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THE PROBABLE ORIGIN OF OENOTHERA LAMARCKIANA SER.

HUGO DE VRIES

(WITH PLATES XVII-XIX)

In a series of most interesting articles, B. M. DAVIS has recently tried to prove that mutability might be a result of previous crosses. This view was first proposed by BATESON and SAUNDERS, and applies especially to the phenomena which *Oenothera Lamarckiana* shows when seeds from the pure strain, and even from pure lines within this strain, are sown, as in the experiments I conducted in my experimental garden. DAVIS expected to be able to offer the desired proof by showing that *O. Lamarckiana* might be duplicated by crossing two other species of the same group. Up to this time, as a matter of fact, he has not succeeded in producing any form which comes sufficiently near *O. Lamarckiana* to be compared with it.¹ But if he had succeeded in doing so, evidently it would not have been a proof for his assertion, unless his hybrid should show the same degree of mutability as does *O. Lamarckiana*, since we have as yet no means of judging from the morphological characters of a given plant whether its hereditary characters are in a stable or in an unstable condition.

In starting his experiments to produce a duplication of LAMARCK'S evening primrose, DAVIS was unfortunate in the choice of the species for his combination. He chose *O. biennis* L. and a

¹ For a successful duplication of an elementary species by means of crossing, see *Oenothera biennis* × *O. cruciata* Nutt. in Gruppenweise Artbildung, p. 311.

form which he assumed to be *O. grandiflora* Aiton. It is evident that the first condition of success in such work consists in the purity and the immutability of the species which are to produce the hybrid. If they are already in a mutable condition, it is to be expected that their hybrids, or at least some of them, may combine the different lines of mutability of their parents; and at all events, the mutability of such a hybrid would be no proof that this phenomenon may be produced by means of crossing. On the other hand, if the species to be crossed, or even only one of them, were not pure, the hybrid might inherit this impurity and show phenomena which might easily be mistaken for mutations.

It so happens that *O. biennis* is in a condition of mutability analogous to that of *O. Lamarckiana*, although not developed to the same high degree. From time to time it produces dwarfs, which are distinguished from it by exactly the same two characters which differentiate the dwarfs of *O. Lamarckiana* from their mother species, namely, low stature and sensitiveness to the attacks of some species of soil bacteria.² Moreover, STOMPS has shown that *O. biennis* may, although very rarely, double the number of chromosomes in its sexual cells, which in *O. Lamarckiana* produces the two mutants *O. gigas* and *O. semigigas*.³ As is now generally admitted, *O. gigas* results from the pairing of two mutated sexual cells, each of which had a double number of chromosomes. *O. semigigas*, on the other hand, is produced by the pairing of a sexual cell mutated in the same way, with a normal gamete; therefore it possesses only 21 chromosomes (14+7), while the number in *O. gigas* is 28. As yet, only *semigigas* mutants have been observed coming from *O. biennis*, and it is obvious that the double combination must be much rarer. As a proof of this special kind of mutability in *O. biennis*, however, the observations of STOMPS are wholly sufficient.

In quoting these facts, DAVIS says that if it can be shown "that tested strains of this *biennis* are able to produce new forms of specific

² STOMPS, TH. J., Mutation von *Oenothera biennis* L. Biol. Centralbl. 32:521-535. 1912; also ZEYLSTRA, H. H., *Oenothera nanella* De Vries, eine krankhafte Pflanzenart. Biol. Centralbl. 31:129-138. 1911. Vergl. ferner: Gruppenweise Artbildung 1913:296-304.

³ STOMPS, TH. J., *op. cit.* p. 533.

rank or even marked varieties, the mutationists would have much stronger evidence in support of the mutation theory than that based on the behavior of *O. Lamarckiana*.”⁴ After conceding this strong position to his adversaries, DAVIS subjects the results of STOMPS to a rather sharp criticism, which, unfortunately, is based upon a confusion of two wholly distinct types, namely, *O. biennis* L. var. *cruciata*⁵ and *O. cruciata* Nutt. He says: “It should be made clear that the form (*O. biennis cruciata*) is recognized in the more recent taxonomic treatments as a true species sharply distinguished from types of *biennis* by its floral characters,” and “a cross between these types must certainly be regarded as a cross between two very distinct evolutionary lines and its product as a hybrid in which marked modifications of germinal constitution are to be expected.”⁶ But, as a matter of fact, the Dutch *O. biennis cruciata* differs from *O. biennis* only in the characters of the petals; in all other respects it is wholly the same, and therefore evidently only a subordinate variety of this species. It has not been dealt with in recent taxonomic treatments, since it occurs almost exclusively in the sand dunes of Holland, where it is produced from time to time by mutation from the mother form (first observed in 1900), without having been able until recently to multiply in the field so as to produce a persistent local variety.⁷

On the other hand, *O. cruciata* Nutt. is quite a different species, with narrow, brownish green leaves, and a different type of branching, of spikes, and of fruits. It grows wild in New York and Vermont, and is well known to all students of the American flora. By some authors it has been considered a variety of *O. biennis*, and this probably is the chief cause of DAVIS’ confusion. The character and the behavior of its hybrids with *O. biennis* have been amply dealt with in my *Gruppenweise Artbildung*.

In the experiment of STOMPS, the dwarf and *semigigas* mutations were produced by hybrid strains of *O. biennis* and *O. biennis*

⁴ DAVIS, B. M., Mutations in *Oenothera biennis* L.? Amer. Nat. 47:116-121 (especially p. 116). 1913; see also *op. cit.* 47:540-596 (especially p. 567). 1913.

⁵ Die Mutations-Theorie 2:599. 1903.

⁶ Amer. Nat. 47:117. 1913.

⁷ Die Mutations-Theorie 2:599. 1903.

cruciata, and it was assumed that such strains would behave as true species in all characters not related to the differentiating marks of the petals. It must be conceded, therefore, that the cross of these two forms may be treated "as though it were the combination of forms within the same species, which have similar germinal constitutions" (DAVIS, *op. cit.* p. 117).

But the most clear and simple way of obviating this whole objection is evidently to sow seeds of *O. biennis* of pure descent upon the same large scale as in the former experiment. This has been done, and a dwarf and a *semigigas* form have been produced by this pure line, besides some other mutations.⁸ They had the same characters as the former ones, and now provide us with the "strong support" asked for by DAVIS. Moreover, they show that his choice of *O. biennis* for a proof of the assertion that mutability might be produced by crossing immutable species was a most unhappy one.

The second condition for success in this kind of work is, as has been stated, the purity of the types to be crossed. As already quoted, DAVIS assumes that a cross between two very distinct evolutionary lines may give a hybrid with marked modifications of germinal constitution. This may be applied to his choice of the type which he calls *O. grandiflora*, and which he has made the other parent of his initial cross. He got his seeds from Dixie Landing, Alabama, a locality where BARTRAM had discovered *O. grandiflora* about a century ago. He assumed them to be of the pure species, but a culture which I made in my garden from seeds kindly supplied to me by Mr. DAVIS proved to be a mixture, and thereby threw a distinct doubt upon the purity of the station. For this reason I visited Dixie Landing in September 1912, and had the good fortune to be accompanied by Mr. H. H. BARTLETT, of Washington, well known for his systematic researches among the wild species of this group. We found the station in a most desolate condition. A small-flowered species, *O. Tracyi*, in almost all respects different from *O. grandiflora*, had migrated into the same old cotton fields and mixed everywhere with the species of BAR-

⁸ STOMPS, TH. J., Parallele Mutationen bei den Oenotheren. Ber. Deutsch. Bot. Gesells. 30: Heft 3, 1914.

TRAM.⁹ On no single field was the original form pure; it was always mixed to such a degree with *O. Tracyi* and with their hybrids that we found it impossible to collect undoubtedly pure *grandiflora* seed from this locality. Moreover, the intermediate types were so numerous (over a dozen) that it was difficult to regard all of them as normal hybrids between only two parents. To produce such a diversity of forms, either one or both of the parents must have been in a mutating condition, or more than two species must have combined in the crosses. In both cases, the material can hardly be considered as a fit starting-point for experiments bearing upon the causal relations of crossing and mutability.

Recently I have shown that besides *O. biennis* some other species of *Oenothera* are actually in a state of mutability, and especially has one of the most common American types thrown off marked mutants in my experiment garden.¹⁰ The degrees of development of this condition, however, are very different in different species. In some of them mutations occur rarely, but they serve to throw a doubt upon the stability of those forms for which no positive results have as yet been won. In other words, we may say that almost all the nearest allies of *O. Lamarckiana* are open to the suspicion of sharing at least some degree of the mutability of this species. There is no use, therefore, in trying to produce mutability by crosses of species of the same subgenus (*Onagra*) in order to show that this phenomenon is only a result of crossing, as is asserted by DAVIS.

Moreover, I might point out that the question should be dealt with from a general standpoint and not be limited to the evening primroses. If it should be true that phenomena like those of *O. Lamarckiana* could be produced by crossing immutable species, it would, of course, be of much higher scientific value to produce them in other families or genera, or at least in the other subgenera of the evening primroses. The chance of finding immutable parents for a cross would be far greater and the proof could be given as easily and in many cases with less amount of mechanical work

⁹ DE VRIES, HUGO, and BARTLETT, H. H., The evening primroses of Dixie Landing, Alabama. *Science N.S.* 35:599-601. 1912.

¹⁰ *Gruppenweise Artbildung*, pp. 296-312. 1913.

and space in the garden. The line of work chosen by DAVIS seems to me to be necessarily without any chance of success.

Besides his experimental work, DAVIS has made some historical researches to discover the origin of *O. Lamarckiana*.¹¹ Unfortunately, he has neglected to visit the Museum d'Histoire Naturelle at Paris, where the herbarium of LAMARCK is preserved, and where other valuable documents concerning the first appearance of our species are to be found. For myself I visited these collections in 1895 and reported on the results of my investigations in my *Mutation theory* (vol. I. pp. 437-444 of the English edition). In October 1913 I repeated my visit and compared the authentic specimens with the remarks made upon them by DAVIS. I regret to say that, through his ignorance of the available evidence, DAVIS has been led to conclusions which are fully contradicted by the herbarium material, both of the "Herbier de Lamarck" and of the "Herbier général" of the Museum. As we shall see, the origin of *O. Lamarckiana* is the same as I have pointed out in my book.

In the herbarium of LAMARCK, *O. grandiflora* (Lam.), which later was renamed by SERINGE and called *O. Lamarckiana*, the name it still bears, is represented by two large flowering specimens. When I studied them in 1895, they were loose on their sheets and bore together the no. 12, indicating that they corresponded with no. 12 *O. grandiflora* of the *Encyclopédie méthodique, Botanique*, by LAMARCK.¹² About 1900 they were fastened on new sheets and the numbers have been lost.¹³ For convenience, I shall call these specimens *A* and *B*, the former being represented by our pl. XVII, while a photograph of *B* has been published by DAVIS.¹⁴

¹¹ DAVIS, B. M., Was LAMARCK's evening primrose (*Oenothera Lamarckiana* Seringe) a form of *Oenothera grandiflora* Solander? Bull. Torr. Bot. Club 39:519-533. pls. 37-39. 1912; A much desired *Oenothera*. Plant World 16:145-153. 1913; The problem of the origin of *Oenothera Lamarckiana*. New. Phytol. 12:233-241. 1913.

¹² The Mutation Theory 1:442. 1901.

¹³ The herbarium of LAMARCK was acquired by the Museum d'Histoire Naturelle in 1886. Vergl. BONNET, ED., L'herbier de LAMARCK, son histoire, ses vicissitudes, son état actuel. Jour. Botanique 16:129-138. 1902.

¹⁴ DAVIS, B. M., Was LAMARCK's evening primrose (*Oenothera Lamarckiana* Seringe) a form of *Oenothera grandiflora* Solander? Bull. Torr. Bot. Club 39:519-533. 1912. See pl. 37.

Unfortunately, these two specimens do not belong to the same elementary species, but the question as to which of them is to be considered as the authentic specimen has been answered by all authors in the same way, with the exception of DAVIS. According to the general agreement, *A* (pl. XVII) is the type of the species. DAVIS has not seen this specimen, and has based his judgment upon the communications of botanists concerned with systematic rather than with elementary species.

The plant *A* corresponds exactly with *O. Lamarckiana* Ser. as it is now universally cultivated and as I know it from my own cultures. The specimen is evidently a side branch, picked in the autumn, and the flowers, although very large, are not quite so large as may be seen in July and August. It bears no fruits, but the sexual organs of the flowers and the form of the flower buds do not leave the least doubt concerning its identity. The stigma lobes are widely spread and raised by the long style high above the tops of the anthers, and this is one of the best characters of *O. Lamarckiana*. The buds are conical and thick, and not thin as in *O. grandiflora* Ait. For comparison, I have given a group of flower buds (pl. XVII), picked in the autumn also, from my pure cultures. All the other marks correspond to those of the present species, although of course not all of them distinguish it from allied forms.

This sheet bears the label, "d'Amérique sept., tige rameuse, haute de 3 à 4 pieds," in the handwriting of LAMARCK. The description in the *Encyclopédie* says of the origin of the species: "Cette espèce est originaire de l'Amérique septentrionale. On la cultive au jardin du Muséum d'Histoire Naturelle (V.S.)."¹⁵ The description, however, quotes some points which are not visible on the herbarium specimen, nor on specimen *B*. It is therefore clear that the author knew his plants from another source still, probably from the living material of the Jardin des Plantes. The most interesting point for us is the description of the fruits: "Le fruit est une capsule courte, cylindrique, glabre, tronquée légèrement, quadrangulaire, n'ayant environ que le tiers de la longueur

¹⁵ V.S. ("vidi siccum") means that the diagnosis is based on herbarium material.

du tube calicinal.”¹⁶ This description wholly agrees with the fruits of the present species, especially if we remember that LAMARCK based his description on a comparison with the only other large-flowered form he knew, *O. longiflora*. The short fruits at once distinguish our species from the allied types, such as *O. suaveolens* Desf. and *O. grandiflora* Ait., which have thin and proportionally long fruits.¹⁷

This character of the fruits shows that the description of the *Encyclopédie* has been based upon specimen *A* and not upon the other one. For, although *B* lacks fruits also, it belongs to an elementary species which has long and narrow fruits, as we shall soon see. Here I might point out that in systematic researches of this kind, more value is to be attached to published diagnoses and descriptions than to the material preserved in a herbarium. The older systematists, as a rule, did not take much care of their material, even if they were very careful of their descriptions.¹⁸ The herbarium specimens are often found without their names and without any indication concerning their origin. The rule “descriptio praestat herbario” applies in our special case, even as it does in many others. In our case, the description is relatively complete and clear, while in the dried specimen only part of the characters are represented.

For all these reasons I cannot agree with DAVIS, who says (p. 519) that I made an incorrect determination of the material of my cultures, when I identified it with LAMARCK’s plant of 1796. The authentic specimen of LAMARCK and the description in the

¹⁶ *Encyclopédie méthodique, Botanique* par LAMARCK, Tome IV, 1796. pp. 550-554, “Onagraise.” Twelve species of this genus are enumerated, *O. longiflora* being no. 4, *O. corymbosa* no. 11, and *O. grandiflora* no. 12. A copy of the diagnosis of this last one may be found in my *Mutation theory* (p. 441) and in the article of DAVIS. The article in the *Encyclopédie* is not signed and was probably written by POIRET, who prepared many articles in vol. IV, and wrote the whole of the later volumes. In the herbarium of Paris some of the specimens may be seen quoted with the authority of POIRET, as, for example, on the sheet of *O. suaveolens* Desf., where above that name is written *Oenothera grandiflora* Poiret *Encyclopédie*. (Cf. pl. 39 of the article of DAVIS.)

¹⁷ *L’Oenothera grandiflora* de l’herbier de LAMARCK. *Rev. Gén. Botanique* 25: 1914.

¹⁸ Cf. BONNETT, *op. cit.* p. 138.

Encyclopédie correspond as closely with the characters of my plants as dried specimens and descriptions expressed in words ever can do.

On the contrary, the specimen *B* is surrounded with doubts. DAVIS has given a very elaborate description of this branch, comparing it with my *Lamarckiana*. The sheet bears the label: "*Oenothera* [*grandiflora*] nova spec. flores magni lutei, odore grato, caulis 3 pedalis." The fact that the name *grandiflora* is placed in brackets shows that LAMARCK did not wholly trust his identification of this plant with the other one. Perhaps the words "nova species" indicate that he took it to be possibly a different species. Later, POIRET discovered the identity of this specimen with *O. grandiflora* Aiton Hort. Kew,¹⁹ as has been indicated by DAVIS. And in DE CANDOLLE'S *Prodromus* (3:47. 1828), SERINGE separated the two types, describing *O. grandiflora* Ait. and *O. Lamarckiana* (SER. MSS) as different species.

The words "odore grato" point to *O. grandiflora* Ait., which has fragrant flowers, while the flowers of *O. Lamarckiana* Ser. are almost without odor. In the original description no mention is made of the odor, and this shows once more that the specimen *B* was not the authentic one for this description.

DAVIS has compared the branch *B* with some of his hybrid strains from Dixie Landing²⁰ and finds a close resemblance. Perhaps the plant of LAMARCK was a chance hybrid found in the Jardin des Plantes, and in this case, as DAVIS says, "we can have no certainty as to the characters of an individual plant unless its seeds have been grown in large cultures."²¹ At all events, it is not backed by other herbarium material in the Museum d'Histoire Naturelle, so far as I know. If POIRET'S opinion that it belongs to *O. grandiflora* Ait. is correct, then it has evidently not served as a basis for the description of *O. grandiflora* Lam. (*O. Lamarckiana* Ser.). In *O. grandiflora* the fruits are thin and relatively large, for example,

¹⁹ *Encyclopédie méthodique*. Suppl. IV, p. 141. 1816. See DAVIS, p. 522.

²⁰ At Dixie Landing, Alabama, only hybrid strains of *O. grandiflora* and *O. Tracyi*, perhaps mixed with other species too, are to be found. See Science *op. cit.* p. 399. 1912.

²¹ DAVIS, B. M., A much desired *Oenothera*. Plant World 16:148. 1913.

3 cm. long and 3 mm. wide; while those of *O. Lamarckiana* may measure 2.5 cm. in length and 6 mm. in width, making a ratio of $\frac{10}{1}$ in the one case and $\frac{4}{1}$ in the other.²² The description of the fruits as short, as given by LAMARCK, evidently points to the second and not to the first case.²³

Summing up the main results of this discussion, we find that specimen *A* of the herbarium of LAMARCK closely corresponds to the *O. Lamarckiana* Ser. of the present time, and has been taken by almost all authors for its prototype. The specimen *B* differs from it in its general aspect, in the words "odore grato" on its label, and in the opinion of POIRET that it belongs to *O. grandiflora* Ait., this opinion pointing to long and narrow fruits. Personally, it impressed me as having been brought into the herbarium of LAMARCK only later on, and as having been placed in the cover of *O. grandiflora* Lam. with a doubt shown by the placing of the name in brackets.

The best proof for the fact that *A* and not *B* is the authentic specimen of *O. grandiflora* Lam. is perhaps given by the specimen in the herbarium of Father POURRET, which was given to the Muséum d'Histoire Naturelle by Dr. BARBIER in 1847.²⁴ It bears the name *Oenothera grandiflora* Lam. written in the clear and beautiful handwriting of the clerk of POURRET. In the same cover there is another sheet of POURRET's collection, on which the same clerk wrote *Oenothera biennis*. Unfortunately, DAVIS, who did not visit the Museum, has mistaken this one for the one studied by me,²⁵ and has accordingly published a photograph (pl. 38) and a description of it. It is easily seen that this specimen really comes nearer to our present *O. biennis* L. than to anything else.

²² *L'Oenothera grandiflora* de l'herbier de LAMARCK, *op. cit.* fig. 1, b and c.

²³ DAVIS (*op. cit.* p. 523) lays great stress on the tips of the sepals, but I cannot find a well defined difference between the two species in this character. He calls attention to the word "sétacé" in LAMARCK's description of the sepal tips: "this has been translated by DE VRIES (*Mutations-Theorie*, p. 317. 1901) as "dicke." The French, however, is from the late Latin word *setaceus*, derived from "seta," a stiff hair or bristle. The meaning, therefore, is exactly the opposite of that given by DE VRIES." If the reader will kindly look up my book at the page quoted by DAVIS, he will find that I have translated "sétacé" by "fadenförmig."

²⁴ The Mutation Theory, Engl. ed. 1:442, note 2.

²⁵ Bull. Torr. Bot. Club *op. cit.* p. 527.

The plant which POURRET called *O. grandiflora* Lam. is represented on our pl. XVIII. It agrees wholly with the present *O. Lamarckiana* Ser., and in all respects. It was fastened on its sheet by the clerk of POURRET and consists of two flowering spikes and two separate flowers. The stigma lobes are seen spread above the anthers in the normal way. The specimens were picked at the beginning of the flowering period and bear no fruits; obviously they were main spikes. They will be recognized at once as *O. Lamarckiana* by anyone who has seen living cultures of this species. As I have quoted in my *Mutation theory* (*loc. cit.*), SPACH has written on this sheet "*Onagra vulgaris grandiflora* Spach," which remark also proves the identity with *O. Lamarckiana* Ser. The printed label says "Collection de l'Abbé POURRET, extraite de l'herbier légué par M. le Dr. BARBIER en 1847." The main spike measures about 40 cm., the smaller one about 20 cm.

In my book I have also referred to a specimen of *O. suaveolens* Desf. At that time I did not know the Alabama species and believed that *O. suaveolens* Desf. and *O. grandiflora* Ait. were synonyms, as almost all authors did. Therefore I used the two names promiscuously. Last summer, however, I cultivated, side by side, *O. suaveolens* Desf. from Fontainebleau, collected by Dr. BLARINGHEM, and *O. grandiflora* Ait. from Castleberry, Alabama, collected by myself with Mr. BARTLETT. They proved to be wholly different species.²⁶ So far as I know, the large-flowered Oenotheras, which are now relatively common in the western departments of France, all belong to *O. suaveolens* Desf., at least all the specimens and cultures on which I based my opinion in 1901 did. The specimen of the Muséum d'Histoire Naturelle, which I referred to especially, has been described by DAVIS from a photograph which is reproduced on pl. 39 of his paper. DAVIS, who did not know the *O. suaveolens* as a separate species, called it the flotsam of the herbarium (p. 529); it is, on the contrary, the authentic specimen of DESFONTAINES, bearing on the label the name *suaveolens* written by DESFONTAINES himself. The smaller plant, fastened on the same sheet, has another label, saying only *O. grandiflora*, and seems to me to have been fastened on this sheet subsequently. The

²⁶ *L'Oenothera grandiflora* de l'herbier de LAMARCK, *loc. cit.*

larger one, however, corresponds exactly with the species which is now growing in many thousands of specimens near Samois on the eastern limit of the Forêt de Fontainebleau, where I visited the different stations with Dr. BLARINGHEM in October 1913. The long fruits and the thick flower buds do not leave the least doubt concerning the identity of this specimen.

The most interesting discovery in this field of historical research, however, is that of a specimen of *O. Lamarckiana* Ser. in the collection of MICHAUX, described recently by BLARINGHEM.²⁷ I had the advantage of studying this sheet myself, when I visited Paris in October 1913. The printed label says "Herb. Mus. Paris, Herbar de l'Amérique septentrionale d'ANDRÉ MICHAUX." There is no further indication of the locality and no name. The specimen is a main spike, picked in the beginning of the flowering period, and without fruits (pl. XIX). It is excellently preserved and corresponds in all respects to my cultures of *O. Lamarckiana* Ser. The lobes of the stigma are seen to be widely spread above the anthers. The flowers and flower buds are exactly those of the present species.

ANDRÉ MICHAUX died in 1802, after having traveled during twelve years through the eastern United States from the Hudson River to Carolina. His celebrated collection constitutes one of the best sources of our knowledge of the flora of those parts of America at the end of the eighteenth century, that is, of the same period in which LAMARCK published his volumes of the *Encyclopédie*. His herbarium is at present at the Muséum d'Histoire Naturelle at Paris, and his plants were described after his death by his son FRANÇOIS ANDRÉ MICHAUX in a book entitled "ANDRAEAS MICHAUX, Flora boreali-americana, sistens characteres plantarum quas in America septentrionali collegit ANDRAEAS MICHAUX."²⁸ MICHAUX had the habit of collecting seeds of as many species as possible, besides his herbarium specimens, and of sending them to Europe to be sown.

²⁷ BLARINGHEM, L., *L'Oenothera Lamarckiana* Seringe et les Oenothères de Fontainebleau. Rev. Gén. Botanique 25:1914.

²⁸ Editio nova, 1820, Paris. The genus *Oenothera* is dealt with in vol. I on p. 214; the plant is given under the name of *O. biennis*. For the ground covered by his travels, see the preface and the article of BLARINGHEM.

This beautiful specimen proves that *O. Lamarckiana* Ser. was a component of the flora of the eastern part of Northern America at the end of the eighteenth century, and that it has come down to us as completely unaltered as may be shown by old herbarium specimens. Moreover, it tends to make it at least very probable that the European strains, or at least some of them, are derived from the importation of seeds by MICHAUX. The specimen *A* in the herbarium of LAMARCK, designated as "d'Amérique sept.," probably belonged to this same strain.

The exact situation of the locality where MICHAUX collected this specimen is, of course, unknown. Much stress is laid by many authors upon the fact that no wild station for *O. Lamarckiana* has been discovered lately in any part of the United States. This argument evidently loses the main part of its weight when we know that it was observed by such a well known botanist as MICHAUX. Moreover, this situation is not peculiar to *O. Lamarckiana*; on the contrary, the same condition prevails for the other European species, *O. biennis* L., *O. muricata* L., and *O. suaveolens* Desf., whose original stations in the United States and Canada have not been rediscovered. Even *O. grandiflora*, which is known to occur in Alabama in different localities, is observed there to grow on cultivated soil only, especially on old fields of corn and cotton, and no one knows whence it came. Therefore, if our present ignorance of the origin of *O. Lamarckiana* is adduced in order to throw a doubt on its reality as a good species, the same doubt is attached to its nearest allies, and, in fact, to all the dozens of elementary species of the group *Onagra* which are now being found wild on waste fields and along roadsides all through the United States. Autochthonous stations are not known for any of them.

A most valuable contribution to the clearance of the historical data concerning the origin of *O. Lamarckiana* Ser. has been brought forward by DAVIS in his criticism of the alleged Texan origin of the present cultivated strain. This was introduced into the trade by Messrs. Carter and Co. of High Holborn in the neighborhood of London, about the middle of the last century. These horticulturists offered the seeds as coming from Texas. But, since then, no botanist is known to have seen the plant in that state, and DAVIS

suggests (p. 523) that the statement might, perhaps, have been caused by a mistake.²⁹ Now, it is well known that such details are, as a rule, given more in the interest of advertising than in that of pure science. Moreover, no horticulturist likes to offer for sale seeds with the announcement that the same form may be found as a wild flower in his own country.

O. Lamarckiana has been, for many years at least, a component of the flora of England, growing in many localities, especially on the sand dunes along the coast. The most universally known station is that of St. Anne's on the Sea, near Liverpool, which has been studied by BAILEY, GATES, and other botanists, and where the species occurs in thousands of specimens. DAVIS received seeds from different English stations and recognized the plant in the cultures derived from them (*op. cit.* p. 237). In Lancashire the species locally grows together with *O. biennis* L., exactly as it does in the sand dunes of Holland. In such cases it produces hybrids such as I have described under the names of *laeta* and *velutina*, and as DAVIS has isolated as small-flowered races from those English localities (p. 237).

Now, if we agree with DAVIS that the seeds of Carter and Co. were derived from some English station, the probability at once arises that these English stations themselves owe their origin to the introduction of seeds from America, either by MICHAUX himself or by some other botanist of the same period. The history of the species would then become a very simple and clear one. In this respect it becomes of interest to look at the figure published in 1807 in SMITH'S *English Botany* (vol. VI. *pl.* 1534).³⁰ According to the description accompanying this plate, the "specimen was gathered on the extensive and dreary sand banks on the coast a few miles north of Liverpool, where millions of the same species have been observed by Dr. BOSTOCK and Mr. JOHN SHEPHERD growing perfectly wild and covering large tracts between the first and second range of sand hills." In this same locality *O. biennis* L. and *O. Lamarckiana* are now growing in the same abundance of individuals, partly separated and pure in different valleys and

²⁹ See DAVIS in *New Phytol.* 12:234. 1913.

³⁰ Cf. DAVIS, *op. cit.* p. 532.

partly in mixtures which are known to contain also their hybrids. The specimen of 1807 is designated *O. biennis*, but both the flowers have the lobes of their stigma above the anthers, which is a differentiating mark of *O. Lamarckiana*. Moreover, it is the only decisive detail, all other characters of the figures applying equally to both species. If it is allowable to trust to this detail, we should be entitled to conclude that the station of Liverpool contained both forms as early as 1807, even as it is known to do at the present time. In this case, *O. Lamarckiana* must be assumed to have been introduced into England about the time of MICHAUX and LAMARCK, and a common origin for the specimens of their herbaria and the wild stations in England becomes highly probable.

The strain of Carter and Co. has been identified by LINDLEY as *O. Lamarckiana* Ser., and the high authority of this eminent botanist confirms my own determination of the same strain, made by comparing it with the authentic specimen of LAMARCK.³¹

At all events, the adduced facts indicate a very simple history of our species, which has come down to us unchanged, so far as we know, from the original American habitat.³² There is no reason to suppose that it originated as a garden plant, and none at all to subject it to all the doubts ordinarily brought forward against the purity of descent of horticultural forms in general, simply on the ground that some garden plants are of known hybrid origin. *O. Lamarckiana* has remained unchanged through more than a century, and has kept as true to its type as any good wild species. "It is exceedingly fortunate," says DAVIS (*op. cit.* p. 527), "that the plant which serves as the type of *Oenothera Lamarckiana* Ser. should have come down to us so well preserved that there is scarcely a doubt of its identity." But the identity is with the species as it is still known under that name. Whether the species

³¹ DAVIS says (*op. cit.* p. 531) "the identification by LINDLEY of these plants with *O. Lamarckiana* Ser. was undoubtedly incorrect," but he does not give any reason for this assertion.

³² DAVIS says (*op. cit.* p. 530) "that *Lamarckiana* has come down to us greatly modified, that its parentage is far from pure, that it is in fact of hybrid origin." This assertion, which is not based upon any facts, is clearly contradicted by the preservation in excellent condition of the three specimens of LAMARCK, POURRET, and MICHAUX, not known to DAVIS.

was in the same condition of mutability at the time of its first appearance as it is now, is of course a different question.³³

Summing up the results of this historical investigation, we may say:

1. *Oenothera Lamarckiana* Ser. is represented by specimens in the herbaria of LAMARCK, POURRET, and MICHAUX (pls. XVII-XIX), and is, so far as this material enables us to judge, at the present time exactly the same plant as it was at that period. It has come down to us, through more than a century, as unaltered and as constant as true species usually do.

2. It has been a component of the flora of the eastern United States, where MICHAUX collected it and whence LAMARCK derived his specimen.

3. At the present time it is a component of the flora of England, and is as well established in that country as is *O. biennis* in different parts of Europe.

4. The strain which is now in cultivation, and which was introduced into the trade about the middle of the last century, was probably derived from some wild English locality, which itself may have come from an introduction into Europe of the seeds collected either by MICHAUX himself or by some other botanist of his period.

AMSTERDAM

EXPLANATION OF PLATES XVII-XIX

Plate XVII

Oenothera grandiflora Lam. (*O. Lamarckiana* Ser.): the authentic specimen in the herbarium of LAMARCK, two-thirds natural size, referred to as *A* in the text; in the left upper corner a bunch of flower buds of my culture of 1913, dried and pressed, is given for comparison, and photographed together with the main specimen.

Plate XVIII

Oenothera grandiflora Lam. (*O. Lamarckiana* Ser.): the specimen in the herbarium of Father POURRET, one-third natural size; on the label is written *Onagra vulgaris grandiflora* Spach.

³³ Über die Dauer der Mutationsperiode bei *Oenothera Lamarckiana*. Ber. Deutsch. Bot. Gesells. 23:382. 1905.



OENOTHERA LAMARCKIANA SER.

HERBARIUM OF LAMARCK



Vries, Hugo de. 1914. "The Probable Origin of *Oenothera Lamarckiana* Ser." *Botanical gazette* 57(5), 345–361. <https://doi.org/10.1086/331325>.

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