

## AN ACCOUNT OF THE CRUCIATE-FLOWERED OENOTHERAS OF THE SUBGENUS ONAGRA.

HARLEY HARRIS BARTLETT.

The so-called cruciate-flowered *Oenotheras* are those in which the petals are linear or narrowly oblong instead of broadly obovate. The first one which was described, and the only one, in fact, of the subgenus *Onagra* which has ever received a distinctive name, was called *Oe. cruciata* by Nuttall, on which account the character of having linear petals has come to be known as cruciateness. The origin of cruciateness is at present a matter of no little interest to geneticists. Some of them hold to the belief, based, it must be said, upon the traditional systematic treatment of *Oenothera*, that all the cruciate-flowered races either belong to *Oe. cruciata* Nutt. or else have acquired the character of cruciateness by hybridization with that species. In this paper the writer records his conclusion that cruciateness has originated independently in several lines of descent and that the aggregate formerly called *Oe. cruciata* must therefore be resolved into several species and varieties. In accord with this conclusion, he has named and defined some of the cruciate-flowered *Onagrae* which his cultural studies have shown to be constant and distinct.

The original *Oe. cruciata* was found in Massachusetts by Nuttall who sent specimens of it to several botanists. He never described the species himself, and the name was first published as a synonym of *Oe. parviflora* L., by Seringe.<sup>1</sup> The earliest description was that of George Don,<sup>2</sup> who cultivated the plant in 1824 and later characterized it in his General History of the Dichlamydeous Plants, where the name

<sup>1</sup> Seringe, in D. C. Prod. 3: 47. 1828. "*Oe. cruciata* Nutt. in litt. ex herb. DC. et Mercier."

<sup>2</sup> Don, G. Gen. Hist. Dichlam. Pl. 2: 686. 1832. "*Oe. cruciata* (Nutt. mss.) stem reddish, rather hairy; leaves lanceolate, acuminate, denticulate, glabrous but the upper ones are rather downy; flowers sessile; petals linear, rather shorter than the anthers; calycine segments reflexed, linear, mucronate, longer than the petals, but about equal in length to the stamens; lobes of stigma thick, conniving, or spreading a little; capsule cylindrical, hairy. ♂ H. Native of North America. Flowers small, yellow. Cross-petalled Evening Primrose. Fl. July, Aug. Clt. 1824. Pl. 2 to 4 feet."



is ascribed to Nuttall. In 1835 Spach<sup>3</sup> described a collective species *Oe. chrysantha*, which included, as varieties, three species of earlier authorship—*Oe. muricata* "Murr." (as *Oe. chrysantha*  $\alpha$ : *grandiflora* Spach), *Oe. parviflora* L. (as *Oe. chrysantha*  $\beta$ : *parviflora* Spach) and *Oe. cruciata* Nutt. (as *Oe. chrysantha*  $\gamma$ : *cruciata* Spach). Torrey and Gray<sup>4</sup> likewise treated *Oe. cruciata* as a variety, but whereas Spach had reduced the allies of *Oe. biennis* to two species, these authors ranged them all as varieties under *Oe. biennis*. The names *Oe. biennis* var. *cruciata* T. & G. and *Oe. cruciata* Nutt. are strict synonyms.

*Oenothera biennis* var. *cruciata* "with singularly small and narrow linear-oblong petals, and smooth pods" ran through all the editions of Gray's Manual, from the first to the fifth, with no specific statement of geographic range. In the sixth edition, however, we find the statement that "var. *cruciata* Torr. & Gray, with small narrow petals, appears to be merely a rare garden (?) sport. E. Mass." The change appears to have been made because no wild specimens of *Oe. cruciata* had ever been collected, or at any rate none had been preserved in public herbaria, between the time of Nuttall's original discovery of the species (probably 1822 or 1823, soon after his arrival in Cambridge), and 1889, a period of more than sixty years. Cultivated specimens, collected in the Harvard Botanic Garden in 1856 and 1875, were the only material of the species known to Watson, the editor of the sixth edition of Gray's Manual and a monographer of the genus *Oenothera*. His surmise that *Oe. biennis* var. *cruciata* might have originated as a garden sport shows clearly that until comparatively recent years such a form has had only a traditional status as a wild plant in this country.

We have seen that Don cultivated the true *Oe. cruciata* in 1824, and there is no intrinsic improbability but that the form which is still found in European botanic gardens is genetically related to it. It is more likely that the form cultivated at the Harvard Botanic Garden in 1856 and 1875 was a reintroduction from Europe than that it had been continuously in cultivation since Nuttall's time. Of course, it may have had an independent origin. Since the variability of the petals

<sup>3</sup> Spach, E. *Mönographia Onagrearum*. *Nouv. Ann. Mus.* 4: 355. 1835.

<sup>4</sup> Torrey and Gray, *Fl. N. Am.* 1: 492. 1840. "*Oe. biennis* (Linn.)  $\epsilon$ . *cruciata*: petals (abortive) linear-oblong, shorter than the stamens; tube of the calyx 2-3 times the length of the segments; capsules nearly glabrous.—*Oe. cruciata* Nutt.! in *DC. l.c.* (under *Oe. parviflora*)."



in the European garden form shows that it has been hybridized with some broad-petaled species, and cannot therefore be considered typical of *Oe. cruciata*, de Vries<sup>5</sup> has named it *Oe. cruciata* var. *varia*. He used this nominal variety for the crosses between "*Oe. cruciata*" and other species which are described in the second volume of *Die Mutations-theorie*. Because of its unknown, mixed ancestry it was an undesirable type for use for further experiments. De Vries, therefore, wrote to this country for seeds of the true *Oe. cruciata*, which he had no reason to suspect was not well known here, for Small<sup>6</sup> had only recently (1896) restored it to specific rank, under the name *Onagra cruciata*, and had cited it not only from Massachusetts but also from Vermont. The Vermont record was probably based upon specimens collected by Grout at Brattleboro and Vernon; the localities were later published in the *Flora of Vermont*.<sup>7</sup>

In response to his request, de Vries received seeds and rosettes from MacDougal, collected at Sandy Hill, New York, near Lake George, and seeds from Robinson, collected at Jaffrey, New Hampshire—all supposedly *Oe. cruciata*. These were grown at Amsterdam in 1903. The material from Sandy Hill included two very distinct types, both of which were found among the plants from seeds as well as among those from rosettes. The differences between the types were slight, but striking and absolutely without transition. Most of the individuals had rather broadly linear petals and comparatively thick flower-buds. The rest had narrowly linear petals and slender flower-buds. Robinson's seeds from Jaffrey gave a third type, diverging from both of the others in its much longer calyx tube and more slender stem, inflorescences and foliage. De Vries<sup>8</sup> interpreted his findings as follows: "It seems not improbable that *Oenothera cruciata* includes a group of lesser unities, and may prove to comprise a swarm of elementary species, while the original strain might even now be in a condition of mutability." In regard to the two types from Sandy Hill, he said: "Probably two elementary species were intermixed

<sup>5</sup> De Vries, H. On Atavistic Variation in *Oenothera cruciata*. Bull. Torr. Bot. Club 30: 75-82. 1903. Also *Die Mutationstheorie*. 2: 100. 1903.

<sup>6</sup> Small, J. K. *Oenothera* and its Segregates. Bull. Torr. Bot. Club 23: 169. 1896.

<sup>7</sup> Brainerd, Jones and Eggleston. *Flora of Vermont*, 1900, p. 63.

<sup>8</sup> De Vries, H. *Species and Varieties*, 1905, p. 590. See also letter quoted by MacDougal, Vail, Shull and Small, *Mutants and Hybrids of the Oenotheras*, 1905, p. 12.



here, but whether one is the systematic type and the other a mutation remains to be seen."

MacDougal<sup>9</sup> has stated definitely that the New Hampshire type appeared as a mutation from one of the Lake George types in his cultures of 1903 and 1904, at the New York Botanical Garden. His statement follows: "The cultures of 1904 included over sixty specimens of *O. cruciata* which reached the adult stage, and included not only the two forms which he [de Vries] had observed to arise from the seed and roots sent him from this place, but also the third obtained only from material from New Hampshire. It is obvious, therefore, that one form arises spontaneously from one of the other two forms suddenly, and dried specimens from the crop of 1903 in the New York Botanical Garden show that it originated in this manner here in the first year of cultivation, although the second half of the same lot of seeds sent to Professor de Vries failed to give rise to it in Amsterdam" (*l. c.*, p. 13). "*O. cruciata* as it exists at the present time in the cultures of the New York Botanical Garden and in the Botanical Garden of Amsterdam is composed of three elementary species, which are fairly distinct and without intergrading forms. A careful analysis of the occurrence of the group leads to the inevitable conclusion that one of the forms is in a mutating condition" (*l. c.*, p. 52).

MacDougal defined and figured his three elementary species of "*Oe. cruciata*" but quite unaccountably failed to say whether his cultures of 1904 were grown from garden seeds of the previous year or from more of the original wild seed which he had planted in 1903. If the 1904 cultures were a second generation, it stands to reason that he would have known which of the Lake George types was in a mutating condition, and would not have written, referring to the origin of the third form, "The evidence at hand, therefore, seems to confirm the suggestion as to the mutability of the species, but nothing may be said as to which of the types constitutes the parent" (*l. c.*, p. 13). If, on the contrary, the 1904 cultures were from wild seed, MacDougal had no evidence whatever that one of the Lake George types was "in a mutating condition." On either supposition as to the source of the 1904 seed, his conclusion, far from being "inevitable" is not even plausible.

The original seed collection from Sandy Hill was doubtless gathered

<sup>9</sup> MacDougal, assisted by Vail, Shull and Small. Mutants and Hybrids of the *Oenotheras*, 1905.



from individuals of two different species, growing at the same locality, as is so frequently the case with closely related species of the subgenus *Onagra*. This explanation of the source of the two species which De Vries differentiated at Amsterdam is amply verified by the fact that wild rosettes from the same locality as the seeds proved to belong to the same two species. If it were not for a suspicion that two of MacDougal's types were in reality non-hereditary seasonal phases of the same species, one might almost as readily believe that there were three species in the mixed seed collection as that there were two, and thus explain the supposed mutation. MacDougal said of the third type that all the individuals of it completed their seasonal development much earlier than the other two. It seems not impossible that the set of plants which developed early in the season may have appeared so different from later plants of the same form as to be mistaken for a mutation. Several times in the writer's experience with the *Oenotheras*, a culture has consisted of two types of plants, those which went through the life-cycle of a biennial, forming a dense rosette which persisted for weeks, even though the plants, by virtue of being started early in the spring under glass, completed their development in one season, and those which went through a strictly annual life-cycle, forming only a transitory rosette of a few leaves before they become cauline. Since the annual type is lower and less robust, due probably to its not having elaborated a reserve food supply for use during the period of rapid growth, one might easily be misled into interpreting it as a mutation.

After MacDougal gave up his work on *Oenothera*, his cultures were continued by Dr. Geo. Harrison Shull. Shull, however, cannot supply seeds of the questionable third form of "*Oe. cruciata*" and writes that he has never cultivated it. Of three lots of seed which were originally turned over to him, two yielded the same type.

Even if we assume that MacDougal's third form was really distinct, there is no reason to believe that he correctly identified it with Doctor Robinson's New Hampshire type. De Vries characterized the latter as having a strikingly longer hypanthium than either of the Lake George types, whereas MacDougal figured his dubious third type as having a shorter hypanthium than one of the Lake George forms. Moreover, it appears that MacDougal never cultivated the New Hampshire type, but made his identification merely from de Vries's very brief account of it.



The writer believes that the two Sandy Hill types (and probably also the New Hampshire type) are distinct taxonomic units which for the present at least must be treated as species. Neither of them is the same as *Oe. cruciata* Nutt. There is a possibility that they are the cruciate-flowered varieties of thus-far undescribed broad-petaled species, and that further collections may discover their true relationships in this direction. The cruciate character has probably arisen many times in totally unrelated strains, so there is no reason to believe that our three types are of necessity derivatives of any common parent species, even if they are true species in the sense that cruciateness is only one of a group of correlated characters by which each differs from its nearest ally.

During the summer of 1913, the writer had the two Vermont strains in cultivation from seeds furnished by Professor de Vries, but not the New Hampshire strain. The latter has not been grown recently at Amsterdam. As a matter of fact, de Vries has continuously maintained only one of the Sandy Hill types in his cultures; the seeds of the other which he sent were old and germinated poorly, although a sufficient number of plants were obtained for a taxonomic study. It turned out that neither of the Vermont types corresponded with the original *Oe. cruciata* of Nuttall, the type specimen of which is preserved in the Candolleian Herbarium. Through the kindness of M. Cas. de Candolle a photograph of this specimen was obtained, which is reproduced as figure 1. There is also one of Nuttall's original specimens in the Herbarium of the Philadelphia Academy of Natural Sciences, which the writer has carefully compared with the types sent by de Vries. Not only are the latter distinct from *Oe. cruciata*, but in the writer's opinion they are specifically distinct from one another.

After the writer had reached this conclusion, and had planned to publish the two Lake George types as new species, he learned, quite by accident, that Shull had likewise assigned names to them, which he would soon have published in connection with a discussion of certain genetic experiments. In order not to cause Shull any inconvenience, the writer proposed that the species be published with technical diagnoses in this paper, but under the names which Shull had provisionally given them and had attached to a great many specimens and permanent photographic records. It is with Shull's approval that the names *Oe. atrovirens* and *Oe. venosa* are here proposed under our joint authority. In justice to Doctor Shull, however, it is only



fair to state that he does not altogether agree with the writer as to the specific independence of the two forms. Thus, under date of September 26, 1913, he writes: ". . . I must confess that I prefer to consider them as subspecies of *Oe. cruciata* Nutt. and would have published them as such if left to my own initiative. But of course if you are consistently describing everything which is genotypically distinct and morphologically distinguishable as species, these forms certainly deserve the same treatment."

The so-called *Oe. cruciata* of recent collectors, of which numerous specimens have accumulated in our herbaria since 1890, seems to consist not of one species or group of genetically related species, but of the cruciate varieties of several independent broad-petaled species, together with a number of species in which the cruciate character has probably become specific. In other words, *Oe. cruciata*, *sensu latiore*, is a purely artificial group, the components of which must ultimately be distributed according to their true relationships. The writer believes that cruciate variations of any species of *Onagra* are likely to occur as bud sports or germinal mutations. The almost certain origin of the cruciate variety of true *Oe. biennis* on the sand dunes of Holland is a case in support of this belief. One solitary individual of this variety was found by Ernst de Vries in August, 1900, growing with the typical form on the dunes near Santpoort. No such form had hitherto been known. As de Vries<sup>10</sup> pointed out, it could not have originated by hybridization with any other cruciate form, since there was no such form in Holland at the time except the rare *Oe. cruciata* var. *varia* of botanic gardens. Quite aside from the extreme improbability that two normally self-pollinated strains growing at a great distance should have been crossed, it will suffice to point out that *Oe. cruciata* var. *varia* de Vries, is characterized by a dark red coloration of the stems and foliage which is dominant in all its hybrids. In the cruciate variety of *Oe. biennis* there is no such coloration. The writer's cultures of 1913 included fifty plants of it, from seeds sent by de Vries, descended from the original plant found by his son. They were a uniform lot, and differed in no respect from *Oe. biennis*, *sensu strictiore*, other than that the petals were linear instead of obovate. The variety can, therefore, hardly be regarded as other than a mutation, the occurrence of which gives a tangible clue to the manner in which other cruciate forms have arisen.

<sup>10</sup> De Vries, H. *Die Mutationstheorie*, 2, 1903, p. 599.



During the past summer the writer grew fifty plants of an undetermined *Oenothera* from Springfield, Missouri, the seeds of which were collected from one individual by Mr. P. C. Standley. All were strictly uniform except for one plant, of which a single branch bore cruciate instead of broad-petaled flowers. The petals of the cruciate flowers would be characterized as narrowly oblong rather than linear, thus contrasting strongly with those of the cruciate variety of *Oe. biennis*, for instance, but nevertheless strikingly divergent from the petals of normal flowers. Doctor Shull suggests in a recent letter that his experience would lead him to suspect that the occurrence of such a bud variation indicated recent hybridization with a cruciate strain. In this connection de Vries's experience with *Oe. cruciata* var. *varia* is of interest. He found that this variety, in which the petals are inconstant in form, segregated roughly into three groups, a purely cruciate-flowered, an intermediate and an atavistic (broad-petaled) group. Except for rare cases of bud variations which showed a return to the cruciate type, the progeny of the broad-petaled group were constant. Although it is by no means impossible that the broad-petaled Springfield strain is a segregate from a hybrid between a broad petaled and a cruciate strain, the likelihood of such an origin is not great. Thus far no cruciate-flowered *Oenothera* is known from Missouri, and none has been collected nearer than Mobile, Alabama, or Washington, D. C. Although the cruciate bud variation of the Springfield strain has not yet been tested for constancy in a second generation, it seems to be of sufficient interest to justify calling attention to it in connection with a discussion of the origin and relationships of the cruciate types.

Davis<sup>11</sup> has recently published an adverse criticism of a paper by Stomps<sup>12</sup> on mutation in the Dutch *Oe. biennis*, which is based entirely upon a misconception of the relationships of the cruciate *Oenothera* of the sand dunes of Holland. It was perhaps unfortunate that de Vries named this plant *Oe. biennis* var. *cruciata*, in view of the fact that the same name had been formerly used by Torrey and Gray for *Oe. cruciata* Nutt., and may even again be taken up as the valid name for the older type if ideas as to the limits of species continue to shift. Davis made the error of regarding de Vries's homonym as a synonym of *Oe. cruciata*.

<sup>11</sup> Davis, B. M. Mutations in *Oenothera biennis* L.? Am. Nat. 47: 116-120, 1913.

<sup>12</sup> Stomps, T. J. Mutation bei *Oenothera biennis* L. Biol. Centralb. 32: 521. 1912.



Nutt., which was treated in American floras for decades as *Oe. biennis* var. *cruciata* T. & G. De Vries evidently anticipated that no confusion would result from the use of the name *Oe. biennis* var. *cruciata* a second time, because of the fact that he was recognizing the former var. *cruciata* as a species. That misunderstanding has arisen is clear from the following extracts from Davis' article: ". . . we find that the so-called 'mutants' were not derived from the pure Dutch *biennis* of the sand dunes but from a cross between this race and a type designated *O. biennis cruciata*. This fact seems to the writer of fundamental importance in judging the conclusions of Stomps. It should be made clear that the form '*O. biennis cruciata*' is recognized in the more recent taxonomic treatments as a true species sharply distinguished from types of *biennis* by its floral characters. Whatever may have been the origin of *O. cruciata* or its possible relationship to *O. biennis*, a cross between these types must certainly be regarded as a cross between two very distinct evolutionary lines and its product a hybrid in which marked modifications of germinal constitution are to be expected. . . . Stomps assumes that the *cruciata* in Holland is a mutant from the Dutch *biennis*, but his belief rests upon no direct evidence. *Cruciata* has never appeared in the extensive cultures of the Dutch *biennis* grown by de Vries and Stomps. Neither have we any direct evidence that the American *cruciata* has come from any form of *biennis*. It is true that the species *cruciata* and *biennis* appear to be closely related, but it is equally clear that they constitute very distinct lines each with a long period of evolutionary independence. I cannot see the justification for Stomps's attitude when he treats a cross between the *biennis* and *cruciata* of the sand dunes of Holland as though it were the combination of forms within the same species which have similar germinal constitutions. Stomps lays emphasis on the purity of his material of *biennis* and *cruciata* which had been carried along for several years in pure lines from original wild plants of the sand dunes. He states that the crossing of these two forms is concerned alone with the floral peculiarities of *cruciata*, since in all other characters the two types are the same. It seems to the writer hardly possible that lines so well established as *biennis* and *cruciata* can be absolutely the same in all respects except that of flower form, although this is obviously the most important point of difference. The American forms of *cruciata* are exhibiting among themselves remarkable differences of germinal constitution."

As already stated, the writer has cultivated *Oe. biennis* var.



*cruciata* de Vries, and has found it to be, as de Vries and Stomps have said, quite indistinguishable, except as to floral characters, from the true Dutch *Oe. biennis*. It is quite impossible that it has any relationship with the older *Oe. cruciata* Nutt. That it has originated as a mutation from *Oe. biennis* not only once, but several times, independently, seems the most likely explanation of its sporadic occurrence. In his latest book, de Vries<sup>14</sup> states that he has received living specimens from Prof. H. Klebahn, collected on the Lüneburg heath. Its presence in Holland at several localities besides Sandpoort has also been reported to him. Although rare, it seems to be of rather wide distribution, and decidedly worthy of taxonomic recognition. Since the name *Oe. biennis* var. *cruciata* is preoccupied, and therefore likely to continue to be a source of confusion, the writer proposes to substitute for it the new designation *Oe. biennis* var. *leptomeres*.

*Oenothera cruciata* of the American Manuals has been reported only from New England and northern New York. It is represented in the Gray Herbarium by specimens from Nova Scotia (Sable Island, Macoun); Maine (Madison, Lexington and Cornish, Fernald; Cumberland, Chamberlain and Knowlton); New Hampshire (Surry, Fernald; Rollinsford, Parlin; Dublin, Robinson); Vermont (Brattleboro, Grout; Vernon, Robinson); New York (Axton, Adirondack Mts., Rowlee, Wiegand and Hastings); and Massachusetts (Rockport, Cape Ann, Bartram; Northampton, Robinson). Seeds from these or any other localities would be very welcome to the writer of this article. Doctor Robinson has again been so kind as to collect seeds of a cruciate *Onagra* at Jaffrey, New Hampshire, which will be grown during the coming summer. There is little doubt that careful cultural study will bring other cruciate strains to light from the region of New England and northern New York, in addition to *Oe. cruciata* (*sensu strictiore*), *Oe. atrovirens* and *Oe. venosa*.

Although no cruciate *Onagrae* have hitherto been reported from the region south of New England, Doctor Shull has had an undescribed species from Long Island in cultivation for several years. It will be treated in a future paper. The writer has cultivated two others, one from Mobile, Alabama, which must be studied another season before it can be described, and a second from Montgomery County, Maryland, to which the name *Oe. stenomeres* is here given.<sup>15</sup>

<sup>14</sup> De Vries, H. Gruppenweise Artbildung, 1913, p. 298.

<sup>15</sup> Since this article was submitted for publication Bicknell (Bull. Torr. Bot.



*Oenothera stenomeres* has now been under observation through four generations. The starting point of the pure line was a half grown cauline annual plant which was transplanted to the writer's Bethesda garden from Chevy Chase, Maryland, a suburb of Washington, in midsummer of 1910. It was not known to be a cruciate plant until it flowered, but cruciate plants had been seen in the same general locality in 1909, and have been observed frequently every summer since then both at Bethesda and Chevy Chase. Ten plants were brought to maturity in 1911, 16 in 1912, and 106 in 1913. Not until the last year did the strain show any noteworthy variation, although, to be sure, the cultures were very small. In the fourth generation, however, there were at least three mutations in the culture of 106 plants. One was a practically self-sterile plant, otherwise indistinguishable from the type, the second had very large, thick buds and short, thick fruits, and the third was a remarkable plant which the writer is inclined to consider as perhaps the most striking example of mutation which has thus far been reported in any species of *Oenothera* except *Oe. Lamarckiana*. This plant was unusually stout and hairy. About midsummer the growth of the main stem and of all the branches but one was stopped by the development of a large rosette, in every way like the winter rosettes of the biennial strains, at the end of each stem. In this condition the plant remained through the rest of the summer and fall, except that the exceptional branch flowered normally. The form proved to be completely fertile to its own pollen and formed large, well-filled capsules. The flower buds were densely pubescent, which is not the case in the type, but the most remarkable character of the plant was that the petals also were densely hairy. All of the cruciate *Onagreae* appear to have a few scattered hairs on the petals (a microscope is often necessary for their detection) but the petals of this plant were so thickly covered with long appressed hairs that they appeared canescent in the buds, a day or two before flowering time, when they had not yet reached full size. Although larger, the petals of the mutation were narrow, as in all the other plants of the species, and were yellow at maturity.

A further discussion of this very interesting mutation is reserved until its seeds shall have been grown. For the present it will suffice Club 41: 79. 1914) has published *Oenothera stenopetala*, a cruciate-flowered ally of *Oe. Oakesiana*, from the island of Nantucket. It seems to be clearly distinct from any of the species treated here.



to point out (1) that it occurred in the fourth guarded generation of the strain, (2) that the species is strictly self-pollinating because the stamens surround the stigmas and because the flowers generally open only imperfectly or not at all, (3) that any accidental crossing with a broad-petaled species would have been evident in the next generation, (4) that until the year when the mutation was found there had been no other cruciate strain in the garden or vicinity with which it could have accidentally crossed, (5) that the densely hairy petals constituted an absolutely discontinuous variation, for in all the other plants of the strain they were glabrous except under microscopic examination, and (6) that the new character could not have been introduced into the strain by hybridization, inasmuch as no other *Oenothera* with which it could have crossed has hairy petals.<sup>16</sup> The new mutation may be called *Oe. stenopetala* mut. *lasiopetala*.<sup>17</sup>

<sup>16</sup> De Vries (Bull. Torr. Bot. Club 30: 75-82. 1903) reports considerable variation in the degree of pubescence of the petals of *Oe. cruciata* v. *varia*. This form is of garden origin and is known only in European botanic gardens. In America there seems to be no *Onagra* of which the petals appear other than glabrous to the naked eye.

<sup>17</sup> The writer proposes that a trinomial system of nomenclature be used for mutations of garden origin, in order to set them clearly apart from forms of which cognizance must be taken in floras. Gates has made the suggestion that mutations be indicated by placing the abbreviation "mut." between the terms of the binomial. According to his practice, for example, the name of *Oe. lata*, the well-known mutation from *Oe. Lamarckiana*, would be written *Oe. mut. lata*. The use of a trinomial system, however, would appear to have decided advantages over a binomial system. Gates, for instance, has reported the discovery of a mutation from *Oe. biennis* parallel to *Oe. lata*, which he has called *Oe. biennis* mut. *lata* in order that the name might show the parallelism of the two variations. Certainly it is very helpful to be able to use the same mutational designation in such cases, and a trinomial system makes it possible to so do consistently. The use of the trinomial for all mutations would not imply anything about the degree of differentiation of any particular mutation; in other words, the category *mutatio* would indicate manner of origin rather than kind of variation. *Oe. gigas* de Vries is a mutation of specific rank; probably most botanists would consider *Oe. brevistylis* to be of varietal rank. If it were considered desirable, the abbreviations "mut. sp." and "mut. v." (*mutatio specifica*; *mutatio varietalis*) might be applied as follows: *Oe. Lamarckiana* mut. sp. *gigas* and *Oe. Lamarckiana* mut. v. *brevistylis*. The latter variation is found wild in Holland; if it were necessary to include it in a flora the name would be *Oe. Lamarckiana* var. *brevistylis*. The former has been introduced into this country; if it spreads and must be taken account of by systematists the name would stand as *Oe. gigas*.



## KEY TO CRUCIATE ONAGRAE DISCUSSED IN THIS PAPER

- Free sepal tips distinctly infraterminal, *i. e.*, separated in bud.
- Free sepal tips very densely pubescent with appressed, sharp hairs. *Oe. cruciata.*
- Free sepal tips thinly pubescent, not markedly more so than the upper part of the bud.
- Main stem and basal branches with numerous lateral flowering branches. Hairs of calyx segments below free tip of two types, cylindrical and acute. *Oe. venosa.*
- Main stem and basal branches simple below the inflorescence. Hairs of calyx segments below free tip all cylindrical. *Oe. atrovirens.*
- Free sepal tips terminal, *i. e.*, appressed to one another at the base in bud.
- Main stem bearing either a flowering branch or a flower in every axil. *Oe. biennis.*  
*var. leptomeres.*
- Main stem with a few flowering branches below the terminal spike, which pass gradually into abbreviated non-flowering branches toward the middle of the stem. *Oe. stenomeres.*

## OENOTHERA CRUCIATA Nutt.

The specimen in Herb. Phil. Acad. appears to be identical with the specimen in Herb. de Candolle (v. figure 1). It consists of the terminal part of a large branch (or main stem?) bearing one flowering branch in the lowest axil. Stem red on side exposed to the sun, otherwise green, with pubescence of two types,—long spreading or ascending sharp hairs mostly red-tuberculate at base and a thin scarcely visible indument of short, acute, crispate hairs. Upper leaves lanceolate, distantly repand-denticulate, broadest near the base and tapering to the acute or acuminate apex, somewhat pubescent on both sides with appressed sharp hairs. Bracts of the inflorescence lanceolate, broadest near the middle, upper ones with some hairs of the cylindrical, thin-walled, round pointed type. Hypanthium about 33 mm. long, very slender, densely puberulent with cylindrical hairs and sparsely pilose with long, sharp hairs. Calyx segments 10–11 mm. long, puberulence more sparse than on hypanthium and pilosity more dense: free tips about 2 mm. long, densely appressed-pilose, distinctly infra-terminal and well separated in bud. Buds somewhat clavate. Ovary 7–8 mm. long, with both the short, cylindrical and long, sharp, hair types.—Massachusetts, Nuttall, 1825.



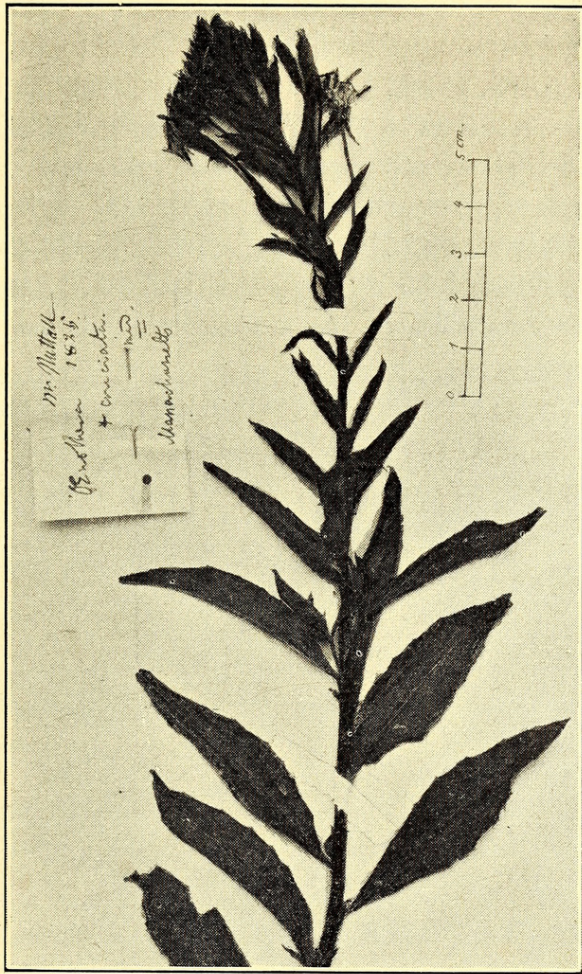


FIG. 1. *Oenothera cruciata* Nutt. Photograph of the type specimen at Geneva, sent by M. Cas. de Candolle.

***Oenothera atrovirens* Shull & Bartlett, sp. nov.**

Biennis. Rosula matura 3.5–4 dm. diametro, altero anno caulem proprium ramosque radicalis simul emittens, foliis spatulatis atroviridibus acutis, maximis ca. 20 cm. longis, 3–4 cm. latis, secus costam paululum bullatis, ad basin versus minime profunde et distanter sinuato-dentatis. Planta matura ca. 9 dm. alta ex caule proprio semper obliquo ramisque ca. 12 multum brevioribus radicalibus patentibus constans, utrisque superiore parte subnutantibus. Caulis proprius infra inflorescentiam simplex, solum ramulos foliis breviores nunquam florentes gerens; inflorescentia vel ex spicis pluribus brevibus densissimis composita vel raro simplex. Rami radicales cauli similes



sed brevioribus ramulis axillaribus plerumque parvissimis rosulatis instructi; inflorescentiae saepissime simplices. Caules in latere ad solem spectante rubri, altero latere virides vel coloribus duobus sparsi, pilis triformibus tenuiter vestiti, I paucissimis longis acutis basi rubrotuberculatis, II multis minutis subappressis valde verrucosis, apicem versus angustatis sed obtusiusculis, III aliisque minutissimis laevibus ampulliformibus. Folia atroviridia subnitida, pendula vel reflexa, anguste lanceolata sinuato-denticulata, maxima ca. 12 cm. longa, 1.5 cm. lata, mediocria ca. 6 cm. longa, 1 cm. lata, tenuissime

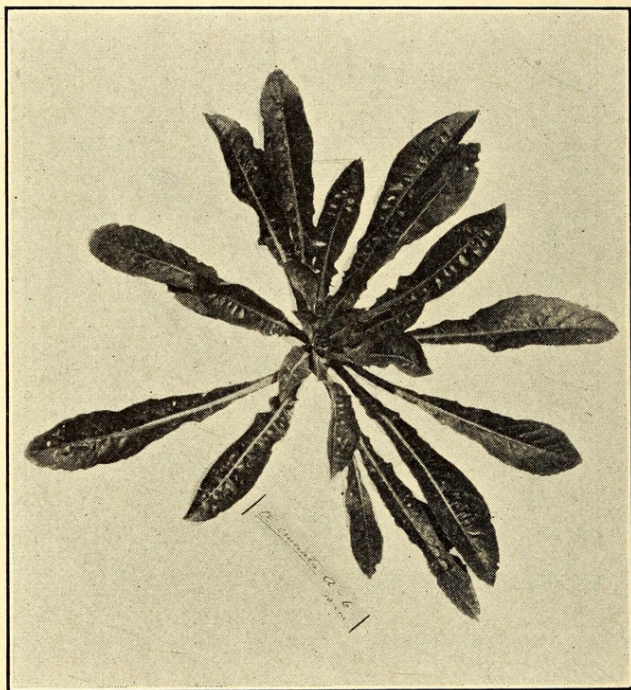


FIG. 2. *Oenothera atrovirens* Shull & Bartlett. Mature rosette. (The label is 10 cm. long.)

puberula, utrinque pilis brevibus acutis subverrucosis, supra aliis etiam minutis ampulliformibus commixtis. Bractee inferiores ovato-lanceolatae foliaceae floribus breviores, superiores juventate ovariis aetate fructibus paulum longiores, lanceolatae acuminatae apice rubrae, utrinque fere glabrae sed paucissimis pilis ampulliformibus praeditae, margine pilis subulatis laevibus acutis basi dilatatis eis foliorum longioribus dense ciliatae. Hypanthium 25–34 mm. longum 2.2 mm. crassum apicem versus abrupte expansum, sparse viscido-pubescens, pilis pluribus cylindricis apice rotundatis et paucis multo



brevioribus ampulliformibus. Calycis segmenta ca. 14 mm. longa inferiore parte pilis cylindricis vestita, apicibus liberis 3.5–4 mm. longis infraterminalibus pilis subulatis eis bractearum marginis similibus praeditis. Petala oblonga 8–9 mm. longa, 2.5 mm. lata, supra glabra, subtus pilis sparsis ornata, aliis laevibus acutis cum aliis cylindricis intermixtis. Ovarium 11–12 mm. longum fere glabrum, pilis sparsissimis acutis laevibus longitudine valde variantibus aliisque minutissimis ampulliformibus vestitum, ad anthesin ex rhachi recte divergens. Fructus maturi densissime aggregati ascendentes, saepe 30 mm. longi, fere teretes, prope basin ca. 7 mm. crassi, sursum angustati, apicibus liberis brevibus emarginatis.—Seeds collected near Sandy Hill (now Hudson Falls), New York, 1902, distributed by D. T. MacDougal and now cultivated in several gardens. Type (from a cultivated plant) *Bartlett* 3500, in U. S. Nat. Herb., nos. 693736–7. This is the "*Oe. cruciata*" of de Vries's *Gruppenweise Artbildung*.

***Oenothera venosa* Shull & Bartlett, sp. nov.**

Biennis. Rosula matura ei *Oe. atrovirentis* valde similis, sed colore aliquantum pallidior. Planta matura 7–9 dm. alta ramosissima. Caulis proprius infra spicam terminalem multos ramos floriferos saepe usque ad basin ferens; rami radicales quoque ramosi nunquam simplices. Caules maculosi; pilis paucissimis basi rubrotuberculatis, multis similibus verrucosis longitudine valde variantibus absque tuberculo rubro ad basin, et sparsis ampulliformibus. Foliorum pubescentia ut in *Oe. atrovirenti*; margo argutius dentata; positio vel patens vel modice reflexa, nec pendula. Bractee foliaceae non deciduae eis *Oe. atrovirentis* ampliores, inferiores interdum fructibus bis terve longiores, apice rubrae, in superiore pagina margineque pilis aliis acutis subverrucosis aliis vel subclavatis vel cylindricis apice rotundatis sparse tectae, subtus pilis uniformibus acutis. Hypanthium 26–38 mm. longum, ca. 1.8 mm. crassum; pilis biformibus aut acutis sublaevibus aut cylindricis apice rotundatis. Calycis segmenta ca. 20 mm. longa, pilis paucis eis hypanthii similibus praedita; appendicibus liberis 5–5.5 mm. longis conspicue infraterminalibus apice rubris. Petala lineari-oblonga ca. 9–10 mm. longa, 1.8 mm. lata, solum supra pilis sparsis cylindricis vestita. Ovarium pubescens, pilis intermixtis, aliis acutis laevibus cum aliis cylindricis. Fructus quam in *Oe. atrovirenti* distantiores, ca. 25 mm. longi, fere teretes, prope basin 6.5



mm. crassi, modice pubescentes, pilis conspicuioribus ascendentibus acutis.—Seeds collected near Sandy Hill (now Hudson Falls), New York, 1902, distributed by D. T. MacDougal. Type (from a cultivated plant) *Bartlett* 3501, in U. S. Nat. Herb. nos. 393738–40. <sup>(6)</sup> *even*

***Oenothera biennis* var. *leptomeris* Bartlett nom. nov.**

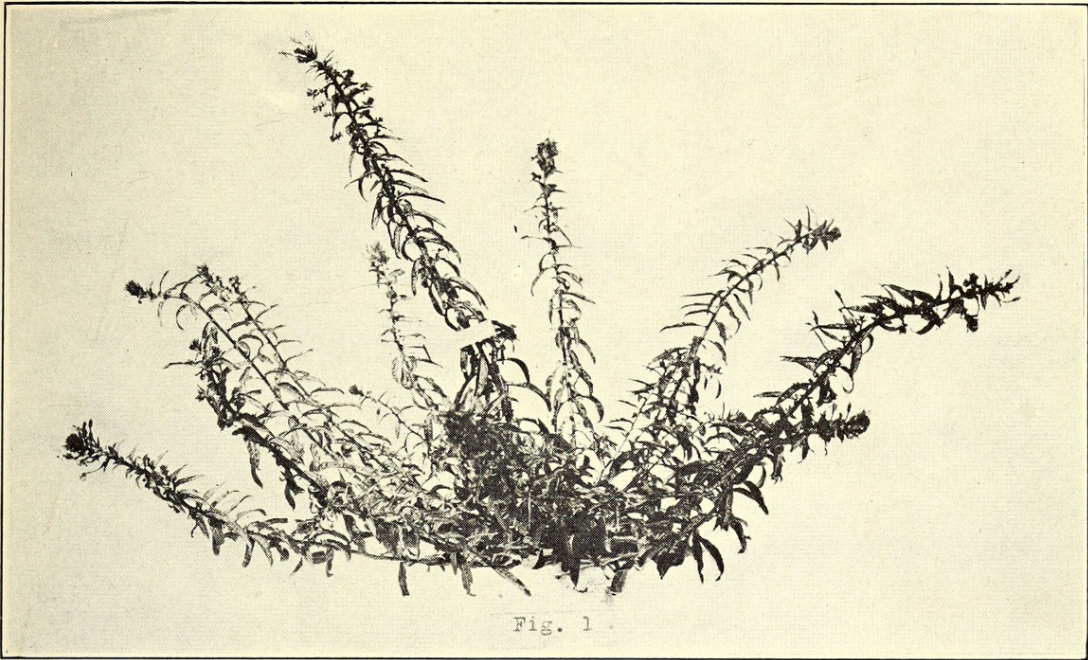
*Oenothera biennis* var. *cruciata* de Vries non T. & G.

A speciei forma typica differt solum petalis lineari-oblongis.—The cultivated line originated from seeds of a plant discovered at Santpoort, Holland, *Ernst de Vries*; known from other localities in Holland and from Lüneberg, Germany, *Klebahn*.

***Oenothera stenomeris* Bartlett, sp. nov.**

Annua. Rosula ex paucis (ca. 10–14) foliis constans, maximis ca. 20–22 cm. longis, 4–4.5 cm. latis, acutis vel obtusiusculis, infra mediam valde sinuato-dentatis, cito caulem et interdum 3–5 ramos radicalis emittens. Planta matura 10–12 dm. alta. Caulis proprius inter mediam spicamque terminalem ramos floriferos ferens, superiores ac longiores primo florentes, demum inferiores ac breviores quos plerumque in ramulos brevis non florentes gradatos sunt. Rami numerosi plantae partis inferioris cauli proprio omnino similes sed breviores, nec in ramos superioris partis transgradientes. Caules rubri et virides, pilis longis acutis rubrotuberculatis sparsi et aliis similibus sine tuberculo rubro, longitudine variantibus, plerumque minutis, pubescentes. Folia ovatolanceolata in medio caule ca. 15 cm. longa, 4 cm. lata, utrinque acuta, modice sinuato-dentata, pilis acutis vestita. Bracteae lanceolatae fructibus et ovariis tertia parte longiores, tenuiter pubescentes, margine pilis aliis acutis verrucosis, aliis ampulliformibus ciliatae. Hypanthium ca. 35 mm. longum, 1.5–1.8 mm. crassum, pilis paucis acutis arcuatis praeditum. Calycis segmenta ca. 14 mm. longa pilis eis hypanthii similibus praecipue supra mediam sparse vestita; apicibus liberis terminalibus, 2.5 mm. longis dense pilosis, saepissime (in floribus cleistogamis vel subcleistogamis) basi persistenter adnatis. Petala lineari-oblonga, 10–11 mm. longa, 2 mm. lata, extus prope apicem pilis paucis subulatis acutis ornata, intus glabra. Stamina stigmata aequantia. Ovarium ca. 12 mm. longum, etiam pilis acutis solis indutum. Fructus modice congesti, ca. 2.2 cm. longi, sparse pilosi, apicibus liberis brevibus truncatis.—Chevy Chase and





BARTLETT: CRUCIATE-FLOWERED ŒNOTHERAS.









BARTLETT: CRUCIATE-FLOWERED ŒNOTHERAS.









BARTLETT: CRUCIATE-FLOWERED ÆNOTHERAS.







Bethesda, Montgomery County, Maryland. Specimens from garden plants, *Bartlett* 2717 and 3146 (type, in U. S. Nat. Herb. nos. 693733-5.).

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EXPLANATION OF PLATES XIX-XXI

PLATE XIX, FIG. 1. *Oenothera atrovirens* Shull & Bartlett. Flowering plant. (The small label is 10 cm. long.)

FIG. 2. *Oenothera venosa* Shull & Bartlett. Flowering plant. (The small label is 10 cm. long.)

PLATE XX. *Oenothera atrovirens* Shull & Bartlett. Inflorescence and details.

PLATE XXI. *Oenothera venosa* Shull & Bartlett. Inflorescence and details.





Bartlett, Harley Harris. 1914. "An account of the cruciate-flowered *Oenotheras* of the subgenus *Onagra*." *American journal of botany* 1(5), 226–243.

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