceolate, spreading, more or less crinkled; hypanthium 3.5-4.5 cm. long, mostly with some red, soft-hairy and glandular-pubescent; sepals 2.3 cm. long, usually reddish, soft-hairy and glandular-pubescent, usually with elevated papillae; sepal-tips 2-3 mm. long; petals pale yellow, orange-red in age, 2-2.5 cm. long and wide; filaments 1-1.5 cm. long; anthers about 1 cm. long; style equaling petals; stigma-lobes yellowish, 5 mm. long; capsules tending to have some red on each face, 2.5-3.5 cm. long, about 5 mm. thick near base, soft-hairy, strigose and glandular-pubescent, sometimes with red papillae; valves truncate at tip; seeds 1.5-1.9 mm. long.

Plantae ramosae, 5-15 dm. altae; caulibus viridibus vel rubris, muricato-hirsutis, strigulosis et in inflorescentia glanduloso-pubescentibus; foliis basali- bus late elliptico-oblanceolatis, apice obtusis, sinuato-serrulatis, crispatis; laminis 10-15 cm. longis, 3-5 cm. latis, base in petiolos alatos 5-10 cm. longos angustatis; foliis caulium lanceolatis, planis, 7-15 cm. longis, 1.5-2.5 cm. latis, subacutis, pilosis et substrigosis, cum pilis marginalibus subpatentibus; inflorescentia 2-4 dm. longa, muricato-hirsuta, strigosa et glanduloso-pubescente; bracteis infernus late lanceolatis, ascendente-divergentibus, superioribus lanceolatis, patentibus, crispatis; sepals 2-3 em. longis, apicibus 2-3 mm. longis; petals 2-2.5 em. longis; capsulis 2.5-3.5 cm. longis, 5 mm. crassis; seminibus 1.5-1.9 mm. longis.


This proposed subspecies is near ssp. eu-Hookeri in most features, but is more northern and western in distribution and is characterized by its smaller flowers and larger seeds. Material seen, OREGON: Jackson Co., Wimer, E. W. Hammond 142 (NY). CALIFORNIA: Del Norte Co.: Crescent City, J. W. Thompson 488 (DS,WTU), beach at Crescent City, Munz 14386 (POM), cult. at Claremont, Munz 14698 (NY, POM), Crescent City, H. E. Parks 8321 (UC); 6 miles south of Crescent City, J. P. Tracy 15602 (UC); near Requa, E. A. McGregor in 1921 (DS). Humboldt Co.: Willow Creek, Abrams 7168 (DS); 2 miles south of Cape Mendocino, Wolf 9307 (RSA); 3 miles south of Cape Mendocino, Tracy 4968 (UC). Siskiyou Co.: Yreka Creek, G. D. Butler 1799 (DS,POM,UC) approaching Oc. strigosa, Butler 1024 (POM,UC); north side of Mt. Shasta, H. E. Brown 485 (NY,UC). Trinity Co.: Carville, Mrs. E. C. Van Dyke in 1931 (CAS), H. M. Hall 8695 (UC) approaching strigosa. Marin Co.: Marin-Sonoma Co. line east of Aurora School, J. T. Howell 23027 (CAS, RSA), with sepals less hairy than usual. From WASHINGTON, western Klickitat County comes a series of specimens by W. N. Suksdorf which have puzzled me greatly and which although far removed from the normal range of this subspecies seem very near to it. They are too papillose on the sepals for ssp. angustifolia; their sepals are too papillose and red for ssp. ornata, yet the flowers are rather large for ssp. Wolfii, to which they seem nearer than to anything else. They are are follows: Vila, Suksdorf 10603 (BH); Bingen, Suksdorf 2066 (GH), 5859 (BH,GH,DS,NY), 7807 (BH).
1 (d). Oenothera Hookeri subsp. hirsutissima (Gray) Munz, grad. nov.


Oe. biennis var. hirsutissima Gray, Pl. Fendl. 43, 1849, as nomen subnudum; ex Watson. Proc. Am. Acad., 8: 579, 1873; ex Brewer & Watson, Bot. Calif. 1: 223, 1876, with more description, but applicable only in part.

?Oe. hirsutissima de Vries, Mutationstheorie 1: 327, 1901.


PLATE II, FIGS. C-H; MAP I

Plants 3-15 (20) dm. tall, branched from base, hirsute and muricate, also strigose; stems usually with some red, often strongly angled in upper parts, with few or no gland-tipped hairs, rather densely leafy; rosette-leaves plane or crinkled, narrow-oblanceolate, sinuate-serrulate, mostly acute at apex, the blades 15-30 cm. long, 2-3 (5.5) cm. wide, densely strigose and pilose on both surfaces, sometimes with some longer hairs also, usually with marginal hairs appressed, veins and margins sometimes reddened; petioles 5-18 cm. long; cauline leaves elliptic-lanceolate, 5-15 cm. long, 1-2.5 cm. wide, subacuminate to acute, subentire to sinuate-serrulate, with 9-11 principal veins on each side of the midrib, usually densely pilose or pubescent on both surfaces, the hairs appressed with some longer stiffer ones on veins, marginal hairs mostly appressed, leaves more or less crinkled, spreading-ascending; inflorescence 2-5 dm. long, typically both hirsute-muricate and grayish with appressed, non-glandular hairs, many-flowered, simple or branched; first bracts flaring, usually exceeded by buds, lanceolate, gray-hairy, later bracts narrow-lanceolate, flaring, twisted; hypanthium 2.5-4 cm. long, reddish, pilose and pubescent; sepals 2.5-3.5 cm. long, usually with some red, rather densely appressed-hairy, with well-formed papillae especially toward apex, with little or no gland-tipped pubescence; sepal-tips 2-4 (5) mm. long, slender; petals pale yellow, aging salmon to purplish, 2.5-3.5 cm. long, somewhat wider, not always apically notched; anthers 10-12 mm. long; style equal to petals; stigma-lobes yellowish, 4-5 mm. long; capsules 2-3 mm. long, 4.5-5 mm. thick, hirsute and muricate, as well as strigose, the valves truncate; seeds 1.2-1.6 mm. long.

Type locality, valley of Santa Fe Creek, near Santa Fe, New Mexico, the type collected by Fendler in 1847 (GH). Ranging from Utah and southern Colorado to Kansas, Chihuahua, and Sonora, but most abundant in Arizona and New Mexico, where it is quite common in moist places in the valleys and even rather dry situations in the mountains. Thus its area is largely that of ssp. Hewettii (irrigua) with which it intergrades, but it is generally lower in stature, much more muricate and with more spreading hair, as well as papillose sepals. For the most part the two subspecies occupy different ecological niches within their geographic area, hirsutissima being more montane than Hewettii.

Material seen, UTAH: Weber Co.: Ogden Canyon, Pammel & Blackwood 3737 (GH); 8 miles north of Ogden, Maguire, Richards & Maguire 4191 (POM); near
**PLATE II.**

*Oe. Hookeri* ssp. *angustifolia*. Fig. A, inflorescence, x $\frac{1}{2}$. Fig. B, hairs, both spreading and gland-tipped, x 5.

*Oe. Hookeri* ssp. *hirsutissima*. Fig. C, rosette-leaf; Fig. D, cauline leaf, both x $\frac{1}{2}$. Fig. E, seeds, x 5. Fig. F, hairs with basal papillae, x 5. Fig. G, capsule, x 1. Fig. H, inflorescence, x $\frac{1}{2}$.
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(DS,GH,UC); Ramsey Canyon, Huachuca Mts., M. E. Jones 21942 (POM), Goodding 782 (NY), Munz 13260 (GH,NY,POM), cult. by Cleland, Munz 13429 (POM), by Munz at Claremont, Munz 13995 (POM); Huachuca Mts., Jones in 1903 (POM); Miller Canyon, Huachuca Mts., Goodding 234 (GH,NY); Price Canyon, Chiricahua Mts., Goodding 2312 (GH,UC); Barfoot Park, Chiricahua Mts., Blumer 1420 (DS,GH,NY); Wood Canyon, Blumer 1916 (GH). SONORA: Canyon de la Petaquilla, near Rio de Bavispe, S. S. White 3324 (GH); Las Tierritas de El Temblor, Sierra de El Tigre, White 3361 (GH); Canyon de la Cienega Alta, Puerto de los Aserrados, White 3186 (GH); El Rancho del Roble, northeast of El Tigre, White 4187 (GH); La Cruz de las Canadas, E. Lloyd 390 (GH); between San Pedro and Fronteras, C. V. Hartman 899 (GH); San Pedro, Hartman 887 (GH); Las Cuevas, Hartman 169 (GH), CHIHUA-HUA: Janos, G. Thurber 735 (GH); Sierra Madre near Colonia Garcia, C. H. T. Townsend & C. M. Barber 107 toward ssp. Hewettii, (NY,POM), 445 (POM); base Sierra Madre, C. G. Pringle 1489 (GH); Sierra Madre, 40 miles from Guadalupe y Calvo, E. W. Nelson 4818 (GH).

Cleland has given me reports on a number of collections of ssp. hirsutissima: (1) seeds from old plant at roadside 3 miles east of Flagstaff, sent him as Munz 13000a, of this he says “Plants are like large, hoary franciscana, with less color in buds” and gives two plants as having 7 pairs of chromosomes and two with circle 4 and 5 pairs. (2) For my 13260 from Ramsey Canyon in southern Arizona, he found a segregation into 2 classes, the first with darker green leaves having but few red dots when young and typical rosette leaf 21 x 3 cm.; buds tinged with red; capsules red-striped; chromosomes of 3 plants circle 4 and 5 pairs, of 1 plant circle 4, circle 4, and 3 pairs. For the other class which had lighter green and broader basal leaves 19 x 5 cm., with abundant red splotches when young; stems and leaves with very large red stains about the papillae, buds green except for the papillae; capsules red-striped and with stains about the papillae. One plant had 7 pairs of chromosomes, and 1 had circle 4, circle 4, and 3 pairs. (3) From New Mexico he studied my 13277 from Raton Pass and concluded it looked like low individuals of the Ramsey Canyon plants; he found circle 4 and 5 pairs of chromosomes. (4) My Taos collection, number 13279, he grew and felt it resembled very much “Devil’s Gate,” a California plant which I put under venusta, but had narrower, more crinkly leaves. Two plants had 2 circles 4 and 3 pairs; two others had 1 circle 4 and 5 pairs. (5) My 13281, he grew as “Embudo” and found 2 circles or circle 4; and (6) my 13283, his “Albuquerque” showed 2 circles or circle 4, or circle 6 and circle 4, or circle 8 with balanced lethals. On the whole, then, there were more small circles than in California plants.

1(e). Oenothera Hookeri Torr. & Gray subsp. venusta* (Bartlett) Munz, stat. nov.

Oenothera venusta Bartlett, Rhodora 16: 36, 1914.

PLATE III, FIGS. D-G, MAP I.

Plants mostly tall, up to 2.5 m. high and freely branched throughout, rather grayish-pubescent, the hairs long, spreading and often red-papilllose at base, also fine, white and closely appressed or erect, and some shorter ones gland-tipped, especially in upper parts of plant; stems usually reddish, conspicuously

*Oe. Hookeri var. venusta (Bartlett) Munz, stat. nov.
muricate, somewhat angled in upper parts; rosette-leaves narrowly to broadly elliptic-oblanceolate, acute to subacuminate at apex, sinuate-serrulate (sometimes deep to toward petiole), mostly quite plane, sometimes crinkled, white to red on midribs, usually striose on both surfaces and on margins, but marginal hairs sometimes erect, blades mostly 15-20 cm. long, 2.5-3.5 (5.5) cm. wide, petioles 5-15 cm. long; stem-leaves numerous but not crowded, lanceolate, soft-pubescent with some longer hairs on veins, marginal hairs mostly spreading, veins scarcely red, leaf-blades more or less crinkled on margins, with 8-10 main veins on each side of the midrib, inconspicuously serrulate-sinuate, 5-15 cm. long, 1.2-2.5 cm. wide, acute to acuminate at apex; inflorescence up to 8 dm. long, mostly branched, rather lax; bracts generally exceeding buds, appressed at base, but with flaring tips, soft-hairy and with shorter hairs, not much crinkled or twisted; hypanthium mostly green, 4.5 cm. long, pilose and glandular-pubescent; sepals 3-4.5 cm. long, green, pilose to appressed-villous, and glandular-pubescent, generally not muricate, the tips slender, 3-5 mm. long; petals pale yellow, orange-red in age, 3-4.5 cm. long; anthers 12-14 mm. long; style equaling petals; stigma-lobes greenish yellow, 5-7 mm. long; capsule 2.4 cm. long, ca. 5 mm. thick near base, often with red on each face, long- and short-haired, the valves subtruncate at apex; seeds 1.2-1.5 mm. long.

Type locality, San Bernardino, San Bernardino Co., California, the type grown from seed collected by S. B. Parish. This subspecies is found mostly in the coastal drainage of southern California below the yellow pine belt, but material from the west base of the Sierra Nevada is very close to it. It differs from the four subspecies so far discussed by having the sepals relatively free from papillae at the base of the long hairs, although the stems are muricate. It is further distinguished by its tallness and tendency to branch throughout.

Herbarium material studied, CALIFORNIA: Tuolumne Co.: Mather, seed sent by H. M. Hall and grown by Cleland as A50, then sent to Claremont and there grown, Munz 13971 (POM), 14090 (POM), 14160 (POM), 14644 (GH,NY,POM); Mather, seeds collected in 1930, grown by Cleland as "Heusi," cult. by Munz, no. 13991 (POM), 14086 (POM). Kern Co.: upper Kern River, Hall 5409 (UC). Ventura Co.: Lyon's H. S., Matilija Canyon, H. M. Pollard in 1944 (CAS), in 1946 (RSA); mouth of Ventura River, Pollard in 1945 (CAS); 5.5 miles southeast of Cobblestone Mt., A. Simontacchi 59 (UC). Los Angeles Co.: Rock Creek, Mohave Desert, Munz & Johnston 11171 (POM); 8 miles west of Ravenna, T. Craig 2015 (POM); Pocoiia Canyon, above San Fernando, M. Hitchcock 26 (POM); Long Canyon, San Gabriel Mts., F. Grinnell, Jr. in 1910 (DS); Soledad Canyon, J. H. Barber 186 (UC); Dalton Canyon, near Pasadena, seed sent by Sturtevant to Cleland and grown as "Dalton," cult. at Claremont, Munz 13988 (GH,NY,POM), 14018 (POM), 14064 (POM); Devil's Gate near Pasadena, seed sent by Sturtevant to Cleland and grown by him as "Devil's Gate," specimen is Munz 13413 (POM), cult. at Claremont, Munz 13970 (POM), 13989 (NY,POM), 14065 (POM); Pine Flats, San Gabriel Mts., West, Sweet & Crow in 1930 (POM) toward angustifolia in habit; San Gabriel Canyon, Abrams 2650 (DS,GH,NY,POM) one of Gray Herbarium specimens toward ssp. grisea; Claremont, C. N. Carter in 1909 (POM); San Antonio Canyon, C. F. Baker 3685 (GH,NY,POM,UC); plant from San Antonio Canyon grown at Claremont, Munz 10000 (POM,UC). San Bernardino Co.: San Bernardino, S. B. Parish 4201 (NY); Harlem Springs, Parish 19302 (GH,UC); 2 miles east of San Bernardino, Munz 13236 (POM), grown at Baltimore as "venusta;"
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Munz 13448 (POM), at Claremont, Munz 13954 (POM), 14597 (POM); Mill Creek, Wolf 2472 (DS,POM); Mill Creek, Hall 13030 seed grown at Baltimore, as “Hall 30,” specimen is Munz 13411 (POM), at Claremont, Munz 13926 (POM), 13969 (POM), 14180 (GH,POM); Fredalba, San Bernardino Mts., Abrams 2787 (DS,GH,NY,POM) toward ssp. angustifolia; Victorville, Parish 10593 (DS,UC); Oak Glen, Munz 13257 (POM). Riverside Co.: Camp Tahquitz, L. Crutcher 13 (POM); 5 miles southeast of Poppet Flat, San Jacinto Mts., Munz & Johnston 8823 (POM). Orange Co.: San Juan Creek, mile below Capistrano, Munz 15569 (GH,POM) toward ssp. eu-Hookeri; Los Alamitos, J. J. Condit in 1908 (UC). San Diego Co.: 1 mile north of San Onofre, Munz 15568 (BH,POM) toward eu-Hookeri; Del Mar, Brandegee in 1894 (UC); San Mateo River, near ocean, I. L. Wiggins 2977 (DS,UC); Mission Valley, Brandegee in 1902 (UC); near San Diego, Mary F. Spencer 113 (NY); near Murray Dam, F. F. Gander A73 (BH); Lakeside, Abrams 3761 in part (DS,NY); Mataguey Creek, Volcan Mts., Munz seed, cult. by Cleland as “Mataguay,” Munz 13462 (POM), cultivated at Claremont, Munz 13957 (POM), 14178 (GH,NY,POM); Palomar Mt., H. P. Chandler 5423 (NY); Jacumba, Munz in 1917 (CU); Buckmans, D. Cleveland in 1884 (RSA); Julian, Hall 13021, seed sent to Cleland, grown at Baltimore as “Hall 21,” Munz 13412 (POM), at Claremont, Munz 13968 (POM), 13977 (NY,POM), 14097 (POM); Vallecitos Creek Canyon, Wiggins 2846 (DS,CAS,UC); Tia Juana River, A. C. Herre in 1902 (DS).

BAJA CALIFORNIA: 15 miles northeast of Ojos Negros on road to Neji Rancho, Wiggins & Gillespie 4111 (CAS,DS,GH,NY,POM,RSA) toward ssp. grisea; La Fresa, trail Vallecitos to Valle Trinidad, Sierra San Pedro Martir, Wiggins 9082 (DS).

As can be seen from going through the above citations, there is intergradation with ssp. angustifolia in the mountains, plants at 4000 ft. or higher tending to be simple and with more red in the calyx; also with eu-Hookeri along the San Diego County coast where plants become heavy-stemmed and sepals muricate and green. Then some plants are intermediate with ssp. grisea in pubescence, so that it is obvious that while venusta in well developed plants is quite a distinct thing, like all these other subspecies in Oe. Hookeri, it apparently exchanges genes freely where it comes in contact with the others.

A number of forms of this subspecies has been studied by Cleland: “Dalton,” “Devil’s Gate,” “Hall 21” and “Hall 30” and “Heusi” were reported by him in Proc. Am. Philos. Soc. 75:339-429, 1935. He found slight differences between the strains, such as in width of leaves, pigmentation of stems and bracts, amounts of pubescence. He got some segregation in the first generation, but was soon able to get plants that came true. For “Dalton” he found 7 pairs of chromosomes, for “Devil’s Gate” 7 pairs in 8 plants examined and circle 4 and 5 pairs in another. “Hall 21” gave 7 pairs in 5 plants, and circle 4 and 5 pairs in a sixth; “Hall 30” had circle 4 and 5 pairs in 2 plants and 7 pairs in a third. “Heusi” showed 2 plants with 2 circles of 4 plus 3 pairs, and 1 plant with one circle 4 and 5 pairs. He reported in considerable detail the results of crossing these various races with each other and with others which I refer to subspecies eu-Hookeri, montereyensis, and angustifolia. He concluded that for the most part there are in California euoenotheras two segmental arrangements which he calls haplo-Hookeri (found in “Hookeri de Vries,” “franciscana de Vries,” and alpha “Hall 30”) and haplo-Dalton (occurring in “Dalton,” “Devil’s Gate,” “Johansen,” “Hall 21,” “Mateo,” beta “Hall 30,” alpha “Heusi,” “Mono”). Thus it will be seen that mostly the plants referred to ssp. venusta differ from
**Oenothera Hookeri** by one segmental interchange. In addition to the races reported by Cleland above, I have had information from him concerning "venusta," with 7 pairs in 3 plants, and "Matagway," with 7 ordinary pairs and 1 extra diminutive pair in 3 plants, and circle 6, 4 ordinary pairs and 1 extra diminutive pair in the 4th plant.


**PLATE III.** FIG. A-G; **MAP I.**

Apparently about 1 m. high, branching from base and above, rather grayish pubescent throughout, with: (1) long divergent hairs, some of which are red-papilllose at base, (2) short finer, dense, and usually appressed hairs, and (3) in upper parts some gland-tipped hairs; stems usually somewhat reddish especially in upper parts, but not intensely so, rather slender, and scarcely if at all angled above; rosette-leaves elliptic-oblongolate, rather flat, not crinkled, with greenish veins, obtuse to acute at apex, sublanceolate to subulate-tornate on margins, appressed-pubescent on both surfaces and margins, with some longer hairs on veins beneath, the blades 5-15 cm. long, 2.5-5 cm. wide; petioles 2-10 cm. long; cauline leaves usually not crowded, lanceolate to lance-oblong, soft-pubescent, with marginal hairs usually appressed, subpubescent to subulate-tornate; acipatic acute, mostly with 10 principal veins on each side of midrib, quite plane, ascending to spreading-reflexed, 1.8-18 cm. long, 0.8-2.0 cm. wide; inflorescence 5-30 cm. long; bracts shorter than buds, hairy, spreading, the lower broadly, the upper narrowly lanceolate; hypanthium green or reddish, 3.5-5 cm. long; pилоe and some shorter gland-tipped hairs; sepals green, sometimes redder in age, not or slightly muricate, pilose and glandular-pubescent, 2.5-3.5 cm. long, the tips 2-4 mm. long; petals pale yellow, mostly orange in age, 3.5-3.5 cm. long, with broad tooth in apical sinus; anthers 11-12 mm. long; style at least as long as the petals, stigma-tubes yellowish green, 3-4 mm. long; capsule 2.5-5 cm. long, 5-4 mm. wide, with fine numerous appressed hairs, and longer divergent ones, sometimes muricate, the valve-tips slender, somewhat emarginate; seeds about 1.5 mm. long.

Type locality, near Boise, Idaho, the type collection made at 2880 ft. elevation, on June 18, 1910, J. F. Macbride 262 (NY, GH in part). The subspecies is mostly rather local in Idaho and southeastern Washington and is taxonomically a weak entity. It is near *sp. venusta* in its method of branching and in sepal characters, but is of distinctly lower stature and more northern range. It resembles *sp. ariziosa* in its low stature and pubescence of sepals, but the sepals are greener and less glandular, the plant is more branched, the leaves less crinkled and the flowers are supposed to be less red in age. Without genetic evidence, since I have no reports on this plant, it seems possibly to show influence of *O. ariziosa*, in the range of which species it occurs.

"Oe. Hookeri var. ornata" (A. Nelson) Muns, stat. nov.
eu-Hookeri by one segmental interchange. In addition to the races reported by Cleland above, I have had information from him concerning “venusta,” with 7 pairs in 5 plants, and “Mataguay,” with 7 ordinary pairs and 1 extra diminutive pair in 3 plants, and circle 6, 4 ordinary pairs and 1 extra diminutive pair in the 4th plant.

1(f). Oenothera Hookeri Torr. & Gray subsp. ornata*  
(A. Nels.) Munz, stat. nov.


PLATE III, FIGS. A-C; MAP 1.

Apparently about 1 m. high, branching from base and above, rather grayish pubescent throughout, with: (1) long divergent hairs, some of which are red-papillose at base, (2) short finer, dense, and usually appressed hairs, and (3) in upper parts some gland-tipped hairs; stems usually somewhat reddish especially in upper parts, but not intensely so, rather slender, and scarcely if at all angled above; rosette-leaves elliptic-oblancoolate, rather flat, not crinkled, with greenish veins, obtuse to acute at apex, subentire to sinuate-serrulate on margins, appressed-pubescent on both surfaces and margins, with some longer hairs on veins beneath, the blades 5-15 cm. long, 2.5-5 cm. wide, petioles 2-10 cm. long; cauline leaves usually not crowded, lanceolate to lance-oblong, soft-pubescent, with marginal hairs usually appressed, subentire to sinuate-denticulate, apically acute, mostly with 10 principal veins on each side of midrib, quite plane, ascending to spreading-reflexed, 4-8 (10) cm. long, 0.8-2 cm. wide; inflorescence 5-30 cm. long; bracts shorter than buds, hairy, spreading, the lower broadly, the upper narrowly lanceolate; hypanthium green or reddish, 3-3.5 cm. long, pilose and with some shorter gland-tipped hairs; sepals greenish, sometimes redder in age, not or slightly muricate, pilose and glandular-pubescent, 2.5-3.3 cm. long, the tips 2.5-4 mm. long; petals pale yellow, mostly orange in age, 3-3.5 cm. long, with broad tooth in apical sinus; anthers 11-12 mm. long; style at least as long as the petals, stigma-lobes yellowish green, 3-4 mm. long; capsule 2-3.5 cm. long, 3-4 mm. wide, with fine numerous appressed hairs, and longer divergent ones, sometimes muricate, the valve-tips slender, somewhat emarginate; seeds about 1.3 mm. long.

Type locality, near Boise, Idaho, the type collection made at 2880 ft. elevation, on June 18, 1910, F. Macbride 262 (NY,GH in part). The subspecies is mostly rather local in Idaho and southeastern Washington and is taxonomically a weak entity. It is near ssp. venusta in its method of branching and in sepal characters, but is of distinctly lower stature and more northern range. It resembles ssp. angustifolia in its low stature and pubescence of sepals, but the sepals are greener and less glandular, the plant is more branched, the leaves less crinkled and the flowers are supposed to be less red in age. Without genetic evidence, since I have no reports on this plant, it seems possibly to show influence of Oe. strigosus, in the range of which species it occurs.

*Oe. Hookeri var. ornata (A.Nels.) Munz, stat. nov.
Material seen, WASHINGTON: Whitman Co.: 1 mile west of Wawaiwai, D. D. Keck 385 (POM,UC); Almota, St. John, English, Jones and Palmer 9261 (UC). Garfield Co.: Ilia, St. John et al. 9237 (UC). IDAHO: Idaho Co.: White Bird Bridge, Range 1 East, Twsp. 28 North, R. J. Davis 3220 (POM). Valley Co.: South Fork Salmon River, Range 7 East, Twsp. 21 North, Davis 2637 (BH). Boise Co.: Sweet, A. Nelson & J. F. Macbride 1631 (BH,GH,NY,UC); Arrow Rock Dam, Range 4 East, Twsp. 3 North, Davis 4079 (POM); Arrowrock Reservoir 7 miles above Boise, Munz 14546 (BH,GH,NY,POM), cult. at Claremont, Munz 14702 (GH,NY,POM), 15273 (BH); Boise Basin, A. Isabel Mulford in 1892 (GH,NY); Boise, June Clark 292 (GH). Owyhee Co.: Sinker Creek, Range 1 West, Twsp. 3 South, Davis 2075 (POM). Elmore Co.: 10 miles west of Atlanta, Boise River road, C. L. Hitchcock & C. V. Muhlick 10077 (BH, CAS); 10 miles east of Featherville, Hitchcock & Muhlick 10411 (BH,CAS).

The only collection of ssp. ornata for which I have cytological information is my 14546, for which Dr. Cleland reports either circle 4 and 5 pairs, or 7 pairs.

l(g). Oenothera Hookeri subsp. angustifolia (Gates) Munz, grad. nov.
Oe. Hookeri var. semiglabra Gates, l.c.; based on a collection by J. G. Lemmon in 1875. There is one such at Gray Herbarium referable to angustifolia, but may not be the type coll. Description supports present disposition.


PLATE II, FIGS. A-B, MAP I.

Plants mostly 3-10 dm. high, the stems tending to be erect to ascending, simple or few-branched from below, reddish, muricate and with some longer spreading hairs, as well as others shorter fine, whitish, appressed, and in upper parts with short, spreading gland-tipped ones; rosette-leaves plane, ob lanceolate, green-veined, sinuate-serrulate, green and usually rather coarsely strigose on both surfaces, with marginal hairs pointing toward apex, blades 10-15 cm. long, 1.5-4 cm. wide, obtuse to acute at apex, narrowed gradually at base into petioles almost as long; cauline leaves gradually reduced up the stem, lanceolate, mostly plane, sometimes crinkled, sinuate-serrulate with color and pubescence of basal leaves, sometimes quite pilose on veins of under surface, mostly acute at apex, the lower leaves gradually narrowed into short petioles, the upper quite sessile, leaf-blades mostly 5-10 cm. long, 0.7-1.5 cm. wide, usually with 10-12 main veins on each side of midrib; inflorescence simple or branched, 1-6 dm. long, with some long spreading hairs papillose at base, some finer appressed hairs, and some finer gland-tipped ones; bracts lance-linear, tending to surpass buds in young inflorescence, mostly 2-3 (4.5) cm. long, spreading in fruit, usually green, the first tending to be crinkled; hypanthium usually red, 2.5-4.5 cm. long, with numerous fine gland-tipped hairs and some spreading; sepals usually red, 2.5-3.5 cm. long, usually with all 3 types of hairs, but not densely pubescent or much papillate, sepal-tips mostly 3-5 mm. long; petals 2-4 cm. long, sometimes wider, sometimes narrower than long, pale yellow,
reddish in age; anthers 8-12 mm. long; style usually exceeding petals; stigmas lobes greenish yellow, 3-8 mm. long; capsule 2-3.5 cm. long, 3.5-5 mm. thick near base, usually with red stripes, with all 3 types of hairs, the valve-tips truncate or slightly emarginate; seeds 1-1.5 mm. long.

Type locality, Asphalt, Utah Co., Utah, the type collection M. E. Jones 5624 (DS, NY, POM, UC). This subspecies ranges in the mountains largely about the Great Basin, namely from southeastern Oregon and eastern California, through Nevada, Utah, and Colorado. With so wide a range, it is variable, especially as to pubescence and as to color of sepals, but on the whole maintains a characteristic habit of growth with low stature and simple stems, as well as plane leaves and tendency to rather reddish hypanthium and sepals. The latter are very little papillose and evidently glandular-pubescent, with the longer hairs few and sometimes almost lacking. The stems, however, are muricate. It is mostly found at considerable elevation, from about 5000 to over 10,000 ft. It intergrades with subspecies Hewettii, venusta, and hirsutissima as can be seen in the citation of specimens in the next paragraph.

Material studied, OREGON: Lake Co.: west side of Crump Lake, Applegate 7630 (DS); Hot Springs, 2 miles north of Lakeview, M. E. Peck 15554 (DS,WTU), with green sepals and toward ssp. Wolfsii. Klamath Co.: east side of Klamath Lake, Williamson River, Munz 14415 (GH,POM), cult. at Claremont, Munz 14701 (POM); near mouth of Williamson River, J. B. Leiberg 709 (UC), Applegate 5923 (DS); Williamson River bridge, Applegate 3673 (UC). Harney Co.: Wild Horse Canyon, Steen Mts., Peck 19121 (WTU). Wallowa Co.: 5 miles above Imnaha, Peck 17511 (DS). IDAHO: Blaine Co.: Corral, Camas Prairie, Macbride & Payson 3811 (DS,GH,NY,POM,UC), Munz 14551 (BH,GH,POM), grown from 14551, Munz 14700 (GH,POM). Owyhee Co.: Twilight Gulch, 8 miles west of Silver City, J. F. Macbride 473, type of Macbrideae (DS,GH,NY,UC), Munz 14540 (GH,NY,POM). Elmore Co.: Queens River, Boise Nat. Forest, F. MacFadden 25262 (CAS). NEVADA: Washoe Co.: Mogul, Truckee R., B. O. Moore & G. E. Franklin 914 (POM); cult. at Claremont from seeds from Reno sent by Lehenbauer, Munz 13923, 13972, 14000, 14088 (all at POM). Humboldt Co.: Rebel Creek, Santa Rosa Mts., P. Train 1269 (POM); Humboldt Canyon, W. Humboldt Mts., Heller 10616 (CAS,DS,GH,NY). Elko Co.: Rowland, Nelson & Macbride 2150 (BH,GH,POM); 8 miles east of Mountain City, N. E. Nichols & L. Lund 384 (POM); Sherman Creek, south end of Rugby Range, Hitchcock & Martin 5695 (POM); Mitchell Creek, south of Harrison Pass, P. Train in 1936 (POM); 1 mile north of Lamoille, B. Maguire & A. H. Holmgren 22043 (BH); 5 miles south of Lamoille Canyon, Nichols & Lund 374 (DS,NY,POM). Lander Co.: 10 miles east of Austin, Munz 16325 (POM); 27 miles south of Battle Mt., F. S. Goodner & W. H. Henning 1030 (NY,NPOM); mouth of Smith Creek Canyon, 41 miles west of Austin, Goodner & Henning 660 (POM). Eureka Co.: Diamond Valley, S. Watson 406 (GH, NY). White Pine Co.: 0.25 mile west of Ely, J. Heinrichs 463 (POM). Ormsby Co.: Eagle Valley, C. F. Baker 1258 (CAS,GH,NY,POM,UC); 3 miles north of Carson City, C. L. Hitchcock & J. S. Martin 5464 (DS,POM,UC); 17 miles west of Carson City, Heinrichs 485 (POM). Storey Co.: 5 miles south of Virginia City, R. A. Allen 497 (POM); 5 miles southwest of Clarks, east of Reno, R. W. Saarni 205 (UC) toward Hewettii in pubescence. Lyon Co.: Wadsworth, I. Tidestrom 10695 (POM), 10717 (BH). Churchill Co.: near East Gate, R. A. Allen 326 (POM); 2.5 miles north of Fallon, Allen 262 (DS,NY,POM) toward Hewettii; Fallon, Tidestrom 10765 (POM). Mineral Co.: 4 miles above mouth of Cory Creek, Wassuk Range, W. A. Archer 6884
Esmeralda Co.: near Carson City, C. L. Anderson 91 (GH), 294 (GH); Chiatovitch Creek, 2 miles west of Kellogg Ranch, Archer 7187 (POM); Fish Lake Valley, R. S. Ferris 6664 (DS). Nye Co.: Cottonwood Creek, 39 miles southwest of Austin, Goodner & Henning 849 (POM); 37 miles southwest of Austin, Goodner & Henning 864 (POM); Round Mt., J. F. Phares in 1915 (DS). Lincoln Co.: Pioche, Maud Minthorn 115 (UC) toward hirsutissima. Clark Co.: Cold Creek, I. W. Clokey 8039 (BH,DS,GH,POM,RSA); Cold Spring Creek, P. Train 1982 (DS,POM); Harris Springs. Charleston Mts., I. La Rivers & N. F. Hancock 565 (POM). CALIFORNIA: Siskiyou Co.: Mt. Shasta, E. Palmer 2520 (UC); Castella, E. E. Smith in 1913 (CAS); Sisson, Eastwood 1300 (GH, NY), Setchell & Dobie in 1902 (UC); Castle Lake Road near Mt. Shasta City, W. B. Cooke 15325 (DS, GH, NY, POM) toward Wolffi. Trinity Co.: 10 miles east of Douglas City, Hitchcock & Martin 5313 (DS, POM, UC). Modoc Co.: Davis Creek, Lura Black 58 (DS), Mrs. R. M. Austin 163 (POM, UC); Ft. Bidwell, Mary Manning 209 (DS, UC); Jess Valley, Warner Mts., F. H. Frost 111 (POM); Big Valley, M. S. Baker in 1893 (NY, UC); Goose Lake, Mrs. Austin & Mrs. Bruce 2254 (UC); Shasta Co.: Morgans Springs, Lassen Butte region, Eastwood 1814 (CAS). Plumas Co.: Genesee Valley, Heller & Kennedy 8861 (DS, GH, NY, POM); Big Meadows, Mrs. Austin 445 (UC). Sierra Co., J. G. Lemmon in 1875, no. 1021 (GH), Amador Co.: Cook's (Wylie) Station, K. Brandegee in 1918 (UC). Mono Co.: Lundy, Maud Minthorn in 1908 (UC); Leevining, Laura Lorraine in 1938 (DS), Hitchcock & Martin 5469 (DS, POM, UC); 4 miles east of Tioga Pass, Hitchcock & Martin 5469 (POM); "Mono" grown from seed sent from Chris Flat, w. Walker River by Johansen, Munz 13465 (POM), 14186 (GH, POM); Mono Lake P. O., J. Price in 1927 (DS); Topaz Lake, A. S. Crafts 430 (POM); Fales Hot Springs, Alice Ottley 1040 (CU); west fork of Owens River, Round Valley, R. S. Ferris 1414 (DS); Mammoth Lakes, M. S. Baker 9099 (CAS). Eldorado Co.: Placerville, K. Brandegee in 1914 (UC), capsule very short. Mariposa Co.: Yosemite Valley, Coville & Funston 1850 (DS, NY); Abrams 4634 (DS, GH, NY, POM), P. B. Kennedy in 1913 (UC). H. M. Hall 9029 (GH, UC). Fresno Co.: South Fork of Kings River, Munz 15931 (BH, CAS, POM); Bubbs Creek, J. T. Howell 16112 (CAS). Tulare Co.: Nine-mile Creek, Culbertson under C. F. Baker 4555 (GH, POM); Camp Alla, Tule-Little Kern Divide, W. R. Dudley 884 (DS). Kern Co.: Ft. Tejon, Xantus de Vesey 27 (GH, NY). Inyo Co.: Deep Creek Ranch, Tidestrom 9915 (GH); Tom's Place, Rock Creek, F. Klyver 216 (DS); Andrews Camp, Bishop Creek, K. Brandegee in 1913 (UC). Cottonwood Canyon, Death Valley region, M. F. Gilman 4295 (POM) toward Hewettii. Ventura Co.: Griffins, A. D. Elmer 3819 (DS, GH, NY, POM). San Bernardino Co.: Big Meadows, San Bernardino Mts., Munz & Johnston 8642 (POM); Green Valley, north base of Sugarloaf Mt., Munz 10764 (POM); Bear Valley, S. B. & W. F. Parish 1668 (DS); Little Bear Valley (now Arrowhead), Parish 1618 (GH) toward venusta. Riverside Co.: Round Valley, San Jacinto Mts., Mary F. Spencer 2201 (GH), sepals very papillose; Strawberry Valley, Hall 2639 (UC) near venusta. UTAH: Salt Lake Co.: Little Cottonwood Canyon, M. E. Jones in 1900 (POM). Uintah Co.: Ashley Creek at 6000 ft., E. H. Graham 7370 (POM); Dinosaur National Monument, near Jensen, Munz 15016 (POM), cult. at Claremont, Munz 15314 (BH, POM). Wasatch Co.: Midway, E. C. Carleton & A. O. Garrett 6704 (NY). Utah Co.: Aspen Grove, Garrett 3371 (NY); 3 miles west of Strawberry Summit, D. D. Keck 780 (DS, GH, POM, UC). Sevier Co.: Mill Hollow, W. P. Cottam 9679 (RSA). Piute Co.: Sevier River below Marysville, Rydberg & Carleton 6968 (NY). Garfield Co.: Panguitche Lake, M. E. Jones 6002s (POM). Kane Co.: mile north of Glendale, Munz 15010 (BH, GH, POM). San Juan Co.: Monticello, Rydberg & Garrett 9169 (NY); south side of Abajo Mts., Rydberg & Garrett 9237 (NY). Washington Co.: Pine Valley, F. W. Gould 1945 (CAS, GH, POM). COLORADO: Fremont Co.: Canyon

Dr. Cleland found “Mono” (Proc. Am. Philos. Soc. 75: 339-429, 1935) which he grew from seed from Mono Co., California, variable in the first generation with “respect to presence or absence of central shoot, leaf breadth, cone color and fruit size” and with two plants having circle 4 and 5 pairs, and two others with 7 pairs of chromosomes. One of these last had a small extra pair and one “a set of 8 extra half-sized chromosomes.” Selecting a strain with paired chromosomes he found that “Mono” differed from *eu-Hookeri* by one segmental interchange and agreed with “Mateo” and various forms I refer to *venusta*. Other races of *angustifolia* which he studied are: “Silverton,” my 13014; “Gunnison,” my 13018; “Salida 1,” my 13019; “Salida 2,” my 13021; and “Ouray,” my 13015. All of these are from Colorado. For “Silverton” he writes in an unpublished report “nearest Mono phenotypically, but less colored and more delicate”; 4 plants showed 7 pairs of chromosomes. “Gunnison” he finds near to “Mono” and to “Salida 1” and “Salida 2”; one plant showed circle 4 and 5 pairs, another circle 6 and 4 pairs, and two had 2 circles 4 and 3 pairs, but he could observe no correlation between phenotypic and cytological features. “Salida 1” and “Salida 2” were very near to “Gunnison” in appearance; the first had 3 plants with circle 4 and 5 pairs, and one with 2 circles 4 and 3 pairs; the second in the single plant examined showed circle 4 and 5 pairs. “Ouray” had circle 4, circle 6, and 2 pairs. On the whole, then, these plants from the mountains bordering the Great Basin tend to deviate from *eu-Hookeri* by more than one segmental interchange.


**Plate IV, Figs. D-H; Map I.**

Plants 1-2.5 m. tall, erect, freely branched, rather loosely appressed-pubescent throughout with fine white hairs and with occasional longer coarser and sometimes more spreading ones; stems usually reddish, sometimes deeply so,

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*Oe. Hookeri* var. *grisea* (Bartlett) Munz, comb. nov.
scarcely if at all muricate; rosette-leaves lanceolate to oblanceolate, sinuate-serrulate, white- or red-veined, somewhat pilose on veins of underside in addition to usual appressed hairs, blades 10-20 cm. long, 2-4.5 cm. wide, often crinkled, acute to obtusish at apex, basally gradually narrowed into petioles 5-12 cm. long; cauline leaves lanceolate, rather dense, subsessile or very short-petioled, pubescent on both surfaces, somewhat pilose on veins beneath, often with marginal pubescence perpendicular to edge, almost plane to somewhat crinkled, with about 10 main veins on each side of midrib, acute to rounded at base, mostly 5-15 cm. long, 0.8-2.5 cm. wide, commonly with small fascicles in the axils; inflorescence commonly branched, up to 6 dm. long, many-flowered, grayish-pubescent on stems, bracts, ovaries, hypanthia and sepals; bracts at apex of young inflorescence flaring widely, older ones narrowly to broadly lanceolate, mostly 1-4 cm. long, spreading and with somewhat recurved tips; hypanthium 2.5-4.2 cm. long, green to reddish under the dense pubescence; sepals 2-4.5 cm. long, not papillose or glandular, green or with faint reddish bands under the pubescence, the sepal-tips 3-6 mm. long; petals pale yellow, mostly orange in age, 2.5-4.5 cm. long; anthers 13-15 mm. long; style usually about the length of the petals; stigma-lobes spreading, greenish yellow, 3-7 mm. long; capsules 2.5-4 cm. long, 4-5 mm. thick, the valves truncate to emarginate, sometimes with faint red bands; seeds 1.3-1.6 mm. long.

Type locality, Riverside, Riverside County, California, the plant grown by Bartlett from seed sent by F. M. Reed. This subspecies is a plant of low elevations in the coastal drainage of southern California and northern Baja California, where it grows in the same region with ssp. venusta, but seems not actually to be with it and to show little or no intergradation or crossing. The two are much the same in their height and free branching, but very unlike in pubescence and papillae. In these respects grisea is near to ssp. Hewettii (irrigua) of New Mexico and adjacent states, but is much taller, has longer less twisted bracts in the inflorescence, as well as larger seeds.

Material studied, CALIFORNIA: Ventura Co.: Ojai Valley, H. M. Pollard in 1944 (CAS) near this. Los Angeles Co.: Lone Pine Canyon, San Gabriel Mts., L. R. Abrams & E. A. McGregor 687 (DS,GH,NY); Live Oak Canyon above Claremont, D. L. Crawford in 1915 (POM); San Bernardino Co.: San Bernardino, S. B. & W. F. Parish 106 (DS,POM,UC), S. B. Parish 4201 (GH,UC). 6489 (DS); 2 miles south San Bernardino, Munz 13239 (GH,POM); Riverside Co.: river bottom at foot of Mt. Rubidoux, Riverside, Munz 13238 (POM), cult. at Claremont, Munz 13956, 14009, 14179 (all at POM); Santa Ana River, Ontario-Corona road, Munz & Johnston 11276 (POM), cult. at Claremont, Munz 13145 (POM), Orange Co.: east of Huntington Beach, L. M. Booth 1190 (POM); 5 miles south of Garden Grove, Munz 14171 (GH,POM), 14171a (GH,POM), 14173 (POM); 6 miles south of Garden Grove, Munz 14176 (BH,GH,POM); Rancho Santa Ana, J. T. Howell 1205 (RSA); San Diego Co.: Lakeside, Abrams 3761 (POM), specimen at NY is venusta; Flynn Springs, F. Youngberg 14 (POM), cult. at Claremont, Munz 13998, 13469, 14030, 14060 (all at POM); Warners Hot Springs, Miss Buttle in 1913 (CAS); Alpine P. O., E. A. Mearns 3944 (DS,NY); Granite, M. F. Spencer 113 (UC); Jamacha Rancho, Sweetwater Valley, G. C. Deane in 1888 (GH); San Diego, Cleveland in 1874 (GH); Otay, I. L. Wiggins 3268 (DS).

BAJA CALIFORNIA: Tecate Valley, Mearns 3768 (DS,NY), Mearns & Schoenfeldt...
Dr. Cleland has sent me unpublished information about three collections of *grisea*: his “Grisea 1,” my 13239; “Grisea 2,” my 13258; and “Flynn Springs,” Youngberg seed. These are from San Bernardino, Riverside, and San Diego counties respectively. He grew also as “Santa Ana,” Munz and Johnston 11276, but I have no report on it. For “Grisea 1” he says, “Differs from ‘Grisea 2’ in stem color, midrib color and broader, yellower less crinkled foliage. Is similar to ‘Santa Ana,’ which has the yellowish foliage of ‘Grisea 1,’ but the narrower more crinkled leaves and the green stem of ‘Grisea 2’; chromosome configuration (1 pl.) circle 4 and 5 pairs; (2 pls.) 7 pairs.” “Grisea 2” had the same configuration. “Flynn Springs” resembled “Santa Ana” in “hairiness and buds, also in character of floral tips, velvetyness of foliage and lateness (in season) of flowering”; its chromosome picture for 3 plants was circle 4 and 5 pairs.

Thus, as in all other subspecies of *Oenothera Hookeri*, there are many races differing from each other in minor regards.

1 (i). *Oenothera Hookeri subsp. Hewettii* Cockerell,

*Oe. Hewettii* Cockerell, op. cit., 204.


*Oe. Hookeri* var. *irrigua* Gates, l.c.

**Plate IV, Figs. A-C; Map I.**

Plant 1-2 m. tall, grayish-strigose throughout with additional longer appressed to somewhat spreading hairs which may be somewhat red-papilllose at base, no hairs gland-tipped; stems mostly freely branched, usually somewhat reddish; rosette-leaves plane or slightly crinkled along midrib, scattered-strigose on both surfaces, the veins little or not colored, blades mostly ob-lanceolate, sinuate-denticulate with marginal hairs mostly adpressed, acute to obtuse at apex, 10-20 cm. long, 2.5 cm. wide, gradually narrowed at base into winged petioles up to 12 cm. long; cauline leaves gradually reduced up the stem, mostly elliptic-lanceolate, generally crinkled on margins, with 10-12 main veins on each side of midrib, subentire to sinuate-serrulate, grayish-strigose, with marginal hairs pointing forward, acute to subacuminate at apex, acute to rounded at base, mostly 5-12 cm. long, 1-1.5 (2) cm. wide; inflorescence up to 5 or 6 dm. long, ashy, many- and dense-flowered; young bracts mostly shorter than the buds, with recurved tips, older spreading-recurved, usually wavy and twisted, grayish, crinkled, sometimes pinkish, mostly lance-linear, 1.5-3 cm. long; hypanthium green or red, 3-4.5 cm. long; sepals 2.5-4 cm. long, green to red, scarcely or not papillose, the tips 3-6 mm. long; petals 2-4 cm. long, about as wide, aging red; anthers 10-15 mm. long; stigma-lobes yellowish, 4-7 mm. long; capsule 2.5-4 cm. long, 4.5 mm. thick, often with reddish bands; seeds about 1 mm. long.
Plate IV.

Oc. Hookeri ssp. Hewettii. Fig. A, inflorescence, x \( \frac{1}{2} \). Fig. B, seeds, x 5. Fig. C, appressed hairs, x 5.

Oc. Hookeri ssp. grisea. Fig. D, inflorescence, x \( \frac{1}{2} \). Fig. E, seeds, x 5. Fig. F, capsule, x 1. Fig. G, cauline leaf; Fig. H, rosette-leaf, x \( \frac{1}{2} \).
Type locality, Abbott Ranch, Rito de los Frijoles, Santa Fe Co., New Mexico, collected by Cockerell in 1912 (type at University of Colorado). Ranging from Nevada and southern Utah to Texas and Chihuahua, Hewettii intergrades with other subspecies as has been pointed out in discussing them. It is also questionably distinct from Oe. elata of central Mexico. In New Mexico particularly, its range overlaps that of sp. hirsutissima, but for the most part it is found in the river valleys rather than in the mountains, hence in a different life-zone.


Dr. R. E. Cleland has sent me cytological data on a number of the plants referred here. His “Durango,” my 13013, showed circle 4 and 5 pairs. His “Sandoval” is my 13282; of it he writes: “This culture was very similar to Las
Cruces, but less strikingly pigmented in stem, buds and fruits, and showed more variation, which, however, was less well defined. No distinct classes were present, a condition reflected in the presence of a variety of chromosome configurations. He found 2 plants with 7 pairs; one with circle 6 and 4 pairs; one
doubtfully with 2 circles 4 and 3 pairs; and 2 with circle 6, circle 4, and 2 pairs. His "Cimarron" was my 18278 and had 7 pairs. His "Las Cruces" was my 18270 and gave two distinct classes: the larger not hirsute on stems, bracts more flaring, less red pigmentation; the smaller hirsute, bracts more erect, more red pigmentation. He could find no cytological correlation with this phenotypic appearance; chromosome configurations ran as follows: 3 plants with circle 6 and 4 pairs, one with circle 6, circle 4 and 2 pairs. Thus, for these collections, chromosome configurations are quite intermediate between the mostly 7 pairs of California plants and the large circles from farther east. That does not mean, however, that these Hewettii or irrigua plants stand out clearly from Hookeri in appearance. Many individuals are difficult to separate from hirsutissima, for example, being quite intermediate in pubescence. Cleland (Genetics 25: 639, 1940) wrote "when the irriguas are crossed with the hookeris, hybrids with intermediate configurations predominate, such as circle 8, or a circle 4 and circle 6. Since intermediate configurations such as these represent minimum differences between the complexes of, in most cases, two or three interchanges, the genoms of the irriguas give evidence of fairly close relationship both to the genoms of the hookeris and to those with which they are normally associated. In short, the irriguas have a variety of segmental arrangements which differ in moderate degree from each other and at the same time also differ in moderate degree from the hookeri arrangements."

2. **Oenothera elata** H.B.K.

*Oe. elata* H.B.K., Nov. Gen. et Sp. 6: 90, 1823.


*Oe. crassipes* Hort. Berol. ex Spach, l.c., pro synon.


*Oe. corymbosa* Sims in Curtis Bot. Mag. 45: t. 1974, 1818, not Lamarck, 1797.

*Oe. Simsiana* Séringe in DC. Prodr. 3: 47, 1828.


*Onagra spectabilis* Spach, l.c.

**Plate V; Map II.**

Plants 6-15 dm. tall, erect, freely branched throughout, the stems usually more or less red, especially above, strongly angled, white-strigulose and with scattered longer more spreading hairs which may have basal red papillae; rosette-leaves narrowly lanceolate to oblanceolate, strigulose on both surfaces, with adpressed hairs on the margins, plane, shallowly sinuate-serrulate, acute to obtuse at apex, the blades 6-20 cm. long, 1-3 cm. wide, gradually narrowed at base into flat petioles 3-12 cm. long; cauline leaves oblong- to elliptic-lanceolate, rather plane, 5-12 cm. long, 1.2-3 cm. wide, mostly with 8 principal veins on each side of midrib, subglabrous to strigulose (especially on veins), with short appressed marginal hairs, leaves gradually reduced up the stem, the
Map II. Distribution of the subgenus *Euwothera* in Mexico. Based on Goode Base Map No. 112. Copyright 1920 by the University of Chicago. Used by permission of the University of Chicago Press.

- Oe. *Jamesii*
- Oe. *Hookeri* subsp. *hirsutissima*
+ Oe. *Jamesii*
- Oe. *elata*.
upper lance-ovate; inflorescence up to 6 dm. long, strigose and with longer divergent hairs some of which may be red-papillose at base, the axis strongly angled; bracts leafy, the lower lance-ovate, upper lanceolate, spreading with recurved tips, all crinkly-margined, soon shorter than buds; hypanthium mostly greenish, 3.5-4.5 cm. long, rather densely pubescent with shorter appressed and longer spreading non-glandular hairs; sepals mostly 2.5-3.5 cm. long, greenish, with pubescence of hypanthium, the tips 1-2 mm. long; petals obovate-rounded, 2.5-4 cm. long, as wide or more so, retuse, pale yellow, aging reddish; filaments about half the length of the petals; anthers 12-14 mm. long; style usually distinctly shorter than petals; stigma-lobes 5-7 mm. long, spreading, greenish yellow; capsule 2.5-4 cm. long, 5-7 mm. thick near base, strigulose and with longer somewhat appressed hairs, obtusely 4-angled, sometimes obscurely banded with red, the valves apically truncate; seeds 1.2-1.7 mm. long.

Type locality, "Crescit in Regno Mexicano"; the type collection, H.B.K. no. 4040, Mexico, Herbarium Paris. The species ranges through the highlands of central Mexico. It is questionably distinct from the Hookeri assemblage from farther north. It is characterized by its thick fruits, broad upper leaves and bracts, short sepal-tips and heavy buds, its short styles. In the garden in Claremont it failed to make rosettes, the axis elongating from seedling stages, but in its native habitat it does of course have rosettes. It intergrades most definitely with Oe. Hookeri through ssp. Hewettii (irrigua) especially in the plants referred to that subspecies in this paper coming from Coahuila and Texas. Munz 15039 and 15042 from near San Pedro, Coahuila resemble it in their short styles and sepal-tips, but have more slender capsules. Cory 9270 and 9631 from western Texas have broad bracts, but long style and long sepal-tips. Other intermediate specimens geographically are likewise difficult to place, but the typical elata seems to be definitely to the south. If the Hookeri assemblage is made to include these central Mexican plants, the name elata has priority over all others.

Material seen, Oe. Simsiana, Erlang 1834, Herb. Fischer, (GOET); Oe. salicifolia Desf. ex ipso. July 28, 1815, Prodr. Herb. (G). MEXICO: HIDALGO: Zimapán, Munz 15048 (BH,GH,POM), cult. at Claremont, Munz 15252 (BH,GH,NY,POM), 15309 (BH,POM). MEXICO: Toluca, seeds from plant in garden as Munz 15075, cult. at Claremont, Munz 15253 (BH,POM), 15308 (BH,POM). DISTRITO FEDERAL: City of Mexico, J. N. Rose & J. H. Painter 7217 (GH,NY); Bosque Chapultepec, Munz 15069 (GH,POM), cult. at Claremont, Munz 15256 (NY,POM), 15303 (POM); Puerto-aereo, Munz 15050 (BH,GH,NY,POM), cult. at Claremont, Munz 15254 (BH,GH,POM), 15307 (BH,POM); Vallée de Mexico, Bourgeau 564 (GH). PUEBLA: Texmelucán, Munz 15067 (BH,GH,NY,POM), cult. at Claremont, Munz 15255 (POM), 15304 (BH,IND,NY,POM); garden at Puebla, seed only, Munz 15076, cult. at Claremont, Munz 15259 (POM), 15305 (BH,POM), 15310 (BH,IND,POM); Acatzingo, Munz 15070 (BH,POM), cult. at Claremont, Munz 15242 (BH,POM), 15310 (BH,IND,POM); Acatzingo, Bro. Arsène 3585 (US), 1586 (US); 6 miles northwest of Cholula, Munz 15074 (BH,NY,POM), grown at Claremont, Munz 15240 (BH,POM), 15306 (BH,POM). GUANAJUATO: Guanajuato, cultivated, A. Dugès 302 (GH).

A rather fragmentary specimen from Guatemala: Volcán Santa Clara, Dept. Sololá, J. A. Steyermark 47089 (POM) seems to belong here, although its sepal
tips are rather long. Another from Huehuetenango, E. W. Nelson 3672 (US) also seems to come here, but more material from Guatemala is needed.

So far as Dr. Cleland has examined *elata*, it has had 7 pairs of chromosomes and thus shows a primitive condition similar to that of *Oe. Hookeri* ssp. *eu-Hookeri*.

3. × *Oenothera erythrosepala* Borb.

*Oenothera suaveolens* f. *erythrosepala* (Borb.) Jávorka, Mag. Flora, 748, 1924.

**Plate VI**

Biennial to short-lived perennial, erect, bushy, 8-12 dm. high; stems coarse, simple or more commonly branched throughout or only above, more or less reddish, rather densely crisp-puberulent and with numerous longer spreading hairs many of which are red-pustulate at their base; rosette well formed, the leaves broadly elliptic-oblancoelate, obtusish at apex, strongly crinkled and sometimes reddish along the midribs, crisp-pubescent on both surfaces, somewhat more coarsely so on veins of under surface, shallowly sinuate-serrulate and crinkled on margins, the blades 8-20 cm. long, mostly 3-5 cm. wide, sometimes almost lobed near base, gradually narrowed into petioles 5-10 cm. long; cauline leaves broadly lanceolate-oblong to ovate-oblong, crinkled, obtuse to acute at apex, with 8 principal veins on each side of midrib, subtrigose on both surfaces, the marginal hairs and those on veins beneath tending to be erect, the blades mostly 5-10 cm. long, 2.5-4 cm. wide, mostly rather abruptly narrowed into petioles 5-20 mm. long, the uppermost quite sessile; flowers mostly in dense simple spikes 1-4 dm. long, grouped in an open branched inflorescence with somewhat angled stems, with the dense pubescence of lower stems and also with gland-tipped hairs; bracts ovate to lance-oblong, spreading, crinkled, concave above, 1-3 (5) cm. long; hypanthium red to green, glandular-pubescent and pilose, 3.5-5 cm. long, 1-2 mm. thick; sepals usually reddish, glandular-puberulent and pilose, connate in 2's or 4's at anthesis, 3-4 cm. long, 4.5-5 mm. wide, the tips 5-8 mm. long, densely pilose and tending to spread in the bud; petals golden yellow, reddish-orange in age, broadly obovate, emarginate, 3.5-5 cm. long, usually somewhat wider; filaments slender, about one-third to one-half the length of the petals; anthers 10-12 mm. long; style somewhat shorter than petals; stigma-lobes yellowish green, 5-7 mm. long, slender; capsule green with red median bands, pilose and glandular-puberulent, somewhat muricate, 2-2.5 (3) cm. long, 5-6 mm. wide, the neck 2-3 mm. long; capsule valves truncate to slightly emarginate; seeds dark, 1.3-1.7 mm. long.

The plants treated here are generally called *Oenothera Lamarckiana* and became known under that name through the activities of de Vries. Unfortu-
nately be misused the name, since *Oenothera Lamarckiana* was originally applied in 1828 by Seringe as a new name for what Poiret had called *Oe. grandiflora* (Lamarck, Encycl. 4: 554, 1798). Poiret's *grandiflora* was not the same as Solander's of 1789, and Seringe renamed the species. At the present writing, Seringe's *Lamarckiana* seems to me to be a synonym of *Oe. suaveolens* Desf., 1804 and 1805. But the plants that de Vries made important through his researches are not the same as Seringe's and unfortunately must have a different name.

I am discussing *Oe. erythrosepala* here, not to give it rank as a species or because I consider it native to the western part of the United States, but it occurs frequently as a spontaneous plant along the coast from San Francisco northward and is easily confused with *Oenothera Hookeri*. Hence, to point out its existence as a wild plant and to distinguish it from that species, it is here included. Its origin and status have been much discussed and the general conclusion seems to be that it is a heterozygous plant with balanced lethals, so reproduces itself. B. M. Davis (Proc. Am. Philos. Soc. 65: 349-378, 1926 and 66: 319-355, 1927) discussed its history in some detail, calling it *Oenothera Lamarckiana* of de Vries, which is the name by which it has gone in genetical literature. Of the botanical names available, the earliest seems to be *erythrosepala* of Borbás. The plant seems different from the western large-flowered species of *Euoenothera* in its broad leaves, as shown by my key to species. From the eastern *Oe. grandiflora* and from *Oe. suaveolens*, both of which also have broad leaves, it differs by its heavily muricate stems, more crinkled leaves, somewhat longer petals (3.5-5 cm. as against 2.5-4 cm.), thicker capsules (5-6 mm. as opposed to 3.5-4.5 mm.), and by fewer main veins in the leaves (about 8 on each side of midrib instead of 10-12).


Oe. erythrosepala. Fig. A, rosette-leaf; Fig. B, cauline leaf, x ½. Fig. C, fruits, x 1. Fig. D, upper stem, x ½. Fig. E, four types of hair; spreading without and with basal papilae; appressed; and gland-tipped; all x 5.

For a discussion of the cytology and genetics of this plant see Cleland (Bot. Rev. 2: 316-348, 1936).

4. OENOTHERA JAMESII TORR. & GRAY.


PLATE VII; MAP III.

Plants winter annuals or biennials, simple and erect, or open- and few-branched from base and/or above, about 1.5 m. tall; stems coarse, often with some red, with fine close white appressed pubescence and scattering longer subappressed hairs, little or not muricate, usually quite strongly angled above; rosette apparently lax, the axis soon elongating, the leaves ascending, elliptic-lanceolate, sinuate-serrulate, appressed-pubescent on both surfaces and on margin, greenish-veined, quite plane, acute at apex, the blades 6-20 em. long, 2-4 cm. wide, narrowed rather abruptly into petioles 2-6 cm. long; cauline leaves not crowded, mostly broadly lanceolate, not crinkled, rather conspicuously sinuate-serrulate, acuminate at apex, appressed-pubescent on margin and both surfaces, spreading to somewhat deflexed, with about 10 principal green veins on each side of midrib, the blades 5-12 cm. long, 2-3.5 cm. wide, the lower acute at base and with petioles 1-2 cm. long, the upper more rounded and subsessile; inflorescence mostly 3-6 dm. long, simple or few-branched, often densely many-flowered, appressed-pubescent to subsericeous; bracts not exceeding buds, the lower lance-ovate, up to 5 cm. long, spreading, somewhat crinkled or plane, appressed-pubescent, persistent, the uppermost lanceolate, ca. 1 cm. long; hypanthium 6-11 cm. long, 1.5-2.5 mm. wide, sometimes reddish, short-pilose and glandular-puberulent; sepals 4-6 cm. long, green to somewhat reddish, strigose, the tips 3-6 mm. long, slender, connivent; petals 3.5-5 cm. long, about as wide, emarginate, light yellow, aging red; filaments about half as long as petals; anthers 18-22 mm. long; style equaling petals; stigma-lobes 5-7 mm. long; capsule 2.5 cm. long, obscurely 4-angled, 6-7.5 mm. thick, appressed-hairy with short fine and longer coarse hairs, the valve-tips narrow and slightly emarginate; seeds 1.5-2 mm. long.
PLATE VII.

Oe. Jamesii. Fig. A, basal leaf, and Fig. B, cauline leaf, x ½. Fig. C, capsule, x 1. Fig. D, seeds, x 5. Fig. E, upper stem, x ½.
Type locality, on the Canadian River, probably in Oklahoma, type collected by James on Long's first expedition (NY). This plant is found mostly in Oklahoma and western Texas, but extends into Coahuila. It is near *Oe. Hookeri* ssp. *Hewettii* and *Oe. elata* in pubescence, but seems amply distinct in its long hypanthium, broad leaves and bracts, more sharply serrulate leaves, thick capsules, larger flowers throughout, and large seeds. Its sharply serrulate leaves, coarseness and strongly angled upper stems suggest influence of *Oe. strigosa*.


In a letter dated February 5, 1946, Dr. Cleland wrote to me that the *Jamesii* race from Parrás has paired chromosomes and the same segmental arrangement as "*Hookeri de Vries,*" but *Jamesii* from Norman has a circle 10, although it does not have balanced lethals. One of the complexes of "*Jamesii Norman,*" my 13575, is similar to the alpha *strigosa* complexes in segmental arrangement, the other complex is similar to the beta *strigosa* complexes. This *Jamesii* has circle 10 and probably an unbalanced lethal condition. *Jamesii* from Bridgeport, my 13580, gives circle 4, circle 6, and 2 pairs and throws segregates having a circle 4 only, or a circle 6 only or 7 pairs. Thus it will be seen that *Oe. Jamesii* in its chromosome configuration is intermediate between *Oe. Hookeri* and more eastern species, that it is near *Oe. Hookeri* ssp. *Hewettii* (*Oe. irrigua*) in this respect as well as in some phenotypic characters, that it has different races that seem to vary somewhat as to origin, if it is correct to place Oklahoma and Coahuila plants together; and they are certainly much alike phenotypically.
Plate VIII.

Oe. longissima var. typica. Fig. A, capsule, x 1. Fig. B, inflorescence, x 1/2. Fig. C, calyx leaf, and Fig. D, rosette leaf, x 1/4.

April, 1949
THE OENOThERA HOOKERI GROUP

5. OENOThERA LONGISSIMA Rydb.


Biennial or short-lived perennial, simple to much branched throughout, normally erect, 1.5 m. tall, the stems angled above, reddish, but of a gray cast because of the short fine appressed hairs, also with some longer coarser hairs which may be somewhat red-papillose at base; rosette leaves oblanceolate, appressed-pubescent on both surfaces and along the sinuate-serrulate margin, acute to acutish at apex, plane, mostly not pigmented on midrib, the blades 10-20 cm. long, 1.5-3 cm. wide, gradually narrowed into winged petioles 5-10 cm. long; cauline leaves grayish green, striate, sometimes pilose on main veins of under surface, linear-lanceolate, rather stiffly spreading-ascending, plane, sub acuminate, remotely and shallowly sinuate-serrulate, with about 10-12 main veins on each side of the midrib, not pigmented on veins, the blades 8-18 cm. long, 0.8-2.2 cm. wide, gradually narrowed at base into petioles up to 2 or 3 cm. long, the upper leaves gradually more reduced and sessile, passing into the sessile, lanceolate, spreading-persistent bracts which are normally 1-3 cm. long; inflorescence 1-6 dm. long, the buds early exceeding bracts; hypan thium 8-12 cm. long, usually more or less reddish; sepals 5.5-15 cm. long, usually reddish, reflexed in pairs, the subulate tips 3-6 mm. long, mostly con nivent; petals pale yellow at anthesis, yellow to orange or reddish in age, obovate, about 4 mm. long, 3.2-4 cm. wide; filaments half as long as petals; anthers 14-18 mm. long; style equaling or exceeding petals; stigma lobes yellow, 4-5 mm. long; capsule subquadrangular, sometimes with red bands, usually 3.5-4.5 cm. long, 1.5-5.5 mm. thick, the free tips ca. 2 mm. long, more or less emarginate; seeds 1.5-2.5 mm. long.

Key to Species

Plant adust, striose, not muricate on stems or glandular-pubescent in inflorescence.

4a. sp. typica.

Plant more or less hirsute especially in upper parts and somewhat muricate on stems, as well as glandular-pubescent in inflorescence.

4b. sp. Clustri.

4a. OENOThERA LONGISSIMA Rydb. subsp. typica* Munz, nom. nov.

4b. OENOThERA LONGISSIMA Rydb. var. Clustri.

Plate VIII: Map III

Plant adust, striose throughout; the inflorescence mostly striose, although some hairs may be longer and somewhat divergent, but not gland-tipped.

Type locality, near the Natural Bridges, Armstrong and White Canyons, San Juan Co., Utah, the type collected by Rydberg and Garrett in Aug., 1911, their no. 9410 (NY). The typical form is found about springy places and seeps below the yellow pine belt, southeastern Utah and northeastern Arizona.

Material seen. UTAH: Grand Co.: Florence Canyon, tributary to Green River from east. E. R. Graham 9967 (POM) toward Oe. Hookeri var. angustifolia. San Juan Co.: Bluff, W. P. Cortman C3238 (POM). Munz 13608 (BISH, HBG, NY, POM), grown at

*Oe. longissima Rydb. var. typica Munz, nom. nov.
5. Oenothera longissima Rydb.


Biennial or short-lived perennial, simple to much branched throughout, normally erect, 1-3 m. tall, the stems angled above, reddish, but of a gray cast because of the short fine appressed hairs, also with some longer coarser hairs which may be somewhat red-papillose at base; rosette-leaves oblanceolate, appressed-pubescent on both surfaces and along the sinuate-serrulate margin, acute to acutish at apex, plane, mostly not pigmented on midribs, the blades 10-20 cm. long, 1.5-3 cm. wide, gradually narrowed into winged petioles 5-10 cm. long; cauline leaves grayish green, strigose, sometimes pilose on main veins of under surface, linear-lanceolate, rather stiffly spreading-ascending, plane, subacute, remotely and shallowly sinuate-serrulate, with about 10-12 main veins on each side of the midrib, not pigmented on veins, the blades 8-18 cm. long, 0.8-2.2 cm. wide, gradually narrowed at base into petioles up to 2 or 3 cm. long, the upper leaves gradually more reduced and sessile, passing into the sessile, lanceolate, spreading-persisting bracts which are normally 4.5 cm. long; inflorescence 1-6 dm. long, the buds early exceeding bracts; hypanthium 8-12 cm. long, usually more or less reddish; sepals 3.5-4.5 cm. long, usually reddish, reflexed in pairs, the subulate tips 3-6 mm. long, mostly connivent; petals pale yellow at anthesis, yellow to orange or reddish in age, obovate, about 4 cm. long, 3.2-4 cm. wide; filaments half as long as petals; anthers 14-18 mm. long; style equaling or exceeding petals; stigma-lobes yellowish, 4-5 mm. long; capsule subquadrangular, sometimes with red bands, usually 3.5-4.5 cm. long, 4.5-5.5 mm. thick, the free tips ca. 2 mm. long, more or less emarginate; seeds 1-1.5 mm. long.

**KEY TO SUBSPECIES**

Plant ashy-strigose, not muricate on stems or glandular-pubescent in inflorescence. 4a. *ssp. typica*.

Plant more or less hirsute especially in upper parts and somewhat muricate on stems, as well as glandular-pubescent in inflorescence. 4b. *ssp. Clutei*.


*Oe. longissima* Rydb. l.c.

**PLATE VIII; MAP III.**

Plant ashy-strigose throughout, the inflorescence mostly strigose, although some hairs may be longer and somewhat divergent, but not gland-tipped.

Type locality, near the Natural Bridges, Armstrong and White Canyons, San Juan Co., Utah, the type collected by *Ryder and Garrett* in Aug., 1911, their no. 9410 (NY). The typical form is found about springy places and seeps, below the yellow pine belt, southeastern Utah and northeastern Arizona.

Material seen, UTAH: Grand Co.: Florence Canyon, tributary to Green River from east, E. H. Graham 9961 (POM) toward *Oe. Hookeri* ssp. *angustifolia*. San Juan Co.: Bluff, W. P. Cottam C2526 (POM), Munz 13008 (BH, GH, NY, POM), grown at

*Oe. longissima* Rydb. var. *typica* Munz, nom. nov.
Baltimore by Cleland, Munz 13450 (POM), at Claremont, Munz 13909 (NY,POM), 14035 (POM), Bluff, Munz 13009 (NY,POM), Munz 13010 (BH,POM). ARIZONA: without locality, O. Kuntze 23252 (NY). Navajo Co.: grown by W. N. Clute at Joliet, Ill., from seed from Betatakin Cliff ruin, Aug., 1919, flowered Aug., 1921 (NY). Coc­

The only collection of this for which Dr. Cleland made a cytological study was my 13008, concerning which he writes “A Grisea-like plant, with unusually long hypanthia and smaller leaves. Plants less robust (perhaps due to infection). One would place the type near to the hookeri alliance on phenotypic grounds.” Two plants were investigated and gave circle 10 and 2 pairs of chromosomes. Thus in the large circle it resembles Oe. Jamesii and must be removed from typical Hookeri by about the same number of segmental interchanges. From the former species, however, it is quite distinct phenotypically in its narrower leaves, less sharply serrulate margins, somewhat smaller sepals and petals, with shorter anthers, more slender capsules and smaller seeds. It occupies a more western range with definitely different ecological situation. It looks much like Oe. Hookeri ssp. Hewettii (irrigua) in pubescence and coloration and narrow leaves, but has not only a longer hypanthium but larger flowers and longer anthers.


MAP III.

Upper parts of plant with long and more or less divergent hairs, as well as short appressed and short gland-tipped hairs; stems more or less muricate with red papillae.

Type locality, War-God Spring, at 7000 ft. on Navajo Mts., Navajo Indian Reservation, Coconino County, Arizona, the type Clute no. 4, July, 1919, (Rocky Mountain Herbarium, number 98480). I am greatly indebted to Professor C. L. Porter of the University of Wyoming for examining for me the type of Oe. Clutei and checking its pubescence. For the most part this subspecies ranges slightly to the west of ssp. typica, that is from southwestern Utah and northwestern Arizona into southern Nevada and adjacent California.

Material seen as follows, UTAH: San Juan Co.: west slope of Navajo Mt., H. C. Cutler 2816 (DS,GH,NY). Washington Co.: La Verken, Munz 15009 (GH,NY,POM), cult. at Claremont, Munz 15297 (BH,NY,POM); canal bank north of St. George, B. Maguire & B. L. Richards, Jr. 15971 (CU). ARIZONA: Coconino Co.: seed from Navajo Mts., in 1919, cult. at Joliet, Ill. by W. N. Clute (NY) probably type material. Mohave Co.: Sawmill Canyon, Selma Braem 52 (DS,POM); 1 mile north of Point Royal, Kaibab Forest, Grand Canyon Nat. Park, Munz 17030 (POM); north rim of Grand Canyon, Eastwood & Howell 6991 (CAS,POM). NEVADA: Clark Co.: seed from Charleston Mts. sent by I. W. Clokey, cult. at Claremont, Munz 14733 (NY,POM),

*Oe. longissima var. Clutei (A. Nels) Munz. stat. nov.
Map III. Distribution of *Oenothera* *Jamesii* and *Oe. longissima*.

△—*Oe. longissima* subsp. *Glutei*
+
—*Oe. longissima* subsp. *typica*
●—*Oe. Jamesii*


Dr. Cleland has studied my 15009 from La Verken, Utah and Eastwood and Howell 6991 from Grand Canyon. He finds these nearer *Hookeri* than is ssp. *typica*, with circle 6 and 4 pairs or with 7 pairs for the former collection and 7 pairs or circle 4 and 5 pairs for the second collection. He says, "like a *hookeri* with very long internodes and hypanthia." Phenotypically *Glutei* resembles *Oe. Hookeri* ssp. *angustifolia* in the red coloration of buds, often rather scantly pubescence on sepals and hypanthium, gland-tipped hairs on same, and muricate stems. It may well have originated from that subspecies.