Proceedings of the Iowa Academy of Science

Volume 17 | Annual Issue

Article 13

1910

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Recommended Citation

Gates, R. R. (1910) "Early Historico-Botanical Records of the Oenotheras," *Proceedings of the Iowa Academy of Science*, 17(1), 85-124. Available at: https://scholarworks.uni.edu/pias/vol17/iss1/13

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EARLY HISTORICO-BOTANICAL RECORDS OF THE OENOTHERAS.

By R. R. GATES.

The present paper is an attempt to trace, as far as possible from available data, the history of the Oenotheras, particularly the largeflowered forms, in cultivation. An effort is also made to recognize, as far as this can be done, the precise characters of the various forms which have been figured or described during the last three centuries. Such records of course vary greatly in accuracy and value, for they are contemporaneous with the development of the science of botany itself. Judging from the number of polynomials applied to them by different authors, the Oenotheras would appear to have been as variable then as they are now. And I may say that my cultures of Oenotheras derived from various sources indicate that at present many of these forms are no less variable or mutable than the O. Lamarckiana of DeVries' experiments.

I have been able to examine a large number of references and plates of Oenotheras—many of them pre-Linnaean—from the valuable sets of Herbals and Icones in the library of the Missouri Botanical Garden. I wish to express my thanks to the Director. Professor William Trelease, for valuable aid in connection with the study of these early records. I am also indebted to Miss Cora J. Hogan, who has aided in deciphering the Snippendale manuscript and has also translated most of the Latin descriptions. I have attempted to trace, as far as possible, the history of O. Lamarchiana Ser., O. grandflora Ait. and (in part) O. biennis L. from these early citations and plates. See also the important historical data supplied by Miss Vail in MacDougal (1903). The degree of accuracy of the plates varies greatly, but in many cases at least, one's conclusions concerning the plants figured can rest on a pretty certain basis, when they have a minute knowledge of the differentiating characters of these forms. O. Lamarckiana and O. grandiflora have often been confused with each other, and there was frequent failure to recognize these two as independent forms. The same is true of O. biennis and O. Lamarchiana. DeVries (1905) has

shown that the O. Lamarckiana now grown in European gardens, and from which the Hilversum cultures were derived, came from Texas, being imported by Messrs. Carter & Sons, London, about 1860. The forms closely resembling O. Lamarckiana, which were grown in European gardens and figured long previous to this, were from another source, and it is now established, from certain records in this paper, that that source must have been in Eastern North America, specifically "Virginia." The record of this last introduction of O. Lamarckiana into England is clear, but the earlier records have been very misty. It is certain, from results communicated here, that a form closely resembling though probably not identical with the O. Lamarckiana race of DeVries' cultures, was the first Oenothera taken to Europe from Virginia, about 1614.

In the case of O. arandiflora, the record of the introduction into Kew in 1778 is perfectly clear, as is also the account of the discovery of O grandiflora in Alabama by Bartram about 1773. (See MacDougal et al 1905, p. 7). The plate of O. grandiflora by Barton, (1821), I regard as undoubtedly representing O. grandiflora rather than O. Lamarchiana, on account of the smooth stem, the slender rounded buds and delicate sepal tips, and the stem leaf (fig. 2), which is not broad at the base, like O. Lamarckiana, but correct for certain races of O. grandiflora. This plate is reproduced by a photograph in MacDougal (1905). Barton describes this plant as native in Carolina and Georgia. It is probable that O. grandiflora was formerly common in that region, and if an introduction of this plant into Europe took place at an earlier date than the one of which we have such a good historical record (as it almost certainly did), it must have been from seeds collected in the Eastern range of the species. It is probable that the Alabama and Carolina plants were not identical, belonging rather to closely related elementary species, but they must have been more closely related than O. grandiflora is to O. Lamarckiana. The differences between these races will be referred to later in this paper.

The volume which served as a starting point in following the early records of Oenothera, was Tournefort's *Institutiones** (1700) p. 302. Here the genus Onagra is characterized, accompanied by a plate (156) illustrating the Onagra flower, fruit and seed with considerable accuracy. At least one of the flowers illustrated is in the *O. biennis* series, with short style and small petals. One with somewhat longer style is apparently shown for contrast. Nine species of Onagra are then enumer-

^{*}See MacDougal (1903), p. 754, for several other historical references.

ated as polynomials. Some of them have since been referred to other genera, such as Jussiaea and Mentzelia. They are as follows:

- (1) Onagra latifolia. Lysimachia lutea, corniculata C. B. Pin. 245.
- (2) Onagra latifolia, flore dilutiore. Lysimachia corniculata non papposa, Virginiana, major, flore sulphureo H. L. Bat.
- (3) Onagra latifolia, floribus amplis. Lysimachia Virginiana, altera, foliis latioribus, floribus luteis, majoribus Cat. Altdorf.
- (4) Onagra angustifolia, Lysimachia angustifolia, Canadensis, corniculata, H. R. Par. Lysimachia Corniculata, lutea, Canadensis, minor, seu angustifolia Mor. H. R. Bles.
- (5) Onagra angustifolia, caule rubro, flore minori.
- (6) Onagra Americana, folio Betonicae, fructu hispido Plum.
- (7) Onagra Americana, foliis Persicariae amplioribus, parvo flore luteo Plum.
- (8) Onagra Americana, foliis Persicariae angustioribus, magno flore luteo Plum.
- (9) Onagra Americana, frutescens, Nerii folio, magno flore luteo Plum.

The reference "Plum" in the last four, is to Plumier's "Description des Plantes de l'Amerique," published at Paris in 1693. An examination of this work showed that neither this nor the later edition (1713) contained descriptions or figures of any Onagras, but Plumier's Catalogue (1703) lists these forms. The explanation doubtless is that these four polynomials had been furnished to Tournefort by Plumier, but the latter had failed to complete his plates for publication in either edition of the work referred to. Later. in Plumier's Plantarum Americanarum the figures are published in the 7th fascicle, 1758. There (6) is referred to Mentzelia while (7) is described as Jussiaea; (8) and (9) are described with polynomials as Oenothera, with a reference to Browne's History of Jamaica (1756). The latter merely gives the polynomials of three "Oenothera" species, but Jacquin lists them in Select. Stirp. Amer. Hist. (1788) and his plate, (Vol. 2, pl. 70) together with the description makes it certain that these are also species of Jussiaea, as might have been expected.

Number (5), with small flowers, is evidently a species of Tournefort. It was afterward referred by Linnaeus to Oenothera fruticosa, (Sp. Pl. p. 346). The plant which Linnaeus meant to indicate by this designation was, however, not what we now know as O. fruticosa, L., which belongs in a different group, but O. muricata, L. as now known. This is shown by Barrelier (1714), who cites Tournefort's Onagra angustifolia, caule rubro, flore minore as a synonym for his Lysimachia angustifolia, spicata, lutea, Lusitanica, with a figure (990). This figure is reproduced in plate 3 of this paper, and in comparison with the figure

989, which illustrates one of the *O. biennis* forms, indicates that one of the forms of *O. muricata*, L. was intended, having smaller flowers and narrower leaves than *O. biennis*. Tournefort's species (5) therefore clearly refers to the present *O. muricata* L.

In (4) the reference "H. R. Par." is to Hortus Regius Parisiensis, 1665, which is merely a catalogue of polynomials. "Mor. H. R. Bles." refers to Morison's Hortus Regius Blesensis, 1669. Here (p. 126) is the earliest recognition I have found of a large-flowered and a smallflowered form. In addition to Lusimachia lutea corniculata of Bauhin's Pinax (which is nearest O. Lamarchiana, as I shall show later) are listed two forms which were introduced into the London Garden between 1655 and 1660. These are named Lysimachia corniculata minor lutea Canadensis and Lysimachia lutea flore globoso, Park. Ger. On page 284 of the same work Morison says further. "Lusimachia Corniculata, lutea Canadensis minor seu angustifolia: Haec sola foliorum angustia, aliarum suarum partium; horum scilicet & capsularum seminalium, parvitate differt, a Lysimachia Corniculata lutea majori Cornuti." This form with narrower leaves and smaller flowers probably belonged to O. biennis, or possibly to O. muricata, but in the absence of figures I have not been able to trace it further.

To return to Tournefort, in (3) "Cat. Altdorf." refers to Hoffman's *Flora Altdorffina*, 1677, which I have not seen. This plant is undoubtedly a large-flowered Oenothera from Virginia, and I am strongly inclined to think that it belongs with *O. grandiflora*. The reasons for this will be given later.

The reference "H. L. Bat." in (2) is to Hermann's Horti Academici Lugduno-Batavi Catalogus, 1687, in which are cited Lysimachia lutea corniculata non papposa Virginiana major and Lysimachia lutea corniculata non papposa Virginiana minor from Morison's Plantarum Historiae Universalis Oxoniensis, Part II, p. 271, (1680). In the latter work Morison gives a lengthy description of the former and refers to the large yellow flowers. I shall show later that this is close to O. Lamarckiana Ser. while the other is undoubtedly a form of O. biennis L., probably the "European biennis," which has flowers somewhat larger than our American forms.

The reference to "C. B. Pin." in (1) is to Bauhin's *Pinax Theatri* . *Botanici*, first edition 1623. This plant was also certainly nearer O. *Lamarckiana* than anything else, as I shall show later.

It will be well now to trace chronologically some of the early records regarding Oenothera. I have not attempted to hunt down every reference nor see every plate. But the accuracy of our present knowledge

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of the forms we call *O. biennis* L. *O. Lamarckiana* Ser., and *O. grandiflora* Ait., enables one to decide definitely in many cases which form is referred to in the early descriptions and plates, and in this way a much more accurate knowledge of the history of these forms in Europe can be attained.

The earliest figure of an Oenothera which I have seen is in Alpin's *De Plantis Exoticis*, 1627. This book was published in Venice, and the plants were grown from seeds obtained from an English physician and "philosopher." There is a description (p. 325) under the name *Hyoscya*-*mus* ·*Virginianus* and a crude line-drawing which, with the description, leaves no doubt that this is a large-flowered evening primrose; and it came from "Virginia." The extremely long hypanthia in the drawing are probably exaggerated, but the statement in the description, "Ex singulis vero alarum foliorum cavis exibat petiolus digitali longitudine fere" shows that the flower must have approximated closely to the size of our present large-flowered forms. See plate 1.

The earliest reference to North American Oenotheras seems to be in Caspar Bauhin's *Pinax* (1623) published at Basil. Here (page 245) he enumerates, with polynomials, eighteen species of Lysimachia. His sub-section *Lysimachia lutea* includes some species still retained in Lysimachia and also *Oenothera biennis* L.; his sub-section *Lysimachia siliquosa* is our genus Epilobium; and his *Lysimachia spicata* and *non-spicata* include species of Lythrum, Veronica and Scutellaria. The Oenothera form is described as follows:—

Lysimachia lutea corniculata.

Lysimachiae Virgineae nomine ipsum semen Patavio missum quod anno 1619. in horto eleganter crevit & ex semine deciduo se facile hactenus propagavit.

This reference to p. 245 of Bauhin's *Pinax* is the only one quoted in most of the later citations. One of the copies of the *Pinax* (1623) found in the library of the Missouri Botanical Garden contains a marginal note describing the plant represented by Bauhin's *Lysimachia lutea corniculata*. The owner of this volume who evidently inserted these and other marginal notes, was Joannis Snippendale who I have since learned, (see Andrews, 1910) was about this time connected with the Botanical Garden at Amsterdam. A note on this subject was published in Science (1910). I have since found the source of the Snippendale manuscript. It is to be found printed in an appendix to the *Pinax*, p. 520, and therefore the description, which was especially long and detailed for the time, refers

to plants grown by Bauhin, presumably at Basil.¹ The description mentions that the plants were obtained from Padua (the first botanical garden founded in Europe) and grown in 1619, and the description was evidently written from the living plants. This fixes with certainty the date on which the observations were made, and also shows that the Lysimachia lutea corniculata of Bauhin must be placed in the series of forms coming under Oenothera Lamarchiana, Ser., though not identical with that form in the strict sense. The text of this description of Bauhin, which is appended, together with a translation, reveals the fact that a form very similar to O. Lamarchiana Ser. was originally a wild species in Virginia, and that it was the first Evening Primrose to be taken to Europe.

V. Lysimachia Lutea Corniculata: planta est ramosa ad viri altitudinem assurgens, forma ad Lysimachiam latifoliam purpuream siliquosam accedens: haec ex radice oblonga alba, digitalem crassitudinem superante, paucis fibris capillata, caulis exsurgit initio rotundus, at supra medium, ob plurimos ramos angulosus, subcinereus, laevis, statim a radice in breviores, mox majores ramos, hique in alios late expansos, brachiatus, qui rotundi paucissimis pilis donati, hinc inde maculis parvis rubentibus variegati, ex quibus tanquam ex poris pilus prodit. Folia statim ad radicem plura, oblonga, palmum superantia, latitudine unciam vix excedentia, quae crassa, pallide virentia, laevia in acutum desinentia; quorum inferiora quandoque laciniata, reliqua vero obscure sinuata, per quorum medium costa alba, ut in Lysimachia Chamaenerion dicta, excurrit; ex alarum sinibus pediculus articulatus et rotundus prodit, cujus pars subra articulum triuncialis fistulosa, cui flos magnus, flavus quadrifolius extra folia effertur: qui cum primo florere incipit, quadrangulus est, quo aperto verum Sole tantum lucente, in ejus medio stilus conspicitur, qui viridis ad articulum usque descendit. et apicibus quatuor sulphurei coloris, crucis in modum dispositis, donatus est, quem stamina octo circumstant, quorum quatuor singulis foliis adposita, alia quatuor ipsis interjecta sunt; hisque singulis capitulum oblongum albicans insidet: ipsi vero flori, calycis in modum, folia quatuor oblonga, angusta, pallida subjiciuntur. Fles odoratus est, nonnihil ad Keiri,¹ vel potius Liliasphodeli lutei odorem accedens, ultra diem non persistens, cum is qui sub vesperam aperitur, ad sequentis diei vesperam flaccescat, unde Ephemerum dici meretur. Flore, cum pedicello ad articulum delapso, altera pediculi pars sesquiuncialis, sensim ad uncias binas, etiam ternas oblongatur et in siliquam sive corniculum abit, et propter semen copiosum, nigrum, parvumque, quod continet, intumescit; quod ubi maturuit, ipsa cornicula, quae utringue ad caulis latera numerosa sunt, in quatuor partes dividuntur. Hujus semen, Lysimachiae Virginianae nomine Anno 1619. Patavio accepimus, quod Vere satum, tota aestate et hyeme sine caule remansit: at sequenti anno, circa Veris finem caulescere, et Junio florere coepit; nunc vero ex deciduo semine (annua enim planta est) autumno delabente, singulis annis in hortulo meo copiose et usque in autumni finem floret.

³Curiously enough, most of the later citations of the *Pinax* refer only to page 245, and for this reason the existence of the description in the appendix, which Snippendale evidently copied, was at first overlooked.

¹Probably Cheircinthus cheiri of Willd. Sp. Pl. 3:516.

Matthioli Ephemerum esse suspicatus sum, sed cum nullas, nisi Dioscoridis, notas, adposuerit, nil pronunciare licet.

English Translation.

Lusimachia lutea corniculata is a branchy plant rising to a man's height. Its shape resembles Lysimachia latifolia purpurea siliquosa.¹ It (comes up) from an oblong white root, thicker than the finger, bearing a few fibres. The stem rises round at the base, and above the middle becomes angular on account of the many branches, (is) subcinereous, smooth, branches out right from the root into rather short branches, soon becoming longer, and these branch into others broadly spread out, which (and these) are round (and) supplied with a very few hairs, (and) dotted with small reddish spots, from which, as from pores, a hair protrudes. There are many leaves right at the root, oblong, longer than the palm of the hand, (but) scarcely exceeding an inch in width. These are thick and pale green, slender (and) end in a point; the lower ones are sometimes laciniate, the others in truth obscurely sinuate. Through the midst of them runs a white rib, as in the aforesaid Lysimachia chamaenerion.² From the curves of the wings (i. e. from the axils of the leaves) a jointed round pedicel comes forth, of which the part above the joint is three inches³ long and hollow. On this a big yellow, fourpetalled flower, flares out beyond the leaves. When it first begins to flower, it (the bud) is quadrangular, and opening when the sun is still barely shining, in the midst of it is seen a pistil, which (is) green (and) goes down all the way to the joint, and is furnished with four apices, sulphur-colored and arranged in the form of a cross, around which stand eight stamens, four of which are placed one opposite each petal. The other four are set in between the first (four). On each one of these sets a small whitish head. Four oblong, narrow, pale leaves are set in underneath the flower itself, in the form of a calvx. The flower is fragrant, not unlike the Keiri, but rather more like the odor of the yellow liliasphodel. (It) does not last beyond one day, and when it opens towards evening it wilts on the evening of the following day, from which it deserves to be called Ephemerum, when the flower with its pedicel has fallen off at the joint, the other part, measuring an inch and a half,¹

¹A species of Epilobium.

²Probably Epilobium angustifolium L.

³It is probable that the dimensions stated are only approximately correct and cannot be taken as accurate measurements. In none of these forms, for example, is the hypanthium three inches in length, but such a measurement would answer approximately for the combined length of hypanthium and cone, which is probably referred to here. Similarly, the width of the rosette leaves, given as scarcely more than an inch, is probably only an approximation. The measurement given for the length of the ovary, viz.: 1½ inches, must surely be incorrect.

¹This must be an error. Half an inch would be more nearly correct for any Oenothera of this group comprising O. Lamarchiana, O. grandiflora and O. biennis.

gradually elongates to two or three inches, and grows into a pod or little horn, and swells out because of the abundant little black seeds that it contains. When it (the seed) is ripe, the little horns, which are thickly set on both sides of the stem, are divided into four parts. We received this seed, *Lysimachia virginiana* by name, from Padua in the year 1619, and when it was sown in the spring, it remained the whole summer and winter without a shoot. And the following year it began to send up shoots about the end of spring, and to flower in June: now from the seed falling in the autumn, (for it is an annual plant), it flowers abundantly every year in my little garden until the end of autumn. I suspect it to be Matthiolus's ephemerum,² but since he has stated that there are none known unless those of Dioscorides, there is nothing which permits me to decide.

To enable the reader to follow these records intelligently I should here state that, as the result of cultures of numerous races of O. grandiflora and O. Lamarckiana forms, derived from various sources, as well as from the work of MacDougal, Miss Vail, and others (1907), (see Gates 1909) the main differentiating characters between the two series of forms are seen to be (1) the buds of the former are rounded instead of quadrangular, more slender, with thinner sepals and usually more slender and setaceous sepal tips than O. Lamarckiana forms. (2) The leaves of the mature rosettes in O. grandiflora have conspicuous basal lobes and are thinner than in any O. Lamarckiana forms. (3) Physiologically the O. grandiflora forms agree in partly or wholly omitting the rosette stage, under the same conditions of culture in which it is almost invariably well-developed in all the O. Lamarckiana forms.

The characters described which serve to identify this plant of Bauhin may now be considered. (1) The presence on the branches, of little red dots, each with a hair arising from it. O. Lamarckiana and all its mutants, as well as O. biennis, have a long type of hair,—the one mentioned here,—which is much longer and stouter than the other type and which always arises from a little papilla, the latter being usually red. This type of hair also occurs on the stems of the O. grandiflora from Alabama, but I have reason to believe that it is much less common and frequently absent from O. grandiflora in its Eastern range. This belief is based upon studies of the O. grandiflora forms now growing wild in certain parts of England, which very probably are descended from plants introduced from Virginia at an early date. (2) The rosette leaves are described as oblong, hardly more than an inch in width, thick and pale green, slender and pointed. The lower leaves of the rosette are said to

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²This is probably Lysimachia ephemeruin of Willdenow's Sp. Pl. 1:817.

be sometimes laciniate, the others obscurely sinuate. A careful study of this description, and comparison with the rosette stages of O. Lamarckiana and O. grandiflora forms, leads me to the conclusion that it undoubtedly could not have referred to *O. grandiflorg*, because the leaves are described as long and narrow, thick and pale green, while in O. grandiflora the leaves are not only broad and darker green, usually mottled with red, but are thin and comparatively delicate. The conspicuous lobes or laciniations at the bases of the leaves of the mature rosette. which seems to be characteristic of all the O. grandiflora forms, might at first be thought to be indicated by the words "inferiora quandoque laciniata." but these words would refer more correctly to the inconspicuous lobes or projections not infrequently found near the base of the blade in O. Lamarchiana and others of that series. Taking the rosette characters tout ensemble, they certainly in my judgment picture a plant of the O. Lamarckiana series, while they could not reasonably be held to refer to any form in the O. grandiflora series. Therefore, regarding O. Lamarchiana as a "Linnaean" species, this form should be included within it. On the other hand the description differs in several respects from the typical O. Lamarckiana of cultures. There is no mention of the crinkling of the leaves, but I shall show that this is referred to in an independent description of what was probably the same form. The rosette leaves, if only an inch in width, are certainly much narrower than is usual in our O. Lamarchiana.¹ (3) The fact that the hypanthium or flower stalk is about three inches long and the flower large, of course precludes the plant from being O. biennis or any other small-flowered form. (4) The statement that the bud is quadrangular is important because it again eliminates O. grandiflora as a possibility. The third character referred to then distinguishes the plant from O. biennis, while either the rosette characters or the quadrangular buds are sufficient to make it certain that the plant cannot be O. grandiflora. The only other species which is a possible candidate for this position is O. argillicola McK. The rosette leaves of the latter are very narrow but, though its flowers are large, several other characters, such as the rounded bud and the more or less decumbent stem and branches throw this out of court as a possibility. While the plant described in this earlier account is therefore closer to O. Lamarchiana Ser. than to any other form, and cer-

It has occurred to me that these rosette leaf characters might compare very well with O. *laevifolia*. Is it possible that O. *laevifolia* is not a mutant from O. *Lamarckiana* but has persisted continuously in collections of seeds, since this earliest introduction? If so, it would probably be the form referred to in the Hort. Cliff. (1737) as growing abundantly on the sand dunes of Holland. Against this interpretation is the fact that plants growing on the English constances near Liverpool from an early date, contain the true O. *Lamarckiana* as a prominent constituent of the population, but are not found to contain O. *laevifolia*.

tainly agrees with the latter in all essentials; yet it seems evident that the rosette leaves were narrower than in our type. Moreover, according to the description, there were also secondary branches developed, which is not usually the case in our present O. Lamarckiana. The plants are also said to be the height of a man, which is rather higher than O. Lamarckiana averages in cultures. I shall show later that the O. Lamarckiana now growing wild on the coast north of Liverpool, England, must have originated from the early introduction of O. Lamarckiana from Virginia, while the O. Lamarchiana of DeVries' cultures is known to have come from Texas. In this connection it may be worth noting that this English O. Lamarckiana in my cultures attains a somewhat greater height than the plants of DeVries grown under the same conditions. These differences, however, are of quite minor value and the important features, such as the red papillae on the stem, the general shape of the rosette leaves, the large flowers and quadrangular buds, make it certain that the plant described by Bauhin cannot be excluded from O. Lamarchiana Ser. and placed with one of the other species.

This appendix to Bauhin's *Pinax* contains the oldest description of a North American Oenothera known to exist. Certainly very few American plants, if any, received so accurate a description at such an early date. As an early historic record of the plant this is about all that could be asked for; and it is certainly much more complete and accurate than could have been expected. It shows that the claim frequently made, that O. Lamarckiana originated in cultivation, either through crossing or in any other way, is without sufficient foundation. There has been so much obscurity and doubt regarding the origin and early history of O. Lamarckiana, that a description which proves that a plant closely resembling it, at least, originally grew wild in "Virginia" and was the first Evening Primrose introduced into Europe, must be regarded as of prime importance as an historical record. The fact that the details of De Vries' Mutation Theory have been conceived on the basis of the behaviour of this plant, gives every item of its early history an added import. It should be stated that the fact that O. Lamarckiana was originally wild does not preclude its having arisen in nature through the crossing of races, although this is improbable for other reasons; nor does it show that crossing has not taken place since its introduction into gardens, for undoubtedly such crossing has taken place. But a discussion of these questions is not germane to the present subject, which is merely to trace the historic record of these plants. In regard to this earliest record it should be pointed out that this form could not have

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arisen by crossing during the five years between 1614, when the plants are first said to have been introduced, and 1619, because a single (largeflowered) type was introduced and there was nothing with which it could cross. The earliest record of a small-flowered form I have found in Morison's *Hortus Blesensis* in 1669, previously referred to.

In looking through the later works of Caspar Bauhin, and especially the *Historia Plantarum Universalis* of John Bauhin, I have found no further mention of *Lysimachia lutea corniculata*. In the last mentioned work, Vol. II, pp. 901-908 (1651), the Lysimachias are described and figured, but this plant is not included, most of the species described being evidently Epilobiums. Its absence cannot be ascribed to its being an exotic, for a "Lysimachia" from Argentina in 1595 is described.

In summing up the case it may be said that the references, in the description, to the large flowers, the quadrangular buds, and the shape and other features of the rosette leaves, remove this plant with certainty from either *O. biennis* or *O. grandiflora*. The only discrepancies with *O. Lamarckiana* as we now know it are (1) the rosette leaves scarcely exceeding an inch in width. But this may be an error, because the reference to ovaries an inch and a half long is evidently an error. However, Parkinson, in his *Paradisus*, also refers to the rosette leaves as "long and narrow pale green leaves," so that it seems probable that this plant had narrower and paler green rosette leaves than the one we now cultivate. There also appears to be no mention of the crinkling of the rosette leaves. (2) Secondary branches are not usually formed in our plant, although they may occur. These minor differences are, however, certainly of much less importance than the similarities already pointed out.

The next reference that I have examined is in Parkinson's *Paradisus*, 1629. From his accompanying figure it is uncertain whether the flowers are large or small, but in his *Theatrum Botanicum* (1640) p. 548, he gives a better figure, which shows that this is undoubtedly a large flowered Oenothera. His quaint description is as follows:

Lysimachia lutea siliquosa Virginiana. The tree primrose of Virginia.

Unto what tribe or kindred I might referre this plant, I have stood long in suspense, in regard I make no mention of any other *Lysimachia* in this work: lest therefore it should lose all place, let me ranke it here next unto the Dames Violets, although I confesse it hath little affinity with them. The first yeares of the sowing the seede it abideth without any stalke or flowers lying upon the ground, with divers long and narrow pale green leaves, spread sometimes round almost like a Rose, the largest leaves being outermost, the very small in the middle: about May the next yeare the stalke riseth, which will be in Summer

of the height of a man, and of a strong bigge size almost to a man's thumbe, round from the bottome to the middle, where it groweth crested up to the toppe, into as many parts as there are branches of flowers, every one having a small leafe at the foote thereof; the flowers stand in order, one above another, round about the tops of the stalks, every one upon a short foot-stalke, consisting of foure pale yellow leaves, smelling somewhat like unto a Primrose, as the colour is also (which hath caused the name) and standing in a greene huske, which parteth it selfe at the toppe into foure parts or leaves, and turne themselves downewards, lying close to the stalke: the flower hath some chives in the middle, which being past, there come in their places long and cornered pods, sharpe pointed at the upper end, and round belowe, opening at the toppe when it is ripe into five [?] parts, wherein is contained small brownish seed; the roote is somewhat great at the head, and wooddy, and branched forth diversely, which perisheth after it hath borne seeds."

He also states that the plant "came out of Virginia."

This is very evidently the same plant as the Lysimachia lutea corniculata of Bauhin, though an independent description.

Robert Morison in his *Plantarum Historia Universatis Oxoniensis*, Vol. II., published at Oxford in 1680, used the description of Bauhin as the basis for his description of the same plant. Many parts are repeated word for word, even one or two errors being perpetuated in this way; but there are also a number of minor changes in the order of description and in the order of words, several additions tending to complete the description, and one or two corrections. These will be seen on comparing the Latin of the two descriptions. Morison's description of this and a second (small-flowered) species (p. 271) is as follows:

Lysimachia lutea corniculata non papposa.

7. Lysimachia lutea corniculata non papposa Virginiana major, nobis. Lysimachia lutea corniculata C. B. P. Lysimachia siliquosa Virginiana, Park. Haec Lysimachia peregrina non multis abhinc annis ex Virginia aliisque Americae Septentrionalis partibus, seminibus in Angliam delata & hic sata, ad cubitalem & bicubitalem aliquando altitudinem provenit: folia habet prima glauca, longa, orbiculariter per terram strata, sinuata, mucronata, palmum superantia, latitudine vix unciam excedentia quae sunt crassa, laevia, pallide virentia, & in acutum mucronem desinentia, per quorum medium costa alba, ut in Lysimachia Chamaenerion dicta, excurrit: praedicta folia exeunt ex radice longa, alba, digitalem crassitudinem superante, paucis fibris capillata; caulis exsurgit initio rotundus, at supra medium ob plurimos ramos angulosus, subcinereus, laevis statimque in breviores, mox majores qui rotundi paucissimis pilis donati, hinc inde parvis maculis rubentibus variegati, ex quibus tanquam ex poris pilus exilit. Ex alarum sinubus pediculus articulatus & rotundus prodit, cujus pars supra articulum triuncialis, fistulosa, cui flos magnus, flavus, quatuor petalis constans, extra folia effertur, qui cum primo florere incipit, quadrangulus est, quo aperto vel sole tantum lucente in ejus medio stilus conspicitur, qui

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viridis, usque ad articulum descendit, & apicibus quatuor sulphurei coloris, crucis in modum dispositis donatus est, quem stamina octo circumstant, quorum quatuor singulis foliis apposita, alia quatuor ipsis interjecta sunt: hisque singulis capitulum oblongum albicans insidet: ipsi vero flori calycis in modum foliola quatuor, oblonga, angusta, pallida, subjiciuntur: flos odoratus est, nonnihil ad keiri vel potius Liliasphodeli lutei odorem accedens, ultra diem non persistens, cum is qui sub vesperam aperitur ad sequentis diei vesperam flaccescat, unde Ephemerum dici meretur. Flore cum pedicello dilapso altera pediculi pars sesquiuncialis sensim ad uncias binas, etiam ternas, oblongatur, & in siliquam seu corniculum abit, & propter semen copiosum. nigrum aut fuscum parvumque, quod continet, intumescit, quedque ubi maturuit, ipsa cornicula, quae utrinque ad caulis latera numerosa sunt, in quatuor partes dividuntur: ex semine sato tota aestate & hyeme sequente sine caule remanent plantae folia per terram strata; at sequenti anno circa Veris finem caulescere, & Junio florere incipit, & floret & semina perficit in Autumni finem, atque cum sit biennalis planta ex semine deciduo Autumno dilabente, singulis annis in hortis nostris copiose conspicitur sine caule, adventante secundo Vere caulem erigit & semina sua perficit.

8. Lysimachia lutea corniculata non papposa Virginiana minor, nobis. Haec in omnibus priori convenit, nisi quod folia producat dimidio minora & angustiora; flores pariter dimidio aut saltem multo minores, nec tam alte ascendunt caules; in caeteris omnibus majori convenit.

English Translation.

LYSIMACHIA LUTEA CORNICULATA NON PAPPOSA.

7. Lysimachia lutea corniculata non papposa Virginiana major, our (species). Lysimachia lutea corniculata, C. B. P. Lysimachia siliquosa Virginiana, Park. This Lysimachia, a foreign (plant), was brought by seed not many years ago from Virginia and other parts of North America to England and sown here. It attained a height of one or two ells. It has at first long glaucous leaves, spread out in a circle over the ground, sinuate, mucronate, longer than the palm (of the hand), hardly more than an inch in breadth, which are thick, smooth, pale green, and end in a sharp point. Through the middle of them runs a white rib, as in Lysimachia Chamaenerion aforesaid. These same leaves come forth from a long, white root, thicker than the finger, bearing a few fibres. The stem rises round at the base, and above the middle becomes angular because of the many branches, (is) subcinereous, slender, and immediately branches into rather short branches, soon (growing) larger, and these (branch) into others broadly spread out, which are round (and) covered with a few hairs, and dotted with small reddish spots, from which as from pores a hair springs forth. From

the curves of the wings a jointed round pedicel comes forth. The part of this above the joint is three inches long and hollow. On this a large vellow flower, having four petals, stands out beyond the leaves. (and) when it first begins to flower, it is quadrangular. When open or the sun shines brightly a pistil is seen in the midst of it, which (is) green (and) goes down all the way to the joint, and is furnished with four sulphur-colored apices arranged in the form of a cross. Around this stand eight stamens, four of which are placed one opposite each leaf, the other four are set in between the first (four): and on each one of these sets an oblong whitish little head. Underneath the flower itself four little leaves, oblong, narrow, (and) pale, are set. The flower is fragrant. Its odor is not unlike (that of) the Keiri but rather more like (that of) the yellow Liliasphodel. It does not last beyond one day, (but) when it opens toward evening it wilts on the evening of the following day, whence it deserves to be called Ephemerum. When the flower with its pedicel has wilted down, the other part of the pedicel, an inch and a half long, gradually elongates to two or even three inches, and grows out into a pod or little horn, and this swells up on account of the abundant, black or fuscous, little seeds that it contains; and when it (the seed) is ripe, these same little horns, which are thickly set on both sides of the stem, are divided into four parts. From the seed sown, the plants remain the whole summer and the following winter without a shoot, the leaves spread out over the ground, and the following year, about the end of spring, it begins to send up shoots, and in June to flower, and it flowers and perfects seeds towards the end of autumn, and since it is a biennial plant, from the seed that falls in the autumn, every year it is seen abundantly in our gardens without a stalk. With the coming of the second spring it erects a stalk and perfects its seeds.

It will be seen that Morison gives both species new names and describes them as his own.

If we now make a comparison of the 1619 account of this plant, with the 1680 description, on comparing the Latin, it will be seen that there are a number of additions to the later account. The plant is now found in other parts of North America than Virginia. The sequence of the description has been transposed, the account of the rosette leaves coming first, in logical order. The changes introduced are in many cases corrections of inaccuracies. Thus, in regard to the rosette leaves, "oblonga" is changed to "longa"; "obscure sinuata" hecomes "sinuata"; "mucronata" is added; "glauca," referring to the rosette leaves, doubtless has the post-Augustinian Latin meaning "bluish gray," in

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this case due to pubescene and not to a "bloom" or coating of wax as in modern botanical usage; "quandoque laciniata" of Bauhin's description is omitted entirely as being, perhaps, too infrequent or inconspicuous to find a place in the description.

In regard to the flower, "quadrifolius" becomes "quatuor petalis constans"; "folia," "foliola"; in regard to the seeds, "nigrum" becomes "nigrum aut fuscum," which is much more nearly correct. "Exilit" is perhaps more appropriate than "prodit" applied to the hairs on the stem. Some errors are also perpetuated. Thus, perhaps "latitudine unciam vix excedentia" applied to the rosette leaves; probably "albicans" applied to the anthers; certainly "sesquiuncialis" applied to the length of the ovary at the time the flower falls. The term "non papposa" in the name presumably contrasts Oenothera with the capsule characters of Epilobium.

Morison also gives figures of the two species (*Plant. Hist.* Tab. 11, Sec. 3) under the names *Lysimachia Virginiana latifolia lutca, corniculata, nobis,* Fig. 7 (with large flowers) and *Lysimachia Virginiana angustifolia, corniculata, nobis,* Fig. 8 (with small flowers). Figures of single flowers are also given, the diameter of the large flower being represented as exactly three times that of the small one. These figures are photographed and reproduced in plate 2.

Six years later, in 1686, John Ray in his *Historia Plantarum*, Vol. I., p. 862, gives a similar description, partly copied from Morison, but with many amendations and additions, and the omission of the rosette characters. The original, which is given here for comparison with the earlier descriptions, is as follows:

10. Lysimachia Lutea Virginiana Ger. emac. lutea siliquosa Virginiana Park. lutea corniculata C. B. App. TREE PRIMROSE. Lys. Americana Col. Axochiotl Hernandez.

С. В.

Ex radice oblonga, alba, digitalem crassitudinem superante, paucis fibris capillata caulis exurgit initio rotundus, at supra medium ob plurimos ramos angulosus, subcinereus, laevis [hirsutus,] crassitudine digitali, medulla farctus, & superius punctis rubentibus varie notatus. Folia longa, angusta, in caule crebra, alternatim posita, ad margines sinuata & obiter dentata. Florcs Lysimachiae modo summis siliquis insident magni, tetrapetali, lutei, Primulae veris floribus similes, e calice quadrifolio, pediculo rotundo, articulato donato. In medio flore stylus conspicitor, qui viridis usque ad articulum descendit, & apicibus quatuor sulphurei coloris crucis in modum dispositis donatus est, quem stamina octo circumstant, querum quatuor singulis foliis adposita, alia quatuor ipsis interjecta sunt; hisque singulis, capitulum oblongum albicans insidet. Flos odoratus est, ultra diem non persistens, cum is qui sub vesperam aperitur ad sequentis diei vesperam flaccescat, unde Ephemerum dici meretur.

Flore cum pedicello ad articulum delapso altera pediculi pars sesquiuncialis, sensim ad uncias binas, etiam ternas, oblongatur, & in siliquam sive coniculum abit, & propter semen copiosum, parvum, angulosum, pullum quod continet, intumescit; quod ubi maturuit, ipsa cornicula, (quae utrinque ad caulis latera numerosa sunt) in quatuor partes dehiscunt, quaternis loculamentis quatuor seminum ordines continentia, nulla intus lanugine seminibus adhaerescente. [In singulis foliorum alia singuli flores sedent; cornicula sessilia pediculis carent, ad basin crassiora, sensim versus apicem tenuiora, raris pilis hirsuta.]

Plantam hanc Lysimachiae Americanae titulo describit & depingit F. Columna, Annotat. ad Res medicas Novae Hispan. Nard. Ant. Recchi: & Axochiotl seu Florem aquae praedicti Recchi seu Hernandez, lib. 7. cap. 48, Hist. Mexicana, descriptum & depictum esse existimat, quod & nobis etiam videtur.

Prima qua sata est aestate caulem non edit, verum anno sequente, semine autem ad maturitatem perducto radicitus exarescit.

Camaranbaya Brasiliensis altera species Marggr. huic eadem esse videtur.

11. Lysimachia Virginiana altera, foliis latioribus, floribus luteis majoribus Cat. Altdorf.

Hace praecedente elatior est & major, ut quae humanum interdum altitudinem multum superet,¹ foliis latioribus, & pro magnitudine brevioribus, ad margines minus sinuatis & propemodum aequalibus: floribus etiam multo amplioribus.

In hortis nostris frequentior est praecedente.

Among the many changes in description 10, from the Morison description may be pointed out the insertion of the word "hirsutus," which characterizes the stem better than "laevis"; the word "angulosum" is added to the description of the seeds, and "pullum" substituted for "nigrum aut fuscum." The capsule is more fully described, and the clause "nulla intus lanugine seminibus adhaerescente" contrasts it with the species of Epilobium.

The reference to Hernandez was found to be an independent (earlier) account of a plant which appears to have been O. Lamarchiana. This is the only description I have found in which the crinkling of the leaves is described. In Hernandez's Nova Plant. Anim. et Miner. Mex., published at Rome in 1651, this important independent description is given (p. 882) as follows:

Lysimachia Americana.

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Primae iconis plantam, ni fallimur, vel illi admodum similem, satam habemus ex Virginia Novi Orbis allatam, & sub nomine Lysimanchiae luteae a doctiss. Johanne Pona Veronense nobis cum alijs rarioribus dono missam, cuius flores (pictoris forsan incuria in summo non dense depicti) siliquis insidentes apparent, longo lobulo prodeuntes lutei, qui crescente caule paulatim inter foliorum

¹In a recent visit to St. Anne's-on-the-Sea, on the coast near Liverpool, England, where many large-flowered Oenotheras have been growing wild for a century at least. I observed one rather constant race which seeded itself in an unused back-yard. Its average height exceeded that of a man, and its flowers were correspondingly very large. The other characters were intermediate in some respects between *O. Lamarchiana* and *O. grandiflora*, but much nearer the former.

sinus alternatim, & in spicam disponuntur: marcescentibus vero illis crassescunt siliquae quadratae, duas uncias longae, durae, & perfectae, in quatuor partes dehiscentes: copiosa intus, parva, angulosa, fusca, insipida semina continentes, & facile, vento agitata planta, decidentia, ut necesse sit cum incipiunt dehiscere, colligere. Augusto floret, & Septembri perficitur. Folia sapore insipido, quae prima facie Keiri sive luteae Violae similia videntur, sinibus levibus excavata, quae in caule vix sinuosa apparent, ut facile salignis aequiparari potuerint. Flores fructui insident longo tubulo, foliato capite, qui esti quatuor foliolis constructi sint, non tamen ideo cum Keiri aliquid commune habent, siliqua non bivalvi, non capitata, nec semina compresso: nec etiam cum vera Lysimachia folijs inordinatis, non ternis, nec adstringentibus: fructu diverso cum siliquosa dicta sive Chamaenerio non parum, nisi semina huic non papposa essent. Planta est levifolia, radice longa parum, & fibrosa, lignosa, quae regerminare solet. Iconem expressam addimus. Aliam ejusdem nominis plantam bulbosa radice, infra reperies alterius generis fol. 257.

The accompanying figure is that of an Oenothera with large flowers and the stigma projecting beyond the stamens. The branching of this plant is somewhat unusual, if correctly represented. There are no basal branches, but a few long branches near the top. However, I have seen plants in cultures with this type of branching, and there is so much difference in branching, under different conditions of growth, that this point is of little significance. The point of greatest interest in this description is the statement regarding the leaves, "sinibus levibus excavata." This clearly describes the characteristic crinkling of the leaves of *O. Lamarchiana*, and leaves little, if any, doubt that this plant was *O. Lamarchiana* in the strict sense. The upper leaves on the stem were evidently smooth, as is usually the case in our *O. Lamarchiana*. The comparison with Salix leaves may indicate that they were somewhat narrower than typical *O. Lamarchiana*.

Regarding the origin of these seeds, which were obtained from John Pona in Verona, it is not clear whether the latter had obtained the seeds direct from Virginia or had grown several generations of the plants before sending seeds to Hernandez. This leaves open the possibility that crosses might have taken place in the meantime, but if they did, the same crosses might have taken place in Virginia among the wild plants, so that this contingency does not seem to the writer to be of importance.

The reference to fol. 257 is to a figure and description of another plant in *Rerum Med. Nov. Hisp.*, published by the same author in the same year. This is evidently a Mexican species of Oenothera. The flowers are described as varying from red to yellow.

To return to the description of Ray's species, number 11, I have coneluded probably belongs to *O grandiflora*. Coming from Virginia, it

differed, as I shall show, in certain respects, from the *O. grandiflora* of Alabama which is now in cultivation. But the broader and relatively shorter leaves and the other characters mentioned seem to refer to this form, although all the distinguishing characters which would lead to certainty are unmentioned. The flowers of the reputed Virginian *O. grandiflora* may be somewhat larger than in *O. Lamarckiana*. Moreover, exceptionally tall and robust plants frequently have correspondingly larger flowers. I shall refer to this again later. It is the earliest description I have seen which could refer to *O. grandiflora*.¹

Tournefort, in his *Institutiones* (1700), recognized large- and smallflowered forms, and in 1714 Barrelier gives very instructive figures of three species as follows:

- (1) Pl. 989. Lysimachia latifolia, spicata, lutea, Lusitanica, with the synonym Onagra angustifolia Tourn. Inst. 302.
- (2) Pl. 990. Lysimachia angustifolia, spicata, lutea, Lusitanica, with the synonym Onagra angustifolia, caule rubro, flore minore. Tourn. Inst.
- (3) Pl. 1232. Lysimachia lutea, corniculata, latifolia, Lusitanica, with the synonym Onagra latifolia, floribus amplis Tourn. Inst.

The first two species are small-flowered forms, and it is very probable that they represent races of what are now known as *O. biennis* L. and *O. muricata* L. In plate 989 the spike is very dense, while in plate 990 the petals are deeply emarginate, smaller and the rosette leaves narrower than in 989. The rosette leaves have long petioles in both. The third species has much larger flowers, the leaves are represented as markedly repand-denticulate, sometimes more or less curled. Though there is little basis for judgment, the leaves seem to suggest *O. Lamarchiana* rather than *O. grandiflora*. These figures are reproduced in plates 3 and 4.

The *Hortus Cliffortianus*, published at Amsterdam in 1737, gives (p. 144) two species of Oenothera, with synonomy as follows, the genus Oenothera having been previously characterized by Linnaeus in the *Genera Plantarum*:

1. Oenothera foliis ovato—lanceolatis denticulatis, floribus lateralibus in summo caulis.

Onagra latifolia Tournef. Inst. 302.

Lysimachia lutea corniculata Bauh. pin. 245, 516.

Lysimachia lutea corniculata non papposa virginiana major. Moris. Hist. 2 p. 271.

¹Since writing this I have noticed that L' Heritier, in his description of O. grandiflora (see L' Heritier MS) says "Conf. Onagra latifolia floribus amplis. Tourn. inst. 302," which clearly confirms my conclusion.

Lysimachia lutea corniculata latifolia lusitanica Barr. rar. t. 1232. Onagra latifolia, floribus amplis Tournef. Onagra latifolia flora dilutiore Tournef.

Crescit in Virginia aliisque Americae locis.

It is interesting to note that even at this time he says "Copiose crescit ubique in campis arenosis Hollandiae."

 Oenothera foliis lineari-lanceolatis dentatis, floribus e media caule. Onagra angustifolia, caule rubro, flore minore. Tournef. Inst. 302. Onagra salicis angusto dentatogue folio, vulgo Mithon. Fevill peruy. 3.

p. 48. t. 36.

Crescit in America meridionali prope Chili.

The corolla is described as "flavo rubra." I have not attempted to determine what South American species this is. Tournefort's *Onagra* angustifolia is evidently wrongly referred to it.

Linnaeus, in the first edition of the Species Plantarum (1753), recognizes three species of Oenothera (1:346), O. biennis, O. mollissima and O. fruticosa. The second is a South American form which need not concern us. Tournefort's Onagra angustifolia caule rubro, flore minore is referred to O. fruticosa. As already mentioned, the figure of Barrelier (990), together with his synonomy, makes it quite certain that the plant here designated by Linnaeus O. fruticosa was in reality what we now know under the name of O. nuricata L. The modern O. fruticosa belongs in the sub-genus Kneiffia and has a very different habit, much larger flowers and quite different capsules.

Linnaeus' citation of *O. biennis* in the *Species Plantarum*, 1st Edition, is as follows:

Oenothera foliis orato lanceolatis planis. Vir. Cliff. 33. Hort. Ups. 94. Gron. virg. 154. Roy. lugdb. 251. Gort. E. gelr. 78.
Oenothera foliis ovato-lanceolatis denticulatis, floribus lateralibus in summo caulis. Hort. Cliff. 144.
Lysimachia lutea corniculata. Bauh. pin. 245, 516.
Moris. hist. 2. p. 271. s. 3. t. 11. f. 7.
Habitat in Virginia unde 1614, nunc vulgaris Europae.

The fact that Linnaeus eites as an illustration Morison's fig. 7 (reproduced in plate 2), which is beyond peradventure a large-flowered Oenothera, and ignores all previously published figures of small-flowered species. shows without question that he meant in O. biennis to include only the larger flowered forms. Further, he recognizes that Morison's plant is the same as the Lysimachia lutea corniculata of Bauhin, which, as I have shown, on acount of the quadrangular buds and other characters, undoubtedly belongs in the O. Lamarckiana series of forms, and not to O. grandiflora. Unquestionably, therefore, Linnaeus meant as

the type of O. biennis, one of the O. Lamarckiana series of forms, with large flowers, and he excluded and ignored all reference to any of the small-flowered forms, several very good figures of which were already in existence by the same authors who had figured and described the large-flowered forms. In the *Hort*. Cliff. the synonomy as already given (p. 31 MS.) cites in addition to Morison's Lysimachia lutea corniculata non papposa virginiana major. (which is apparently the same as the plant which he figures under the name Lysimachia Virginiana latifolia lutea corniculata). Barrelier's Lysimachia lutea corniculata latifolia lusitanica with his figure 1232 (reproduced in plate 4). Barrelier cites as a synonym Tournefort's Onagra latifolia floribus amplis, which is, I believe, O. grandiflora. The figure itself is indecisive between O. grandiflora and O. Lamarckiana. Linnaeus, however, in the Hort. Cliff., segregates Ona gra latifolia, floribus amplis Tournef. as differing from the type of his species. It would, therefore, seem probable that while Barrelier considered his species to be the same as Tournefort's Onagra latifolia, floribus amplis, yet Linnaeus decided that Barrelier's plant was the same as Morison's, and that the species of Tournefort was another thing, differing in minor characters. This is in entire accord with our belief that the latter species was really O. grandiflora. Moreover, the close similarity of the names under which these plants of Barrelier and of Morrison were figured (differing only in using Virginiana for lusitanica) would indicate that these two forms were the same. At any rate, it is clear that Linnaeus meant by Oenothera biennis the large-flowered forms of O. Lamarchiana series, and it is possible. though not probable, that he meant to include *O. grandiflora*.

From this time forward large flowered forms are frequently cited or figured under *O. biennis* L., and, as we have seen, these large-flowered forms were undoubtedly the ones to which the name *O. biennis* was originally applied.

O. biennis is stated by Linnaeus to have been brought from Virginia about 1614. The source of this statement, which other evidence shows must be about true, I do not know, but it has frequently been quoted in other works. In the *Hortus Upsaliensis*, (1748) Vol. I, p. 94, Linnaeus says with reference to the plant which he afterwards called O. biennis in the Species Plantarum, "Habitat in Virginia circa 1620, in Europam translata, nunc in Belgio, Italia, Gallia, Germania spontanea," showing the wide distribution of these forms at that early time, a century after their first introduction.

Miller in the Gardener's Dictionary, 6th Edition (1752), under Onagra cites 12 species. Regarding the first, *Onagra latifolia* Inst. R. H.

or broad leav'd Tree-primrose, he says, "The first sort is very common in most English gardens, where, when it has been suffered to scatter its seeds, it will come up and flourish without any care; and many times becomes a troublesome weed: this will thrive in the Smoak of London, so that it is a very proper plant to adorn the City Gardens."

An important record and an accurate (colored) plate of Oenothera, is found in Miller's Figures of plants in the Gardener's Dictionary, the editions of 1760 and 1771 being practically identical. The figures in this work appear to be all natural size. Plate 188 is of *O. pumila* and plate 189, which is dated 1757, contains two figures. It is quite clear that these are what we now know as *O. muricata* and *O. biennis*. Fig. 1 is cited as follows:

"Oenothera foliis lanceolatis dentatis, caule hispido.

Tree Primrose with Spear-shaped indented Leaves, and a prickly Stalk. This is the *Oenothera foliis lanceolatis capsulis acutangulis*, Lin. Sp. Plant. 346. Tree Primrose with Spear-shaped Leaves, and Capsules with acute Angles. Tournefort titles it, *Onagra angustifolia*, *caule rubro*, *flore minore*, Inst. R. H. 302. Narrow-leaved Tree Primrose with a red Stalk and a smaller Flower."

In describing Fig. 1 he says definitely that the style is shorter than the stamina, and this is clearly shown by the figure. As indicated by the synonomy, as well as shown by the figure, this is the *O. fruticosa* of Linn. Sp. Pl. Ed. 1, which I have already shown is the plant we now know as *O. muricata* L. The size of the flowers, as well as the other characters, clearly correspond to certain races of this species, though the stem leaves appear to have been rather broader than typical.

In describing Fig. 2, we have the following:-

"Oenothera foliis ovato-lanceolatis planis, Virid. Cliff. 33.

Tree Primrose with oval Spear-shaped plain Leaves. This is the Oenothera foliis ovato—lanceolatis, denticulatis, floribus lateralibus in summo caulis, Hort. Cliff. 144. Tree Primrose with oval Spear-shaped indented Leaves, and Flowers proceeding from the wings of the Leaves on the upper Part of the Stalk. Tournefort titles it, Onagra latifolia, Inst. R. H. 302. Broad-leaved Tree Primrose; and by Caspar Bauhin, Lysimachia lutea corniculata, Pin. 245. Yellow horned Loosestrife."

The accompanying passage is quoted in MacDougal (1907), p. 5. The characters shown in the figure make it evident that this plant was some race of what we now call O. *biennis*, L. This is shown by the size of the flowers and by the fact that the style is short so that the stamens surround the stigma. This figure would also, however, represent equally well certain hybrids between O. *biennis* and O. *Lamarckiana*. Miller in referring the plant to the species of Linnaeus already cited in the *Hort*. *Cliff*. did the natural thing, seeing that Linnaeus had not made a separate

species for forms with flowers of this size, although, as we have seen, the type of Linnaeus' species was clearly indicated by his citation of figures, both in the *Hort. Cliff*. and the *Species Plantarum*. In later works the large and small-flowered forms were usually referred indiscriminately to *O. biennis* L. Miller's citation of the synonomy of the *Hort. Cliff*. cannot, therefore, be taken as indicating that this plant referred to the type of Linnaeus' description, as this was evidently not the case.

Philip Miller was "gardener to the worshipful company of Apothecaries at their Botanic Garden at Chelsea." I have recently cultivated a race of O. biennis (as we now understand the name, i. e., a plant with smaller flowers than O. Lamarckiana and a short style so that the flower pollinates itself) received under that name from the Chelsea Physic Garden, whose flower characters agree in general with those of our O. biennis, but the rosette leaves and stem leaves are remarkably crinkled and in general appearance much resemble O. Lamarckiana, being quite unlike
our O. biennis races. I mention this case not only to show that numerous races of O. biennis exist, differing widely from each other in certain features, but to emphasize the necessity, in determining any plant from the early records, of considering every character in so far as it can be known, before deciding upon its affinities.

Miller's statement that his plant is "more commonly seen in the Gardens than any of the other species" may be true, or it may indicate a failure to differentiate between this and the large-flowered forms. It seems probable, however, that the large-flowered forms had by this time largely disappeared from the English Gardens. We have seen that the large-flowered form referred to by Ray in 1686 which we have with a large degree of probability determined to be *O. grandiflora* from its eastern range in North America, was more common in gardens at that time than the other large-flowered form (O. Lamarckiana). Later, during the three-quarters of a century intervening between 1686 and 1760 both must have disappeared from cultivation in the English gardens.

It is interesting to note that O. Simsiana is a species with large flowers and a short style, so that the stigma is surrounded by the stamens, as in O. biennis. But this was not introduced into England until 1816 (see Curt. Bot. Mag. 45:1974), where it was raised in the garden of the Marquis of Bath at Longleats, in Wiltshire, from seeds obtained in Mexico. Moreover, its flowers are much larger than those in Miller's figure, and there are other differences. (See also Miss Vail's account in MacDougal, 1907, p. 68.)

From the use of the adjective *planis* in the polynomial cited by Linnaeus from *Vir. Cliff.* 33, it may be inferred that this plant did not have the crinkled character of the leaves as we know them in the present O.

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Lamarchiana. The leaves in the upper part of the stem in O. Lamarckiana, are, however, frequently nearly or quite smooth.

We have shown that the first Oenothera introduced into Europe from Virginia was more closely related to the *O. Lamarckiana* of our present cultures than to any other form, differing from it only in such minor points as the width of the rosette leaves; which seem also to have been of a paler green color, because the Bauhin description and Parkinson agree on this point. But the important independent description of Hernandez in 1651 definitely refers to the crinkling of the leaves. This makes it highly probable that the plant of Hernandez was almost or quite identical with our *O. Lamarckiana*, Ser.

O. GRANDIFLORA AI'L.

The history of the discovery of O. grandiflora in Alabama and its introduction into Kew has already been given by DeVries (1901) and particularly MacDougal (1905, p. 7), and need not be repeated here. But certain interesting data can be added. Before entering upon these it will be advantageous to outline some of the differences between O. Lamarckiana and O. grandiflora as we now know them from cultures (see Vail, 1907, p. 66; Gates, 1909c, p. 131). In *O. grandiflora* the buds bear only a short and inconspicuous type of hair, giving them an almost glabrous appearance (in some cases entirely glabrous), while in O. Lamarckiana and all its mutants there is in addition a long, curved type of hair, arising from papillae and giving the buds a pubescent appearance. The same is true of O. biennis. The same type of hair is found on the stems in O. Lamarckiana and O. biennis, arising from papillae which are usually red, so that the stem is covered with small red dots. O. grandi*flora* from Alabama shows the same condition on the stem, but in some of the forms of O. grandiflora from near Liverpool, England, the long type of hair is frequently almost wholly absent, leaving the stem nearly glabrous. The buds in O. grandiflora are also more slender and rounded. and the sepal tips frequently longer and usually more setaceous than in O. Lamarckiana.

In addition the rosettes are very unlike, the leaves in *O. grandiflora* being smooth, thin, and with a series of characteristic basal lobes, while in *O. Lamarckiana* they are crinkled, thicker, and without the basal lobes. But unfortunately, the rosettes are rarely mentioned, except in connection with recent studies and cultures, and in the very early works.

Professor DeVries has given an account of the history and synonomy of *O. grandiflora* Ait. He prefers to call it *O. suaveolens*, the name introduced by Desfontaines, to avoid confusion on account of the various

forms to which the name O. grandiflora has been applied.¹ The name was first given by William Aiton in *Hortus Kewensis*, Vol. II, p. 2, 1789. in which a figure by L'Heritier, Stirpes Novae, tom. 2, tab. 4, is cited. In the second edition of *Hortus Kewensis*, by W. T. Aiton (1811), the same brief description is given, Vol. II, p. 341, but instead of the L'Heritier plate, a description by Willdenow, Species Plantarum, Vol. II, p. 306 (1789), is cited. Britten and Woodward (1905) have traced the history of a number of plates of L'Heritier, which were intended for a second volume of the *Stirpes Novae* which was never published. Some of these plates are now in the DeCandolle library, some in Moretti's library and some in the library at Kew. Among them is the plate of Oenothera grandiflora, which is referred to in a letter to Dryander dated August 18, 1788. (See Britten and Woodward, 1. c.) Through the kindness of M. Casimir De Candolle I have been able to obtain the original manuscript of L'Heritier, in which his description of O. grandiflora was prepared. M. DeCandolle very kindly forwarded from his library a manuscript of five pages, giving L'Heritier's original description of as many species of Oenothera. The plate (No. 4) of O. grandiflora was, however, not in the DeCandolle library, and if it is still in existence it will probably be found in the library at Kew.¹ I have reproduced here a photograph and transcription of this, chronologically the earliest, description of O. grandiflora, unless we call Ray's brief account (1686) a description. A number of points in the description make it certain that the plant described is O. grandiflora Ait., as we know it, and not O. Lamarchiana. I am greatly indebted to Professor Trelease for valuable aid in deciphering the manuscript and in tracing these records.

It is now possible to show clearly that there were at least two races of $O.\ grandiflora$. The first of these is represented by what I have called the Eastern $O.\ grandiflora$, originally wild in Carolina, Virginia and adjacent regions and well illustrated by Barton in The Flora of North America (Vol. 1, pl. 6), 1821. Certain $O.\ grandiflora$ forms from my cultures of Oenotheras from parts of the coast near Liverpool, England, agree with this form in every respect, which seemingly substantiates my conclusion arrived at from the historical data, that the original introduction of $O.\ grandiflora$ took place at a very early date, from Eastern North America, the English plants being descended from this form the secaped from gardens at an early period.

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 $^{^1\!}See$ DeVries, Mutation Theory, 1909, Vol. I., p. 440 et seq. Also MacDougal et al, 1905, p. 7.

 $^{^1\!}A$ subsequent examination of the plates of L'Heritier in the Kew Library, shows that the illustration of O. grandifiora is not among them.

The O. grandiflora which was introduced into Kew from Alabama in 1760 differs from the Eastern form in a number of minor, though constant, characters, as shown by cultures. Among these differences may be mentioned, (1) in the Eastern form, as figured by Barton and as shown in cultures from near St. Anne's, England, the stem leaves are much broader than in the present Alabama form of my cultures, though the leaves of both agree in being tapering and acute at both ends.¹ (2) The flowers in the Eastern form are fully as large as in O. Lamarchiana, the petals being broad and overlapping in the opened flower, as in O. Lamarckiana. In the Alabama form, on the other hand, the flowers (in my cultures) are considerably smaller and the petals are narrower and more cuneate, so that spaces occur between them in the expanded flower. (3) In bud characters, the "Eastern grandiflora," as determined from the English plants, bears on its sepals a short and inconspicuous type of hair, while the sepals of the Alabama grandiflora are entirely glabrous. (4) On the other hand, the stems of the Eastern grandiflora are frequently almost free from hairs either of the long or short type, while the Alabama form bears, especially on its branches, many of the long hairs arising from papillae: (5) The "Eastern" plants average considerably larger than the Alabama ones. It is possible that some of these distinctions are due to environmental differences and are not permanently inherited.

Among the points in L'Heritier's description of O. grandiflora (which was evidently carefully written, using the Genera Plantarum as a model, though never published) which make it certain that it is this form and not O. Lamarchiana which is described, are the words "folia ovato-lanceolata, utringue acuta," applied to the leaves of the stem. The term ovate-lanceolate has also been applied to the early descriptions of O. Lamarchiana, but the stem leaves of O. Lamarchiana are not so broad as those of some races of O. biennis and O. grandiflora. The stem leaves of O. Lamarchiana Ser., can not be described as acute at both ends, while this is perfectly true of O. grandiflora. The width of the stem leaves, however, given as 3 inches, is exceptionally broad. It is interesting to note that the cotylectons are described as deltoid-lanceolate. I have not observed the cotyledons of O. grandiflora, but I have observed them in a form whose bud characters and other features show its close relationship to O. grandiflora. These cotyledons become characteristically deltoid-lanceolate. This is true, though apparently to a lesser extent, of

[&]quot;The description of O. grandiflora by L' Heritier (q. v.) shows that his (Alabama) plants had very broad leaves. It is therefore probable that both the broad and narrow-leaved races occurred in both the Eastern and Southern range of the species. "For other data regarding the types of hairs and their inheritance in certain Ocnotheras, see Cannon (1909).

the O. Lamarchiana forms. It is a very transient condition in all.

Plate 5 is from a photograph of this page of manuscript. The following is the transcription. The characters of the manuscript were literally transcribed as far as they could be deciphered.

Conf. Onagra latifolia floribus amplis. Tourn. inst. 302. Blaikie.

OENOTHERA GRANDIFLORA.

Cal. Perianthium monophyllum superum inferne tubulosum, apice 4-partitum pubescens. Tubus cylindricus longissimus intus canescens. Limbus quadripartitus dependens; laciniis lineari lanceolatis apice subulatis plerum una altera ve excepta sutis, tubo brevioribus, longit. 2 poll.

Cor. Petala 4. obcordata, argutissime denticulata, s. integra, laciniis calycinis longiora, ad apicem tubi inter divisures inserta, lineata.

Stam. filamenta 8. declinata, fauci calycis inserta, corolla breviora lutea. Antherae lineares biloculares, peltatae, longissime.

Pist. German inferum cylindricum, tetragonum, pubescens, longit. 5 lin. Stylus filiformis intra tubum pubescens extra deflexus, staminibus longior. Stigma maximum quadreilobum?, cruciforme; lobis crassis teretibus patentissimis glutinosis.

Per. Capsula cylindrica, demum subtetragona quadrinervis, quadrilocularis, quadrivalvis, apice primum dehiscens, subvillosa, sessilis, dissepimentis valvulae singulae

(oppositis

(contrariis

ejusdemque substantiae a columella subulata quadrangula discedentibus, longit. 15 lin. diam. 3 lin.

Sem. numerosa, obsolete angulata, columella affixa, fusca, parva.

Spica terminalis, prolifer, erecta, foliacea S. bracteata, pubescens pedalis flores sessiles, lutei, odoratissimi, longit 4. poll. diam. 3. poll. Bracteae lanceolatae, acutae, remote—dentatae, sessiles nisi ter minores in omnia foliis conformes.

Folia ovato—lanceolata, utrinque acuta laxe—dentata, nervosa supra viridia infra pallida pubescentia que, subsessilia alterna, subdependentia, longit, 4-5 poll. diam. 3. poll.

Caulis erectus uti fruticosus, ramosus, rimis corticem abjiciens, rami teretes villosi, scabri, ramuli patuli.

Cotyledones deltoideo-lanceolati, obtusi, sessiles.

O. fol. ovato-lanceolatis, staminibus acclinatis, caule fruticoso.

All five pages of the L'Heritier MS were photographed, and prints together with transcriptions of each page were deposited in the herbarium of the Missouri Botanical Garden. The species described on the four other pages are as follows:

Oenothera paniculata. A line is drawn through the word paniculataand fruticosa L. is written above it. Evidently the writer finally decided that it was not a new species. Similarly, there is a description of O. *lyrata*, this being changed to O. rosea. Another page is devoted to a

https://scholarworks.uni.edu/pias/vol17/iss1/13

description of an Oenothera which is said to be between O. mollissima and O. sinuata, but no name is given to it. The last page is a note on some Onagra from the Banks Herbarium.

It is important to note that Willdenow in his edition of Linnaeus' Species Plantarum (3:306) in 1799, to the polynomial description of O. grandiflora, œ foliis ovato-lanceolatis, staminibus declinatis, caule fruticoso, adds "Caulis, folia et germina glabra," which makes it evident that the long type of hair was almost wholly absent from the stems as well as the buds of these plants. This agrees with the characters of many plants in the O. grandiflora series from England, elsewhere described. They cannot have lost this type of hair through crosses with O. Lamarckiana or O. biennis forms, for the latter both have it. While not strictly glabrous, these plants of O. grandiflora are relatively so compared with O. Lamarckiana and O. biennis, and the older regions of the epidermis often become glabrous by the loss of the delicate type of hair as the epidermal cell walls become thicker.

In 1797 Lamarck, in his Dictionnaire (p. 554), described a new species O. grandiflora, evidently not knowing that this name had already been used by Aiton. (See DeVries 1895, 1901, 1909.) In this description of Lamarck (or rather Poiret; see DeVries 1909, p. 442), which was written only from herbarium material, and the name of which was changed by Seringe to O. Lamarckiana, there are several points which need to be carefully scrutinized because they refer to the differences between O. Lamarckiana and O. grandiflora as we now know them. In describing the calyx, the words "termines par un filet court, setace" are used, referring to the sepal tips. DeVries translates this clause (1901, p. 317) "welche an der Spitze eine kurz, dicke, fadenfoermige Verlaengerung tragen," and the English rendering of the German is "which are terminated by a short, fat, thread-like prolongation." The latter, while an equivalent of the German, is not correct when applied to the French. The difficulty is in DeVries' use of the word "dicke" apparently as an equivalent of the French "setace." This difference is referred to because in O. Lamarchiana and its derivatives, as we know it in cultures, the sepal tips are usually thicker than in O. grandiflora. The words used in the French description really apply better to O. grandiflora than to O. Lamarckiana, but in herbarium material they would probably apply equally well to O. Lamarchiana. The original description also uses the expression "lisses et glabres des deux cotes" in describing the stem leaves. This is of course not true of living material of O. Lamarchiana, except, that the upper stem-leaves (which are the ones usually preserved in an herbarium specimen) are usually nearly free from crinkling. De-

Vries, however (1909, p. 442), assures us that the original specimens from which the description was drawn agree exactly with the O. Lamarchiana used in his cultures, although he says that they by no means represent the mean type of the species in every respect.

De Candolle in the Prodromus (III:46) in 1828 segregates O. grandiflora Ait., O. suaveolens Desf., and O. Lamarckiana Ser. from O. biennis L. O. suaveolens is recognized as probably referable to O. grandiflora Ait., as DeVries has shown to be the case (1895 p. 587), under O. biennis L. are cited as figures Fl. Danica 3:pl. 446 (which seems to represent a race of the "European biennis") and Miller's Gard. Dict., pl. 189, Fig. 2. which I have already referred to as probably a race of our present O. biennis, or perhaps a hybrid between O. biennis and O. Lamarckiana. The O. Lamarckiana of the Seringe Mss, as is well known, was the O. grandiflora of Lamarck's Dictionnaire. Under O. grandiflora Ait. De-Candolle cites Sims in Curt. Bot. Mag., 46 pl. 2068 (1819), to which I may now refer.

Sims distinguishes a form (Λ) which he characterizes as "Caule, foliis, germinibusque glabris" and a form (B) "caule et germinibus, subpubescentibus, foliis calycibusque villosis." The plate refers to the (B) form. I formerly considered that this plate represented O. Lamarckiana rather than O. grandiflora, on account of the rather narrow leaves and the stout sepal tips. A direct comparison of the measurements of the plate with those of a culture of the Alabama O. grandiflora from seeds obtained from Prof. S. M. Tracy, makes it evident, however, that the two agree in practically all their characters and measurements, even in the rather narrowly cuneate petals with spaces between them. The last character is more conspicuous in flowers blooming late in the season. Regarding the difference between his two forms, Sims says, "Except in the slight pubescence of the stem, germen and tube of the calys, and the soft villous leaves, our plant differs in no respect from *Oenothera grandiflora*, of which, therefore, it must be considered as a mere variety." He then says it is a native of Carolina. In cultures of O. grandiflora races from plants naturalized on the Lancashire coast of England, I have found differences similar to those between Sims' forms. Other series of races are found to exist, differing from each other less than the present O. grandiflora and O. Lamarckiana in the strict sense differ from each other. My recent cultures indicate that, however they may have originated, numhers of such races occur and breed true to their peculiarities. When selfpollinated they behave as "pure lines." What their behavior in crossing may be is as yet unknown.

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We have seen that, previous to the introduction of *Q*, grandiflora in 1788, a large-flowered form which was at any rate more closely similar to O. Lamarchiana than to any other species except perhaps O. laevifolia, had been commonly grown in European gardens and illustrated with various figures. This was the first Oenothera to be introduced from the New World, about 1614. Already in 1737 (Hort, Cliff.) it had escaped from gardens and was found growing wild in large numbers in Holland and (Hort. Upsal. 1748) was widely distributed in Europe. It is altogether probable that various races were included in this distribution, even at that time. I have not attempted to trace the earliest references to the occurrence of Oenotheras wild in England, but it was abundant on the coast near Liverpool in 1805, (Sowerby Eng. Bot., 22 pl. 1534) and probably existed there much earlier. Thompson (1905) states that 1837 is the first record of its occurrence wild on the coast of Somerset. He refers to the form as O. biennis L., but it has recently been shown by cultures to include O. Lamarchiana and other forms. For a summary of the distribution of Oenotheras in Europe see A. DeCandolle (1855)(II:710). They are naturalized and growing abundantly in many places.

The Liverpool plants now consist of *O. Lamarchiana* and certain of its mutants, as well as *O. grandiflora* and a great variety of hybrids between these forms. Perhaps it would be equally correct to regard them as a series of intermingling "pure" lines or races. The *O. Lamarchiana* is certainly very closely similar to that of DeVries' cultures, but there seem native to Virginia would belong to a different elementary species from that in Texas.

In 1832 Don (2:685), under the name O. bienms refers to Oenotheras growing in the greatest abundance on the Lancashire coast, north of Liverpool. and also says, "It covers several acres of ground near Woodbridge, Suffolk." The flowers are referred to as "large, pale yellow, and delicately fragrant." In Edwards' Botanical Register (19. pl. 1604) in 1833, a large-flowered form is figured under the name Oenothera biennis var. grandiflora by Lindley. The flowers and the flowering shoot probably represent O. Lamarchiana, for though the shoot is slender and with only slight pubescence, yet the flower buds are rather stout and with short sepal tips as represented, though scarcely decisive. But the leaf (which probably is from the rosette or far down on the stem) is much longer and more narrowly lanceolate than shown by O. grandiflora. This leaf is very narrow even for O. Lamarchiana, but the sessile stem leaves with their broad clasping bases, certainly characterize O. Lamarchiana rather than O. grandiflora.

Baxter in his British Phanerogamous Botany, in 1839, gives a plate (4:257) which seems to resemble *O. Lamarckiana* rather than *O. grandiflora*. But doubtless *O. grandiflora* from its first introduction from Virginia (?) had escaped from English gardens long before the later introduction in 1778, and was growing wild as we now find it, mingled with *O. Lamarckiana* forms. This figure may therefore refer to some hybrid between the two.' It is referred to as *O. biennis*, the only English species.

Dietrich, in characterizing *O. grandiflora* Ait. in the German flora (Gaertnerei und Botanik 6:202) in 1837, describes the leaves as smooth and the capsules as "filzig." The style is described as "so lang als die Staubfaeden." The hairiness of the capsule and especially the short style make it not improbable that he was describing hybrids between *O. biennis* and *O. grandiflora*.

After the time of Linnaeus, the large-flowered Oenotheras are frequently referred to and figured as O. biennis, and in England this practice has continued down to the present time. It is justified, as we have seen, by Linnaeus' citation of figures in his characterization of the species. But in America, where these large-flowered species have long been rare or absent, usage has tended to confine the term to a smallflowered self-pollinating form, and this is what is meant when the name O. biennis L. is used in the present paper. Thus a plant is figured under this name by Sowerby (English Botany 22 pl. 1534) in 1806, and he says "Our specimen was gathered on the extensive and dreary sandbanks on the coast a few miles north of Liverpool, where millions of the same species have been observed . . . perfectly wild, and covering a large tract between the first and second range of sand-hills." The plate has large flowers and answers to O. Lamarchiana rather than to O. grandiflora (See plate 6). However, at this date O. grandiflora was also doubtless naturalized in the same locality, where my cultures have shown that the two species are intercrossing freely, and the plant figured in Sowerby undoubtedly represents one of many such races growing together in that locality. As already mentioned, some O. grandi-

¹I should point out that treating such intermediate races as possible hybrids does not in the least explain their origin from an evolutionary standpoint. Just as there is no such thing in nature as a sharply defined Linnaean "species," but rather a host of more or less independent elementary species which, in open-pollinated forms, are continually intercrossing so that the lines of descent are changing with each generation; so there is no sharp line between a hybrid and a pure form. By self pollinating during successive generations, the individuals will be found to breed true to smaller and smaller differences, except when mutations occur. If such "pure" individuals are then pollinated from some other race, no one can say how closely or distantly that race should be related to produce a hybrid rather than a "pure" strain. In nature, except in strictly self-fertilized forms, the indiscriminate crossing of individuals exhibiting a host of minute character differences, is the normal condition. The process of separating and purifying races by self-pollination is analagous to the chemical process of fractional crystallization.

flora forms are almost wholly lacking in the long type of hair. It may be said that the hybrids between O. Lamarchiana and these O. grandiflora forms, usually at least possess the papillae on the stem which are characteristic of O. Lamarchiana, but their stems and buds are less hairy, the long type of hair being present but much less numerous than in O. Lamarchiana. The rather smoothish aspect of the stem and buds in the plant figured lead one to believe that it was probably a hybrid between O. Lamarchiana and one of these O. grandiflora forms. My cultures of Oenotheras from this region show certain races, having similar characters. It is probable that some races of O. grandiflora in its eastern range differed from the present O. grandiflora in Alabama, in having a very few of the long type of hair.

I regard these plants of *O. Lamarckiana* and *O. grandiflora* now flourishing on the English coast, as most probably derived from escapes from the English Gardens, such escapes having probably taken place early in the seventeenth century, from the plants introduced from "Virginia" about 1614. *O. Lamarckiana* is known to have been abundant on the English coast as early as 1805, long before its (second) introduction into Kew in 1860. Among the Oenotheras at St. Anne's I could find no small-flowered forms, so that *O. Lamarckiana* could not have originated here from a cross between *O. grandiflora* and *O. biennis* races. Neither is there any probability that *O. biennis* has occurred here formerly and has since died out, for the self-pollinating forms invariably set more sets than the open-pollinating, and thus have a better chance to multiply in the struggle for existence.

It will therefore be possible to compare this—the "Virginian Lamarckiana"—with the "Texas Lamarckiana" which formed the basis of De Vries cultures, if my hypothesis regarding the origin of the English plants is correct.

After O. Lamarckiana was introduced from Texas in 1860 it was figured in the Floral Magazine (2 pl. 78) in 1862 and copied by Lemaire in the Illustration Horticole (9 pl. 318) in the same year. As already stated, this was the source of the O. Lamarckiana of DeVries' cultures.

To return to the history of *O. grandiflora* Ait. there seems to be good evidence that this species was taken to Europe from its Eastern range in Carolina, Georgia, and the adjacent region, at least as early as 1669, i. e., long previous to its introduction into Kew from Alabama in 1778. Since that early introduction it has escaped from botanical gardens, just as did *O. Lamarchiana*, and is now growing wild in various parts of Europe. It is found abundantly in western France (Gillot, cited by De-Vries, 1909, p. 443) and in other parts of the continent.

DeVries (1909 p. 441 footnote), in discussing O. grandiflora, says, "My investigations in the herbarium at Paris have convinced me of the identity of the form I cultivate as O: suaveolens Desf. (O. macrantha Hort.) with the form described by Desfontaines. Both of them have flowers of the same size as those of O. biennis." This is explained by the fact that the European O. biennis has larger flowers than the American races, though smaller than O. Lamarchiana, while the Alabama O. grandiflora has flowers which are also, in some cases, distinctly smaller than in O. Lamarchiana.

From the fact that the Oenotheras established on the sand dunes of the English coast north of Liverpool include O. Lamarchiana and O. grandiflora, where they have freely multiplied and intercrossed since at least 1805, and probably much earlier, the conclusion is scarcely avoidable that this O. Lamarchiana must have been derived from the early introduction of these plants from Virginia, for the Texas plant was not introduced until 1860.

At one stage in the progress of these historical investigations I thought it probable that O. grandiflora had been introduced into this English locality much later, i. e., since the introduction of this plant from Alabama in 1778. It seems improbable, however, that both O. Lamarckiana and O. biennis would be taken over from Virginia, and O. grandiflora remain behind. As already stated, I believe that Ray's species number 11 belongs to O. grandiflora. It seems not improbable that the absence of later recognition of two large-flowered forms may have been due to subsequent crossing in gardens, which is very likely to have occurred and which (as I have found from my cultures) would tend to obscure the distinctions between the two species, by creating intermediates. For instance, the statements of Lindley in Edwards' Bot. Register 19 pl. 1604, (1833) in which the figure of a plant which is most like O. Lamarchiana Ser. is given under the name O. biennis var. grandiflora, show that very probably the limits between O. biennis L., O. Lamarchiana Ser. and O. grandiflora Ait. had been largely obscured and eliminated by spontaneous crossing in gardens during the long period of their cultivation.

Miller. in the Gardener's Dictionary, in 1807 (Vol. 2 Part 1) cites under Oenothera, O. biennis, O. grandiflora, O. parviflora, O. muricata, O. longiflora, O. fruticosa, and others. The plant referred to under O. biennis is described in part as follows: "Germ sessile, an inch long or more; on the top of this is the tube of the calyx, from an inch to almost two inches in length, and narrow, spreading out at the top into four acute segments, villose on the outside, an inch in length, bent down by

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pairs when the corolla expands and then rolled inwards." The corolla is described as one and a half to nearly two inches in diameter.

From this description and the careful measurements it is evident that this plant had small flowers about the size of the American O. biennis. The synonymy and other statements, which were copied from book to book, cannot be taken as meaning anything in the present connection. Contemporaneously (1806) Sowerby, as we have seen, pictures a largeflowered form closely resembling O. Lamarckiana, under the name O. biennis, so that it is quite evident that at this time no distinction was drawn between O. biennis and O. Lamarckiana forms, although O. grandiflora had been segregated.

The condition of the plants now growing wild and freely intercrossing on the sand-dunes near Liverpool, is probably somewhat similar to what it was in their original home in Virginia, although it is probable that in their original habitat the individuals were much more scattered. owing to the nature of the habitat and the competition of other plants. For this reason, crosses between the different species were much less likely to occur, but that such crosses did occasionally occur there can be no doubt. It seems characteristic of species which have become "weeds" in another country, that they grow in large numbers of individuals closely aggregated in localized areas, while in their native habitat they are more uniformly scattered over larger areas, taking their part in the regular flora of the country. The reasons for this difference in distribution I shall not discuss here. In the case of the open-pollinated Evening Primroses, it is not at all improbable and indeed may be regarded as certain, that crosses between different forms did occasionally occur where their ranges of distribution overlapped. In the case of the three species we are considering here, it is probable that before the white man's invasion of the continent, all three were to be found over a large part of the country. Since then the small-flowered, close-pollinated O. biennis and its related forms, such as O. Oakesiana, O. muricata and O. fruticosa, have continued to maintain themselves, while the open-pollinated O. grandiflora seems to have nearly or quite disappeared from its Eastern range in Virginia and Carolina, and O. Lamarckiana seems to have become quite extinct on this continent.

It would seem, therefore, that the close-pollinated species have been more successful in their competition with the conditions introduced by civilization, than the open-pollinated forms. This might be expected, because in close-pollinated forms seed production is always certain to follow flowering, while in open-pollinated species, with increased enemies

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and lessening numbers, the amount of seed-production may fall below the minimum necessary for the perpetuation of the species.

Dr. W. O. Focke, of Bremen, first identified the Oenotheras near Liverpool, England, as belonging to *O. Lamarckiana*. Charles Bailey, in a more recent account of this vegetation (1907a, b) concludes that their introduction probably came from sweepings of grain-ships and docks and in grain for poultry from America. It seems more probable, however, that they originated as escapes from English gardens at a very early date.

In concluding this examination of historical records it should be said that I have endeavoured to present the documents and other evidence from which my inferences and conclusions have been drawn, in such a way that the reader who examines the evidence can judge for himself of the justice of the conclusions deduced. I have not been biased in favor of any theory of the origin and history of *O. Lamarckiana*. I have shown that a form very closely resembling *O. Lamarckiana*, except in certain rosette characters, was originally wild in Virginia, but it has never seemed to me that the question whether *O. Lamarckiana* has been hybridized or not is of great significance in connection with the interpretation of the mutation phenomena in these open pollinated forms, which must have experienced crossing in nature before their introduction into gardens. It is, however, a matter of much importance to determine that a form at least closely similar to *O. Lamarckiana* was the first Oenothera introduced into cultivation.

In nature, the individuals of all open-pollinated species are hybrids, in the sense that many more or less diverse elements have contribuated to their ancestry. In making cultures from wild open-pollinated forms I have been impressed with the variability of the first generation in cultivation in comparison with forms which have been selfed for a number of generations. It is of course necessary, in breeding, to select certain individuals for later generations, and if these are self-pollinated the resulting races are sure to show increasing uniformity in later generations. If space for cultures permitted that every individual could thus become the starting point for a race, it would be found that each such individual would originate a race showing slight peculiarities. In the last analysis, as Jennings¹ has remarked, the differences between races would be found to go down to the limits of observation and measurement. The occasional appearance of mutants, or marked departures from the type which breed true, is of course another matter.

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¹Jennings, H. S. Experimental evidence on the effectiveness of selection. Amer. Nat. 44: 136-145. 1910.

It may be pointed out that the mutants of O. Lamarchiana all have certain features in common, which they also share with the parent form. These (See Gates 1909) include (1) the presence of the long type of hair on the stems and buds, arising from papillae which, on the stems, are red; (2) the quadrangular shape of the buds; (3) the large flowers with long style. It has sometimes been suggested that the phenomenon of mutation in O. Lamarckiana is a form of hybrid splitting, O. Lamarchiana itself being merely a synthesized hybrid. Supposing this were the case, O. grandiflora and O. biennis are the only forms we know which could reasonably be assumed to have been its parents. It is true that O. biennis possesses the first two of the characters mentioned above, in common with O. Lamarckiana and its mutants. But if O. Lamarckiana had been synthesized in this manner, why should all the mutants fail entirely to show either the small flowers with short style, characteristic of O. biennis, or any of the many peculiarities (elsewhere enumerated) of O. grandiflora? All the evidence I can find, from every standpoint, is opposed to such a possible origin for the mutating O. Lamarckiana.

SUMMARY.

To recapitulate briefly the history of the three species Oenothera Lamarckiana Ser., O. grandiflora Ait., and O. biennis L., as far as it is now known, we may say that the form known to Bauhin in 1623 as Lysimachia lutea corniculata (Onagra latifolia, Tournefort, 1700) was a largeflowered Oenothera, undoubtedly more like O. Lamarckiana than any other species, though differing in certain rosette characters from the O. Lamarckiana of our present cultures. This is proved by an appendix in Bauhin's Pinax, and the original discovery of the record was from marginal notes copied into the book by Joannis Snippendale.

The important fact is thus disclosed that a form closely resembling *O. Lamarckiana* was the first Oenothera introduced into Europe from Virginia about 1614, and therefore that it did not originate in cultivation. While the Oenothera of this early record seems to have differed somewhat from our present *O. Lamarckiana*, these differences are small compared with the important characters in which they agree, and make it necessary to include this plant in the *O. Lamarckiana* series of forms.

This description by Bauhin, of plants grown in 1619, is evidently the basis of Robert Morison's description of the same plant in 1680. An independent description in Parkinson's *Paradisus* in 1629, refers to the same plant under the name *Lysimachia Virginiana*. Ray in 1686 in his *Historia Plantarum*, repeats the Morison description with numerous

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changes and additions. Under the name Lysimachia Americana, Hernandez in 1651 gave an independent description of plants from Virginia, (O. Lamarckiana?) in which the characteristic crinkling of the leaves is definitely described. These records are all of prime importance, and the full text of the descriptions is given in each case.

The recognition of large- and small-flowered forms in published works came in 1669 by Morison. When *O. biennis* was first introduced is not determined, but Barrelier (1714) gives three figures, the first of which is probably *O. Lamarchiana* Ser., but may be *O. grandiflora* Ait., the second is *O. biennis* L. and the third *O. muricata* L. (See plates 3 and 4).

The earliest figure of an Oenothera was in Alpin's *De Plantis Exoticis*, 1627, where an evening primrose from Virginia is drawn, under the name *Hyoscyamus Virginanus*. (See plate 1). The seeds were obtained from an English physician, Dr. More, and the plant is very probably the same as Bauhin's *Lysimachia lutea corniculata*.

The races of O. grandiflora which I have been cultivating from near Liverpool, England, have in many cases much broader leaves than the O. grandiflora in my cultures from Alabama. It seems very probable that Ray's species 11 in 1686 was O. grandiflora Ait. introduced from its Eastern range in "Virginia." This was the commonest form in the English Gardens in Ray's time, and it is very probable that the O. grandiflora plants which were flourishing in a wild state on the English coast above Liverpool, and in Suffolk and elsewhere, as early as 1805 and probably much earlier were, like those of O. Lamarckiana, derived from very early garden escapes. I therefore consider it probable that O. grandiflora in its eastern American range had, in part at least, broader leaves than the Alabama form, though both types may have occurred in both regions. Some of the races from Liverpool also have considerably larger flowers with much longer hypanthia than our present O. Lamarchiana. From these facts it seems very probable that both O. grandiflora and O. Lamarchiana were twice introduced into cultivation, these forms having passed out of cultivation and become naturalized in many localities in England and elsewhere, during the long interval of about a century in the former case and nearly two centuries in the latter, between the first and second introductions.

Linnaeus, in his Species Plantarum, cites in the synonomy, as the type of his species O. biennis, Morison's figure of Lysimachia Virginiana latifolia, lutea, corniculata, which is the same plant as Bauhin's Lysimachia lutea corniculata, and which comes in the O. Lamarckiana series of forms, having large flowers and quadrangular buds. Linnaeus also cites the Hortus Cliffortianus in his synonomy, in which is cited

Barrelier's figure of Lysimachia lutea corniculata latifolia lusitanica together with the figure of Morison's already referred to. It is very probable that Barrelier's plant was the same as Morison's. The names used are almost identical but Barrelier cites as a synonym for his plant Tournefort's Onagra latifolia, floribus amplis. The latter is very probably our present O. grandiflora Ait. Linnaeus in the Hort. Cliff. evidently concludes that Morison's and Barrelier's plants are the same, and segregates Onagra latiflora, floribus amplis as a subform. Therefore the type of Linnaeus' O. bicnnis was a large-flowered form in the O. Lamarckiana series and may perhaps, have also included a form in the O. grandiflora series, if Barrelier was correct in his synonomy. But all the figures and names of small-flowered forms were definitely excluded, or rather ignored by Linnaeus.

After Linnaeus' time the small-flowered forms were included indiscriminately with the large-flowered ones under O. biennis L. The large-flowered forms later came to be designated O. biennis var. grandiflora until after the recognition again of O. grandiflora Ait. and O. Lamarckiana Ser. as separate species. Since then the name O. biennis L. has been chiefly confined to the small-flowered forms, although Linnaeus evidently intended as the type of his species the large-flowered forms. We know now that the difference between large and smallflowered species in Oenothera is an important one, involving various other changes in flower parts and connected with the habit of open or close pollination.

Ray described two large-flowered species in 1686. One of these was probably *O. Lamarckiana* and the other *O. grandiflora*, from its Eastern range in Carolina and Georgia. This is described as having broader leaves and much larger flowers.

In 1778 O. grandiflora Ait. was introduced into England after its discovery in Alabama by Bartram. It was described by Aiton, Willdenow, and by L'Heritier whose description (the most accurate) was never published, until reproduced here. Poiret described a plant in Lamarck's Dictionnaire in 1796 under the name O. grandiflora. This was recognized by Seringe to be different from the O. grandiflora of Aiton and Willdenow, and was named by him O. Lamarckiana. In this way was segregated a form which had long been going under the name O. biennis L. These now well-known facts have been brought together by DeVries and MacDougal.

In 1860 O. Lamarckiana Ser. was reintroduced into England from Texas. Seeds were distributed on the continent and this DeVries has shown to be the probable source of the O. Lamarckiana now grown in European gardens, and the source of his cultures. It is not impossible

that this O. Lamarckiana is different from the form whose history we have tried to trace, and which we believe was originally a native of Virginia; but the O. Lamarckiana now growing wild on the coast north of Liverpool, England, and which must have come from the early introduction (according to records which show that it has been growing abundantly there since at least 1805) is found from cultures to be very closely similar to the Texas form from which originated the plant in DeVries' cultures. O. grandiflora Ait. has also been shown, from statements of Bailey, and my own cultures, to be growing wild in the same English locality, and intercrossing freely with O. Lamarckiana and certain of its mutants. It seems probable that both species have been naturalized here since early in the 18th century.

The fact that the small-flowered forms are self-pollinating, gives them . a much better chance in the struggle for existence than the large-flowered open-pollinating species because they have a better opportunity to set seeds. This probably accounts for the fact that the small-flowered forms are now more wide-spread and prevalent in Europe except in locations sparsely covered with vegetation, such as sand dunes, where the open-pollinated forms can aggregate in large numbers. It also probably explains the more or less complete disappearance of the largeflowered forms from eastern North America, since the introduction of eivilization, for with increasing enemies the amount of seed production may fall below the minimum necessary for the preservation of the species.

Missouri Botanical Garden.

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PLATE I. Hyoscyamus Virginianus. Albin's De Pl. Exoticis, p. 324.



PLATE II.

Morison, Hist. Pl. Univ. Oxon. Sect. 3, tab. 11. Fig. 7. Lysimachia Virginiana latifolia, lutea, corniculata, nobis. Fig. 8. Lysimachia Virginiana, angustifolia, corniculata, nobis.



PLATE III. Barrelier, Plantac per Galliam, Hisp. et Italiane observatoe. Fig. 989. O. biennis. Fig. 990. O. muricata.

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PLATE IV.

Lysimachia Americana. Hermandez, Nova. Plant. Anium. et Miner. Mex., p. 882. O. Lamarckiana? Fig. 1232. Borrelier, Plantae per Galliam, Hisp. et Italiam observatoe.

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PLATE V.

L'Heritier MS. description of *O. grandiflora* Aiton. (Published through the courtesy of M. Casimir DeCandolle.)



PLATE VI. Oenothera biennis, Sowerby's English Botany, Vol. 22, pl. 1534. 1806.