# STUDIES OF *LYTHRUM SALICARIA* I. THE EFFICIENCY OF SELF-POLLINATION

A. B. Stout

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The conditions that exist in species with trimorphic flowers permit the investigation of the problems regarding the nature of sex-differentiation and the degrees of compatibility between male and female organs under very favorable circumstances. In these forms the morphological adaptations for cross-pollination are often decidedly correlated with physiological incompatibilities which make cross-fertilization more certain by excluding the functioning of the chance self-pollinations which occur.

In general it is to be recognized that sexual fusions are favored by similarity of the gametes both in genetic constitution and in immediate origin, and that such conditions as trimorphism and self-incompatibility are to be regarded as, in a high degree, secondary and acquired. While these conditions secure the advantages of bringing together gametes of different origins and in greater or less degree of different genetic constitution, they decidedly limit and restrict free fertilization and full productivity.

The combination of morphological trimorphism with physiological incompatibilities as seen in species like *Lythrum Salicaria* may well be regarded as the highest degree of specialization in sex-determination and fertilization that exists in flowering plants. For this species there is the obvious morphological differentiation giving three lengths of pistils and three sets of stamens of lengths corresponding to those of the pistils, with the stamens bearing pollen differentiated as to size, color, and nature of the reserve food material in storage. For the individual, the flower of any particular plant has a pistil of one of the three lengths and a set of stamens for each of the other two lengths. This gives differentiation of forms as such, and in the single plant there is the differentiation that gives two kinds of stamens. Furthermore, this morphological differentiation is decidedly correlated with physiological differentiation. The noteworthy researches of Darwin (1865, 1877) showed that there is marked or even complete sterility to (1) self-pollinations, to (2) intra-form cross-pollinations, and to (3) the inter-form cross-pollinations that are illegitimate (*i.e.*, those that involve different lengths of pistil and stamen). Seed-production was hence found to be more or less limited to legitimate pollinations, which are necessarily crosses.

The specializations in these forms allow no doubts as to their significance such as have often been raised in regard to the colors of entomophilous flowers, for here the adaptations are morphological and depend directly on the agency of insects for their effectiveness in pollination. The relative lengths of the different sets of stamens and of the pistils are unquestionably provisions favoring crossing.

It is, however, obvious that such differentiations are not fundamental expressions of sexual antithesis, since they are all reciprocal in any pair of flowers. Any two plants of any two forms are cross-compatible or cross-incompatible according to whether the cross is legitimate or illegitimate. The differentiations, at least in respect to maleness, that in dimorphic plants are seen in individuals as such and which appear to have definite genetic value are here seen equally well in the two sets of stamens in a single flower. All this emphasizes the fact that the conditions are secondary and acquired in contrast to the more primitive condition of homomorphism and a more general compatibility of gametes.

The generally accepted view has been that the differentiations in this species are well established and very stable. The tendency has been to emphasize, as did Darwin, the evidence that here there is adaptation favoring crossing, and to pass the evidence, which has to some extent been noted, that the adaptations are incomplete. It is to be recognized that such evidence has a very direct bearing on questions of the origin of trimorphism, of the nature of sex-differentiations, and of whether there is still opportunity for further selection in the species either toward greater or toward less restriction of fertilization. It is evidence along these lines that the writer wishes to present in reports, of which this is the first, of investigations with the species.

## The Efficiency of Self-pollination for Plants Grown in Isolation

The writer's studies of *Lythrum Salicaria* were begun in 1917 in testing the self-compatibility of plants grown in isolation from other plants of the same or of related species. On such a plant hundreds of flowers open daily during a rather extended period of time and insect visitors can go from flower to flower, but with no chance, if the isolation is complete, of bringing pollen from other plants of *Lythrum Salicaria.* A large number of flowers are thus involved in the chance for self-fertilization (including here autogamy and geitonogamy), and the results can be obtained for the entire period of bloom. This test does not, however, determine the relative fertility of a plant to pollen of its two sets of stamens, nor does it reveal the need or the efficiency of particular species of insects in the self-pollination of the various forms, which may indeed give results that are highly variable from season to season or from year to year or according to location. However, if seed is produced there is positive evidence of self-compatibility, and the negative results may be tested further by controlled pollinations.

*Short-styled Plants Grown in Isolation.* Two large, well-developed plants several years old were dug from a mixed population growing at the New York Botanical Garden. One (*S no. 2*) was grown in the garden of the

Department of Botany at Columbia University, under the observation of Professor R. A. Harper, and one (*S no. 1*) at the University of Missouri under the care of Professor G. M. Reed. Both plants made vigorous growth and bloomed profusely, but neither plant produced a single capsule during the entire period of bloom of the season of 1917. In 1918 the plant at Missouri suffered severely from drought, and its failure to set any seed that year is not to be considered as adequate evidence of complete self-incompatibility.

The short-styled plant at Columbia University thrived and in the course of its season of bloom in 1918 produced 17 pods. Ten of these contained only mere rudiments of seeds, two contained one good seed (plump and apparently fully developed) each, three had two good seeds each, one had seven seeds, and one had eight. Sixteen of these 23 seeds germinated. In the following year (1919) this plant bloomed more abundantly than in the previous year and produced at least 5000 flowers, and during the entire season 161 pods matured. The seeds in 100 of these pods were counted; the number per pod ranged to 116, and the average was 23.67 (see table 1). This plant grew poorly in 1920, when its roots were separated to make two plants. In 1921 these thrived, and there was abundant bloom but only about 25 pods were produced. The irregular pod production by this plant may involve one or more of several conditions; possibly in 1919 insects may have brought pollen from a distance from plants of this species growing in city parks, or the irregularity may involve the presence or absence of certain insects that are most efficient in causing self-pollination.

*Long-styled Plants Grown in Isolation.* A long-styled plant (*L no. 1*) was grown at Baraboo, Wisconsin, under the care of Mr. William Toole, Sr., a well known pansy specialist. Plants of the variety *rosea* were also growing in the nursery at some distance away, so that some of the seed produced by the plant *L no. 1* may have been due to cross-pollination by insects. But another long-styled plant (*L no. 2*) was grown in what was certain isolation at Pleasantville, N. Y., under the care of Dr. M. A. Howe. Capsules were produced by both these plants. Of the 65 capsules on *L no. 1* in 1917, 16 contained no seeds, 17 contained one seed each, and the highest number of seeds in any capsule was 17. In 1917 a total of 53 capsules matured on the plant *L no. 2*. As shown in table 1, the number of seeds per capsule for this plant was also low, although all but three of the capsules contained some fully matured seeds.

In 1918 both plants produced capsules quite as in 1917, but the capsules on *L no. 2* were somewhat more numerous than in the previous year though still constituting a small proportion of the entire number of flowers.

The capsules produced by these two plants were distributed irregularly but rather indiscriminately throughout the flowering branches. Self-fertilization appeared to be effected with the same frequency and efficiency throughout the flowering period. No very decided seasonal differences appeared in respect to the proportional number of flowers which matured

Table 1. *Self-compatibility in Lythrum Salicaria to insect-pollination, and cases typical for the results obtained for controlled hand-pollinations*

| | Number of Flowers Pollinated | Number of Pods Produced | Number of Pods used in Seed Counts | Distribution of Seed per Pod. Class Groups 1 to 10 | | | | | | | | | | | | | | Average Seed for Pods with Seed |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 0 | –10 | –20 | –30 | –40 | –50 | –60 | –70 | –80 | –90 | –100 | –110 | –120 | –130 | |
| Isolation, Insect-pollination | | | | | | | | | | | | | | | | | | |
| S. no. 1 | ? | 0 | | | | | | | | | | | | | | | | |
| S. no. 2. (1918) | ? | 17 | 17 | 10 | 7 | | | | | | | | | | | | | 3.28 |
| S. no. 2. (1919) | ? | 161 | 100 | 0 | 34 | 30 | 16 | 4 | 5 | 4 | 0 | 2 | 1 | 2 | 0 | 2 | | 23.67 |
| L. no. 1 | ? | 65 | 65 | 16 | 47 | 2 | | | | | | | | | | | | 2.96 |
| L. no. 2 | ? | 53 | 53 | 3 | 47 | 3 | | | | | | | | | | | | 4.85 |
| M. no. 2 | ? | 3000 | 300 | 14 | 202 | 48 | 8 | 7 | 6 | 1 | 5 | 1 | 1 | 1 | 2 | 3 | 1 | 8.91 |
| M. no. 1. (1919) upper ⅓ | ? | many | 71 | 7 | 43 | 12 | 3 | 2 | 1 | 0 | 2 | 0 | 1 | | | | | |
| M. no. 1. (1919) middle ⅓ | ? | few | 31 | 3 | 16 | 3 | 0 | 3 | 2 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | | |
| M. no. 1. (1919) lower ⅓ | ? | few | 40 | 6 | 20 | 3 | 1 | 2 | 2 | 0 | 1 | 1 | 0 | 1 | 2 | 1 | | |
| " total | ? | 1500 | 142 | 16 | 79 | 18 | 4 | 7 | 5 | 1 | 5 | 1 | 1 | 1 | 2 | 2 | | 18.25 |
| Hand-pollination | | | | | | | | | | | | | | | | | | |
| M. no. 1. (1919) | 233 | 134 | 134 | 1 | 28 | 29 | 19 | 20 | 14 | 6 | 5 | 8 | 3 | 0 | 0 | 1 | | 24.61 |
| M. *5–1* no. 13 | 103 | 0 | | | | | | | | | | | | | | | | |
| M. *3* no. 7 | 48 | 8 | 8 | 1 | 5 | 2 | | | | | | | | | | | | 7.00 |
| M. *1* no. 48 | 35 | 6 | 6 | 0 | 1 | 2 | 2 | 1 | | | | | | | | | | 20.33 |
| M. *1* no. 31 | 33 | 4 | 4 | 0 | 0 | 2 | 1 | 1 | | | | | | | | | | 25.00 |
| M. *1* no. 56 | 60 | 9 | 9 | 0 | 0 | 4 | 3 | 0 | 1 | 1 | | | | | | | | 28.33 |
| M. *5–1* no. 25 | 32 | 9 | 9 | 0 | 0 | 0 | 2 | 1 | 0 | 3 | 2 | 1 | | | | | | 50.88 |
| M. *5–1* no. 35 | 32 | 5 | 5 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 1 | | | | | 49.50 |
| M. *1* no. 30 | 37 | 9 | 9 | 0 | 0 | 0 | 2 | 0 | 2 | 1 | 1 | 0 | 1 | 2 | | | | 59.66 |
| M. *1* no. 57 | 40 | 44 | 44 | 0 | 1 | 7 | 3 | 2 | 7 | 3 | 3 | 12 | 5 | 1 | | | | 63.15 |
| L. *4* no. 2 | 55 | 2 | 2 | 0 | 2 | | | | | | | | | | | | | 6.00 |
| L. *1* no. 66 | 68 | 2 | 2 | 0 | 2 | | | | | | | | | | | | | 6.00 |
| L. *2* no. 18 | 50 | 7 | 7 | 0 | 6 | 1 | | | | | | | | | | | | 7.42 |
| L. *1* no. 8 | 49 | 22 | 22 | 0 | 11 | 10 | 1 | | | | | | | | | | | 8.90 |
| L. *5–5* no. 38 | 24 | 6 | 6 | 0 | 2 | 1 | 2 | 1 | | | | | | | | | | 20.00 |
| S. *5* no. 5 | 14 | 4 | 4 | 0 | 1 | 2 | 1 | | | | | | | | | | | 14.00 |

capsules that could be referred definitely to differences in insect visitations or to the constitution of the plants.

*Mid-styled Plants Grown in Isolation.* A plant of this form (*M no. 2*) was sent to Mr. H. L. Skavlem, who grew it at Carcajou Point, Lake Koshkonong, Wisconsin. Mr. Skavlem states that by the middle of July this plant was "over four feet high with an abundance of bloom which continued for about six weeks." The plant bloomed from July 14, 1918, until the first week in September. There were about 35 well-developed main flower spikes ranging from 3 to 14 inches in length, and the total number of flowers produced was estimated at 8,000. This description would apply as well to any well-developed plant of any of the three forms.

This mid-styled plant was decidedly self-compatible in this isolation test. At least 3,000 capsules matured on it in 1917. A total of 300 capsules were examined and counts were made of the seeds present, with results as summarized in table 1. The number of seeds per capsule ranged to 121; twenty-eight capsules had more than 30 seeds each, but 202 capsules contained less than 11 seeds per capsule, and 14 contained only rudiments of seeds. The average number of seeds per pod for those that had good seeds was 8.91. In 1918 the self-compatibility of this plant was quite the same as in 1917.

In making the counts of seeds in 300 capsules (1917 crop) of this plant, position was taken into account. Each branch involved in the counts was divided into three sections of equal length, here designated as the lower third, middle third, and upper third. In the lower third of all branches there were 10 capsules with more than 30 seeds each. It is clear that the average number of seeds per capsule was lower toward the top of the branches of this plant, but smaller capsules and fewer seeds per capsule are, as a rule, to be expected toward the apex. Otherwise the plant was rather uniformly highly self-compatible, and capsules with seeds were produced in a considerable proportion of the flowers subjected to open pollination throughout the entire period of bloom.

Another mid-styled plant (*M no. 1*) was grown in my own home garden. This plant made a vigorous growth and produced in 1917 at least 6,000 flowers. At the close of the season it was found that relatively few of the flowers produced pods during the first two thirds of the period of bloom, but that later nearly every flower produced a pod.

In 1918 it was planned to test experimentally the behavior of this plant, and especially to determine if the marked difference in production of fruit involved changes in the innate ability of the plant to produce fruit or indicated merely some difference in insect-pollination. A large, well-developed long-styled plant was planted by its side. The two began blooming only one day apart. The long-styled plant was allowed to bloom, thus affording opportunity for free cross-pollinations by insects between the two, until the 17th of August, when the long-styled plant was cut down. During the time that both were in bloom nearly all flowers that opened on the mid-styled plant developed fine pods, showing that the feeble production of pods during the early part of bloom as observed in the previous year when the plant was in isolation was not due to an impotence of the pistils. During the rest of the season its performance was quite as in the previous year.

In 1919 the long-styled plant was kept cut down so that no flowers were produced by it, and a series of guarded self-pollinations were made on the plant *M no. 1*. Branches were enclosed in glassine paper bags. Whenever pollen from short stamens was used for pollinations, the flowers to be thus pollinated were opened early in the morning and the long stamens were removed, and then pollen from the short stamens was used later in the day when the anthers were dehiscing.

Legitimate cross-pollinations, using pollen of flowers brought in vials from the experimental plots over a mile distant, were made on 22 flowers during the first 18 days of bloom. The plant was in bloom 55 days. The results obtained for selfing are summarized in table 1 and are shown in more detail in table 2, in which, to facilitate ready comparison, the data are compiled for three periods.

TABLE 2. *Record for controlled pollinations of mid-styled plant no. 1 in summer of 1919*

| | 1st to 18th Day | 19th to 36th Day | 37th to 55th Day |
|---|---|---|---|
| Selfed with pollen of long stamens | | | |
| Failures—no pods | 70 | 35 | 9 |
| Pods produced | 18 | 46 | 70 |
| Seeds per pod—range and average | (0 to 117) av. 34 | (2 to 81) av. 32 | (3 to 82) av. 32 |
| Selfed with pollen of short stamens | | | |
| Failures | 33 | 57 | 47 |
| Pods | 1 | 1 | 1 |
| Seeds per pod | 37 | 10 | 1 |
| Legitimate cross-pollination | | | |
| Failures | 2 | | |
| Pods | 20 | | |
| Seed-range and average | (12 to 176) av. 98 | | |

Of the 140 flowers hand-pollinated with pollen from short stamens, only three produced pods yielding 1, 10, and 37 seeds respectively, but these may have been due to chance pollination with pollen from the long stamens at the time of their removal or with pollen of other flowers which were enclosed in the same bag. The results indicate that the plant remained decidedly if not completely self-incompatible to pollen of its own short stamens throughout the entire period of bloom.

When pollen of long stamens was used in hand-pollinations, the proportion of pods produced increased as the season advanced, and during the last 18 days of bloom there were but 9 failures out of 79 flowers pollinated. The results show conclusively that the self-compatibility in this plant involves fertilizations from the pollen of long stamens, and also that this compatibility actually increases toward the end of the period of bloom. The increase in compatibility affects, however, the number of pods that are formed rather than the number of seeds in a pod. The average number of seeds in the pods that were produced was almost the same for all periods, but the highest number of seeds in any pod was obtained during the first 18 days of bloom.

The 22 legitimate crosses made during the first 18 days gave 20 pods with seeds ranging in number from 12 to 176, with an average of 98 seeds per capsule. These results show conclusively, as do those of open cross-pollinations during the early part of the period of bloom in the previous year, that the pistils of the plant are highly potent during the period of marked self-incompatibility. The decided change in fruit-production s hence due to a change in the physiological relations between pistils and the pollen of long stamens. Pollen from both short stamens and long stamens was examined at frequent intervals throughout the entire period of bloom; there was very little abortion, the pollen was successfully germinated in artificial media, and the use of such pollen in legitimate crosses on several dates during the first 30 days of bloom was almost invariably highly effective in pod- and seed-production. There were in this plant no noticeable evidences of impotence of stamens and anthers, such as are to be seen in some plants of this species.

The branches left to open-pollination produced pods quite as in the year 1917. Several of the main branches were selected and divided into thirds, and seeds in all pods in the lower two thirds were counted; then an equal number of pods from the many pods in the uppermost third were taken at random for counts, the entire number, 142, being as near the number of pods secured from the selfing by hand in which the pollen of long stamens was used as was possible. As shown in table 1, the range for number of seeds per pod and the average were higher for the lower two thirds than in the last third, showing that the change in compatibility involves number of pods formed rather than number of seeds per pod. Comparison shows that the controlled pollinations in which pollen from long stamens was used were somewhat more successful than free open-pollinations, when judged by the average number of seeds produced.

A third mid-styled plant (*M no. 3*) was grown in isolation in the New York Botanical Garden at a distance of about one mile from the location of the plant *M no. 1*. This plant proved to be decidedly less self-compatible to open self-pollination than were *M no. 1* and *M no. 2*, but, as in *M no. 2*, there was quite the same proportion of pods produced throughout the entire season of bloom, no change in compatibility being evident as observed in the plant *M no. 1*.

*Summary*. In these tests seeds were obtained to illegitimate self-pollination of plants of all three forms. Mid-styled plants were most highly self-compatible in respect to the number of pods produced. The pods found were distributed irregularly over the entire period of bloom except for one plant (*M no. 1*), in which it was found that there was an actual change in the degree of self-compatibility to pollen from its own stamens. The results from year to year have been very uniform for all plants, except for the plant *S no. 2*. Its feeble production of pods in 1918, followed by the production of 161 pods in 1919, suggests that the plant is rather strongly self-compatible provided insects make the proper pollinations. It may readily be conceded that the kinds of insects that can most efficiently self-pollinate long-styled and mid-styled plants are not the ones which best self the short-styled plants.

Self-pollination does not appear to be uniformly as efficient in seed-production as are certain legitimate cross-pollinations, at least for the one mid-styled plant *M no. 1* (see table 2). Of the 22 flowers on it that were crossed during the first 18 days of bloom there were only two failures, the highest number of seeds for a capsule being 176 and the average 98. Whether such pollination would be more effective than selfing during the last part of the period of bloom was not tested.

## Self-compatibility Tests by the Bagging Method

A total of about 600 plants have been grown in pedigreed cultures from seed. A considerable number of these have been tested for self-compatibility in the following manner: branches were enclosed in glassine paper bags, and pollinations of flowers opening within were made from day to day. Long-styled plants and short-styled plants were selfed by using the pollen from mid-length stamens, and the mid-styled by use of the pollen of long stamens. In making pollinations, stamens with dehiscing anthers were removed with sterile tweezers and brushed on pistils, leaving an abundance of pollen. In cases of pseudo-proterogyny the fully protruding pistils of partially opened flowers were likewise treated along with pistils of more mature flowers. It appears that in the decidedly pseudo-proterogynous flowers the pistils protrude long before they are receptive to any kind of fertilization, and that highest seed production in compatible fertilizations occurs when pollination is made at or about the time that petals open and pollen is shed. On plants two or more years old, a total of as many as 500 or more flowers were often thus pollinated. On plants in the first year of growth from seed the number thus selfed was often much less.

These tests are undoubtedly less adequate than tests in isolation for revealing feeble grades of self-compatibility and in showing such changes in self-compatibility as are seen in the plant *M no. 1*, but hand-pollinations make certain that pollen in abundance is applied to the stigmas at the time when they are judged to be most receptive.

The general results summarized for each form without reference to lines of descent are as follows:

| | Fully Self-incompatible | Feebly Self-compatible | Medium Self-compatible | Highly Self-compatible |
|---|---|---|---|---|
| Mid-styled plants..... | 64 | 20 | 21 | 7 |
| Long-styled plants..... | 83 | 14 | 0 | 0 |
| Short-styled plants.... | 22 | 1 | 0 | 0 |

An attempt has been made to grade the plants according to whether the self-compatibility is feeble, medium, or strong, the judgment being based on the proportion of selfed flowers that gave pods and the number of seeds produced. Results typical for various grades are given in table 1. The tests made show that many plants of the species are without doubt entirely self-incompatible (*M 5–1 no. 13* in table 1 for example), and that others are highly self-compatible (*M 1 no. 57*), with various intervening grades the grouping of which is neither definite nor accurate.

In these tests mid-styled plants have been more highly self-compatible than plants of the other forms. This is true both in relative numbers that produce fruit to selfing, and in the range to higher grades of fertility. On one plant, *M 1 no. 57*, every flower that was selfed produced a pod, and four other pods were produced in other flowers that spontaneously selfed while enclosed in a glassine bag.

Of the 97 long-styled plants tested in hand-pollinations, only 14 produced pods, and not one gave over 30 seeds in any pod. In all of these the self-compatibility was apparently of a weak grade.

Twenty-three short-styled plants were tested, and only one produced seeds.

The results obtained in the controlled self-pollinations with these plants agree in general with those obtained in isolation tests. A rather large proportion of mid-styled plants are self-compatible in some degree, and nearly half of the plants of this form produced pods containing viable seeds to selfing, and a few were highly self-compatible. There has been no difficulty in finding mid-styled plants to use as parents of self-fertilized lines of progeny. Relatively few long-styled plants produced pods to selfing, and in all such plants the self-compatibility was feeble, few pods being produced and these having few good seeds. Short-styled plants have as a class been decidedly self-incompatible, and of the seedlings tested only one has produced seeds to selfing. The high seed-production seen in the plant *S no. 1* in 1919 was not duplicated by the plant in 1918 nor in 1920 and 1921. There has not been opportunity to test this plant by controlled hand-pollinations as the plants grown from seed have been tested.

## Summary

1. Many plants of *Lythrum Salicaria* are capable of producing capsules and viable seeds to illegitimate self-pollination brought about either by controlled hand-pollination or by insect-pollination in the field. The capacity for self-fertilization still lingers strongly in the species.

2. The proportion of self-compatible plants is greatest in the mid-styled plants, in which also the highest grades of self-compatibility are to be seen. Long-styled plants are, as a class, less self-compatible, and the short-styled plants are still less so. The three forms appear to differ in the capacity for self-compatibility.

3. There are wide variations in the degree of self-compatibility. In the most highly self-compatible form, the mid-styled, there are all gradations between complete self-incompatibility and the highest grade of self-compatibility.

4. The variations in the physiological condition of the sex organs, as

exhibited in selfing, suggests that wide variations may likewise be expected for crossings even for those that are legitimate.

5. One noticeable case of end-bloom self-compatibility was found. This was in a mid-styled plant and involved only fertilizations from pollen of the set of long stamens.

6. The physiological relations of the sex organs in plants of this trimorphic species exhibit quite the same range of variations as are seen in many homomorphic species.

## Conclusion

For the species *Lythrum Salicaria* the evidence of wide variation in the degree of self-incompatibility is definite. The physiological differentiations of the sex organs are incompletely correlated with the apparent structural adaptations for cross-pollination; they are not fixed, constant, and fully achieved either in expression or in heredity, but are fluctuating and intergrading. They still present opportunity for further selection either toward greater or toward less restriction of fertilization.

The persistence of self-compatibility in various degrees of expression, and the apparent difference in respect to self-compatibility seen among the various forms, present strong evidence that self-compatibility was the antecedent condition in the species out of which the present complex of sex relations is still evolving, just as the sets of styles and stamens of different lengths have been developed out of an original homomorphic species.

New York Botanical Garden

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