VIII—Genetical and Taxonomic Investigations in the Genus Oenothera

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Introduction

The present study is the result of combining genetics with taxonomy in the investigation of a polymorphic group of wild plants. It shows a degree of multiformity which was hitherto unsuspected in the genus. All the early genetical work on Oenothera was done with species which had been naturalized in Europe and whose North American home was unknown. Later, DE VRIES (1913) introduced various American forms into cultivation and used them in genetic experiment, but without full taxonomic descriptions. BARTLETT was mainly concerned in describing about twenty-five new species from wild plants of eastern North America brought into cultivation, and the present writer has previously described five, all but one of them from Eastern Canada. Professional taxonomists have paid little attention to the Onagra section of the genus except for the occasional description of a new species from western North America, and the whole number of species now recognized and described is about 70, not counting the 17 new species and 15 new varieties described in the present paper. The reason for the neglect of the taxonomists, even after the mutation work concentrated a great deal of attention on the genus, was no doubt the difficulty that many of the characters are not well shown in ordinary herbarium material. Indeed, cultures are necessary in order to study adequately the characters of these forms; but, on the other hand, species once clearly delimited in this way can be recognized in the field, at least when welldeveloped plants are available, and frequently from the rosette stage alone.

The sporadic collection of seeds from widely separated localities has, however, always in my experience yielded cultures which required description as distinct new species, and this convinced me of the necessity for a much fuller investigation of the distribution of wild American forms before evolutionary conceptions could be adequately applied to the genus as a whole. It was therefore decided, when the opportunity offered, to make as full a genetic survey as possible of the *Oenotheras* to be found in a particular area. In 1932 this developed into a genetic survey of Eastern Canada. Nearly one hundred collections of seeds were made in September and October, 1932, in different parts of Nova Scotia, New Brunswick, Quebec, and Ontario, as well as sporadic collections in Wisconsin, North Dakota, and one in Pennsylvania. Other seeds have been sent to me from collections made in parts of Nova Scotia, New Brunswick, Quebec, New York State, and Saskatchewan. The various donors are mentioned under each species in the detailed description, but I wish particularly to thank Professor Marie-Victorin, who accompanied me

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on a seed-collecting motor journey up the south shore of the St. Lawrence from Bic to Montreal, and Mrs. Winthrop Bell, who has sent many seeds with careful notes of their source and habitat.

From the seed collections of 1932, about 97 cultures were grown at the Courtauld Genetical Laboratory in Regent's Park in 1933. The following year some 126 cultures were grown, mainly a P₂ generation from the previous year, but partly new cultures from fresh seeds sent by Professor Marie-Victorin, Professor Roy Fraser, and others. In 1935, 142 cultures were grown; these were mainly P₃ or P₂ cultures from the original collections, but a few were F₁ hybrids and a number were wild species such as O. biennis L., O. nutans ATK. and BARTL., O. pycnocarpa ATK. and BARTL., O. angustissima, O. eriensis, O. novae-scotiae, O. ammophiloides and O. Victorini. All these species came from areas being investigated, and were therefore of great value for comparison with the new cultures. Many of these cultures were, of course, recognized as belonging to species already described from these or other areas, but many more were found to belong to new species or varieties. From these cultures has gradually developed a new type of investigation, combining taxonomic with genetical methods, treating each culture from a particular wild plant as a unit, and recording the variations and mutations occurring in the cultures through three (or in certain cases two) generations. In certain instances as many as twenty-five cultures have been grown, all belonging to one species.

These cultures have furnished each year a great mass of new material for observation and description. The results are recorded below under the various species and varieties. In addition, cytological investigations have been made, mainly on the 1932 cultures, by Mr. C. E. Ford. By sampling one plant in each of 21 cultures he found in every case a ring of 14 chromosomes in the pollen mother cell nuclei. The individual cases will be recorded under the various species and are listed in Table XXVII. From this and other evidence one can conclude that throughout north-eastern North America, at least so far as the more northern latitudes are concerned, the *Oenotheras* of the *Onagra* group show complete catenation. The few exceptions to that condition thus far found among wild species in North America are as follows: In the large-flowered species O. grandiflora Ser. from Alabama with a ring of 12, its derivative mutation, O. lutescens, being homozygous with 7 free pairs; and O. Hookeri Torr. and Gray from the Pacific coast, California, and northwards.* The latter has 7 free pairs but its ally O. franciscanana BARTL. has a ring of 4. Recent work (Cleland, 1935) indicates that the Californian forms, in strong

* In cultures of O. rhombipetala Nutt. from western N. Dakota, Mr. C. E. Ford has found that it has 7 free pairs of chromosomes, but in petal-shape and other characters this species stands apart from all the Onagras, and it belongs to the subgenus Raimannia. On the other hand, O. Agari, which is naturalized in Australia and is nearly related to O. stricta, belongs in Raimannia and frequently (Sheffield, 1927) has a ring of 14 chromosomes in diakinesis. It has been shown by Hedayetullah (1933) that O. missouriensis Sims has seven free pairs, but this large-flowered species is a perennial with strongly winged fruits and is generally placed in a separate genus, Megapterium. Catenation appears, therefore, to be circumscribed in its occurrence in the Onagraceae—a speciality mainly of the subgenus Onagra.

contrast to the eastern ones, have not gone further than a ring of 4 in their catenation. Forms with small flowers, which are apparently derivatives from O. Hookeri (GATES, 1915), occur further north in British Columbia, however, and it will be important to determine whether these have increased their catenation like the small-flowered northern forms on the eastern side of the continent. It will thus be possible to decide whether, as I suspect, the chromosome ring formation increased to a maximum as the Oenotheras moved northwards both in the east and the West, or whether the western forms lack the power to form a ring of 14 such as the eastern forms possess.

The original seed collections were made, as a rule, from single wild plants. Occasional exceptions to this rule will be mentioned in the text. The seeds from one plant generally yield a culture which is uniform except from the occurrence of an occasional mutation. All such mutations and other derivatives or "segregates" in later generations will be described. That the seeds from a wild plant generally breed true is to be expected, since these forms with small flowers are all normally self-pollinated, and although highly heterozygous yet they remain constant owing to the chromosome catenation.

The geographical aspect of these cultures is also of great interest. Thus if seeds from different plants in the same colony or the same locality are grown, they often yield identical cultures, or the differences may be in single characters such as mean petal-length or the size of the papillae on the stem; or they may be so small that only statistical treatment would bring out a difference in certain characters. Many striking cases have been observed where two adjacent cultures, grown under as nearly identical conditions as can be obtained, show some constant visible difference of this kind which is obviously not environmental in origin. On the other hand, different cultures from the same area usually belong to the same species and frequently show no constant visible difference whatever. Not infrequently two or even more species may, however, be represented in the same area, or even in the same colony. Three years of observations of these various kinds of difference have led to conclusions regarding the nature and evolutionary value of the different types of variation in wild Oenotheras, which will be briefly outlined later in this paper.

From the geographic aspect also it has been of great interest to compare the cultures from adjacent areas and determine as far as possible the geographical distribution and relationships of the various forms. These forms will be described as far as possible in the order of their geographical arrangement, but the present data are sufficient to give only a preliminary conception of the distances to which particular species have spread and the possible lines of their dispersal. Certain forms appear to be coastal and others inland in their distribution. In general, in passing from one area to another, form succeeds form in the way that might be expected, depending on the topography of the country and other conditions. But very occasionally a form appears in an unexpected locality, and such cases may be due to the action of man. The *Oenotheras* nearly all prefer a disturbed sandy soil. Railway embankments furnish such conditions, and *Oenotheras* are frequently

found here. They will therefore tend to spread along railway lines, and certain cases of distribution may perhaps be explained in this way. Seeds may also be carried occasionally in hay and other crops from one part of the country to another. In the main, however, the present distribution appears to be a natural one. disturbed soil of roadsides is a favourite haunt for Oenothera, and it is probable that the activities of man during the last three centuries in Eastern Canada have given opportunities for their spread which did not exist when the country was mainly The clearing of forests, cultivation, and other soil disturbances by man have probably led to collisions between forms which were formerly isolated from each other. Although natural crossing is apparently unusual among these forms, yet it does occur. Owing to the catenation, such hybrids will breed true and will constitute in some cases new species or types generally intermediate between the parents and indistinguishable by any mark from the older species. differences must have arisen under isolation, apparently as gene mutations. From further studies it may be possible to determine how important crossing has been in connexion with the present polymorphic condition of the genus.

A genetic survey of this kind leads to a realization of the endless variety of natural forms in a genus such as *Oenothera*. However detailed it may be, the limitations of space and time make impossible a full analysis of the population of any extended area, or an exhaustive treatment of the contents of even a single colony. Many years of observation lead to the conclusion that any considerable colony of *Oenothera* contains hosts of minute scarcely observable gene differences, as well as a much smaller number of more marked and easily observable differentials. All these differences must apparently have originated at some time as gene mutations. Any strain brought into cultivation from a single plant must of necessity lose the richness of minute mutations which are present in the whole colony from which it is derived. The number of such minute mutations in the species as a whole will be very high. Some of them will be of physiological nature and subject to natural selection. These innumerable minute mutations furnish the materials which Darwin had in mind when he wrote of continuous variations and their natural selection.

The somewhat larger mutational differences which are constantly being observed in the wild *Oenotheras* are in such features as length of petal, wide or narrow petals, red or white midribs, red or green papillae on the stem or the ovaries or the sepals, red or green teeth or glands on the leaf margins, size of papillae on the stem, and so on. There is no evidence that these characters are of any selective value whatever. They occur indiscriminately in many populations and in many species, but they, of course, belong to large linkage groups of characters in which selection of physiological characters may go on from time to time.

All other specific differences are, no doubt, also genically controlled, but in many cases several genes will be involved in a particular character, and genetic analysis in the presence of catenation can only be made after elaborate experimentation. In many such characters it is difficult to separate genic effect from fluctuation and from the effect of luxuriance or favourable conditions of growth. Thus in various

species the later rosette leaves and lower stem leaves tend to be strongly pinnatifid at base, yet this character will only be well expressed in relatively luxuriant plants and may be more or less suppressed if the plant grows under unfavourable conditions. On the other hand, some species, no matter how luxuriantly grown, will not show this character. This brings us to another point, namely, the marked effect of slight environmental differences. Plants grown near a row of trees which cut off some of the sunlight in the late afternoon are markedly smaller in the development of all While this shows that light intensity is a limiting factor in their growth, as is to be expected, yet the resulting differences have to be taken into account in drawing up the descriptions. Among wild plants, which often grow under far from optimum conditions, characters, especially of the leaves, are frequently suppressed These plants also respond strongly to environmental conditions in the later seedling or young rosette stages. In nearly all species, if the plant does not begin to form a stem with internodes by a certain date in the season, which varies from year to year, it will remain a rosette until the following year. other conditions stem formation may begin very early in the development and the rosette will then be omitted altogether.

The seeds for these cultures were sown each year in the greenhouse in February or early March, pricked off into boxes, later transferred to cold frames, and finally planted out about the end of May. The more strongly biennial forms even then have difficulty in forming a stem during the summer season, but many species if brought on too rapidly will, especially in a warm summer, tend to bolt, some of them practically omitting the rosette and flowering early, while others form a full rosette and only come into flower some weeks later. "Late" and "early" plants may occur in the same culture, but the condition is not inherited and is apparently a response to particular temperature or growing conditions at a certain stage of the plant's development. On the other hand, species differ markedly in the strength of their biennial habit, and all degrees occur in this respect.

Investigations of this kind under somewhat different climatic conditions from their natural habitat, necessitate continually keeping in mind the responses of the In general it appears that specific characters are but little affected by the There are, however, certain marked exceptions. climatic differences involved. Thus O. insignis BARTL., a prairie species from Saskatoon (p. 337), grown in England, retains at first its habit of a short stem producing flowers and fruits not only from the lowest internodes but even from the rosette; but many of the plants remain rosettes and flower the following year, producing tall stems without basal flowers, i.e., they at once lose their prairie adaptation. Again O. albinervis from North Dakota (p. 339), where it grows under arid sandy conditions, has smooth leaves with conspicuous silky pubescence, whereas in English conditions of climate and soil the leaves are strongly crinkled and the silky pubescence fails to appear. Under these circumstances the leaves are extraordinarily like those of the mutant O. rubrinervis. These marked changes of habit have been observed, however, only in species brought from the relatively arid Western plains, and not in all of those. For instance, O. rubricapitata (p. 343), a North Dakota species which was found growing by a pond in conditions of partial shade from trees, does not appear to be altered at all when grown in England, and the same is true of most other species.

Another category of characters which appear in Oenothera may be known as evanescent characters. Several such have been observed in these cultures. An example may be taken from O. albinervis (p. 343). Two strains of this species from different localities were identical in every respect except that for a short period one strain showed a pale red spot at the base of the petals in all the flowers, while in the other there was no trace of this spot. Another example of an evanescent character is in O. niagarensis (p. 326), in which, during a part of the season, there is a touch of pale red at the base of the petiole of the stem leaves. Later in the season this completely disappears, but it is always there in the early part of the season and is therefore a specific character. Another striking example is in an undescribed species from St. Jerome near Montreal. Here, throughout the main part of the season the filaments are yellow, as they are in all other species of this group. Towards the end of the season, however, with lower temperature they become brilliant orange to red. This character is uniform in all late flowers of this species and has been observed in two seasons, but no trace of it has been seen in any other species.

I am greatly indebted to the Director of Kew for help given in connexion with these experiments, to Dr. T. A. Sprague, and especially to Mr. N. Y. Sandwith, whose notes on many of the cultures were of great value in drawing up the descriptions; but I am alone responsible for delimitation of the species and varieties. Complete plant specimens from many of the cultures are now at Kew, and several other sets of specimens from the same cultures are being prepared for circulation to other leading herbaria, an original set of representative specimens being retained in the herbarium at King's College. The many photographs which are necessary for descriptive work of this kind have been carefully taken by Mr. C. S. Semmens.

In drawing up the descriptions of the various species, the numbers attached to the various cultures in each year, as well as the number of plants in each culture, are given in the relevant tables. Thus under O. paralamarckiana (Table I), culture No. 1 of 1933 contained 50 plants. Each culture of 1934 was obtained by selfing a plant of the previous generation, unless the contrary is stated. Rarely, where stated, open-pollinated seeds were used if for some reason selfed seeds were not available. In such cases the offspring were usually uniform and like the parent, showing that crossing had not taken place. Thus in the P₂ generation of O. paralamarckiana, grown in 1934, culture 18 contained 25 plants, culture 19 one plant, and culture 124 18 plants. In the text these cultures are referred to as 18.34, 19.34 and 124.34 respectively. in 1935 another P₂ culture of four plants was grown as 19.35, and in the same year eight P₃ cultures were grown, each from selfing a plant of the previous generation, as shown in Table I. Generally, when more than one daughter culture was grown it is because the parent plants showed some difference which required further investiga-It is to be emphasized that in every case throughout the experiments, with a few exceptions to be mentioned, each culture is derived from selfing a single plant

of the previous culture. In the pedigrees of cultures for each species, the particular culture on which the description is based is underlined. Thus for O. paralamarckiana, culture 19 of 1934, is underlined. In a very few cases the description is taken from two cultures, both of which are underlined.

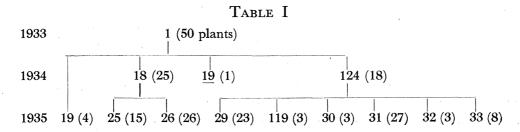
The varying numbers of plants in different cultures depend upon the amount of germination or the space available. In 1933 50, or sometimes 100, plants were grown in each culture. Wild seeds always germinate better than those from plants in cultivation for even two years. The cause of this is unknown, except that it is due to delayed seed germination. The first flowers from a plant produce seeds which show the most marked delay in germination, but even those from the middle of the season germinate badly in comparison with wild seeds. As a single capsule usually produces over 300 seeds, good germination gives far more seedlings than can be grown, but occasional complete failures occur for no accountable reason. Seed germination is also much higher in some of these species than in others.

DESCRIPTIONS AND GENETICAL BEHAVIOUR OF THE SPECIES

Under each species a full description is given followed by a short Latin diagnosis, selecting the main characters. The photographs here published are selected from a much larger number. The relationships and any genetical peculiarities of the species are then discussed. The order of the species is, so far as possible, geographical, beginning with Massachusetts, then New York, then the numerous species and varieties recognized in Nova Scotia and the adjacent portion of New Brunswick, then up the south shore of the St. Lawrence in Quebec, then the Ontario localities around Toronto and Windsor, finally the species from Saskatchewan and North Dakota. These species are collected into Table XXVII (p. 348) to show their geographical distribution and that of their varieties. It will be obvious that even in areas where the most intensive study has been made, still more could be done before the genetic survey could be regarded as complete, while there are large intermediate areas still untouched.

O. paralamarckiana n. sp.

From seeds collected at Penzance, Woods Hole, Massachusetts, September 1932, the original plants growing tall and erect by the roadside. The following cultures have been grown. Those of 1933 and 1934 have already been briefly described



elsewhere (GATES and NANDI, 1935) where photographs of the species and five of its trisomic mutations are published in connexion with a cytological investigation of these forms.

Description—Rosette leaves dull green, ca. 16, narrowly elliptic or elliptic-oblanceolate, apex obtuse to acute or shortly acuminate-cuspidate, 15–27 cm. \times 38–55 mm. (petiole 2·5–5 cm.); midrib white to pale pink above, green on lower surface; leaf usually concave, surface markedly crinkled or bullate, but slightly less so than in O. Lamarckiana, undulation very conspicuous. Margin strongly repand-dentate below, repand-denticulate towards apex, teeth green or red. Indumentum on both surfaces softly \pm erect-pubescent, with rather long hairs of unequal length, midrib also \pm appressed-crispulous pubescent. There is also a second series of sub-appressed-arcuate hairs on mesophyll. Leaves often with one or two obscure liver-coloured blotches.

Stem erect, pale green with red papillae, 60-65 cm. high, hirsute with a longer and shorter series from red or green papillae, also arcuate-crispate-subappressed-pubescent; strongly, thickly ribbed below bracts, basal branches shorter than central stem. Stem leaves elliptic, or lower elliptic-oblong, acute with red or greenish tip, concave, crinkled all over, 9-17 cm. \times 36-51 mm., margin very wavy, repanddentate below, repand-denticulate above, teeth green, midribs white. Both surfaces with erect or suberect pubescence in two series of different length, the largest almost hirsute (fig. 1).

Ovary $8-12 \times 3$ mm., strongly ribbed, densely spreading or patulous-hirsute from red or green papillae, shortly spreading glandular-pubescent and crispate-appressed-puberulous. Hypanthium $18-38 \times 3$ mm., thick, rather sparsely patulous-hirsute and shortly glandular-pubescent. Bud-cone green with yellowish longitudinal stripes, $12-20 \times 6.5$ mm., nearly terete. Sepal tips 2 mm., appressed, pink at tip. Petals $14-21 \times 16-22$ mm., nearly truncate or rounded, not emarginate, opening out to form cup-shaped flower with narrow spaces between the cuneate bases of petals, surviving all day without wilting, tips tending to bend backwards. Filaments ca. 9.5 mm., anthers ca. 5 mm., reaching nearly to top of stigma in bud. Stigma lobes 5-6 mm., more or less spreading in anthesis, ca. 10 mm. above mouth of hypanthium. Ripening fruits green, short and stout, ca. 20×7 mm., with a fine pubescence of long and short hairs (no red papillae).

Diagnosis—Folia radicalia surda viridia, elliptico-oblanceolata, costa alba aut pallida rubicunda, superficies manifeste bullata, undulata; caulis erectus tuberculatis rubris aut viridibus. Folia caulina elliptica, aut inferiora elliptico-oblonga, acuta, concava, bullata, costae albae. Petala 14–21 mm. longa, fere truncata, non intra diem marescentia, stigma circa 10 mm. supra hypanthium.

This species is essentially like a *Lamarckiana* with small flowers, but the leaves are more lanceolate and pointed at the tip than in *Lamarckiana*. The 1933 culture was somewhat shaded by tall trees, and as a result the plants were smaller in size. Plants

grown in full sunlight in 1934 and 1935 were markedly more luxuriant. They show strong resemblance in foliage characters to the well-known specimen in the Jardin des Plantes which DE VRIES identified with O. Lamarckiana. This specimen is figured by DE VRIES (1914, Plate 19) and also by DAVIS (1927, Plate 5) and was obtained somewhere in eastern North America by MICHAUX in the eighteenth century. The luxuriance of MICHAUX's specimen indicates that it was perhaps a garden specimen from seeds collected by him. The foliage of O. paralamarckiana is very similar to

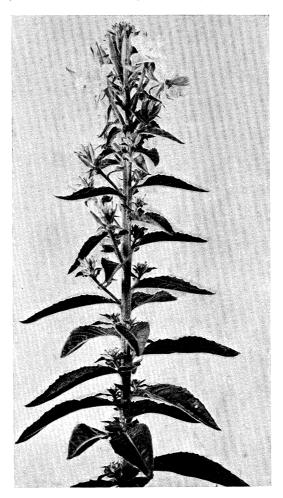
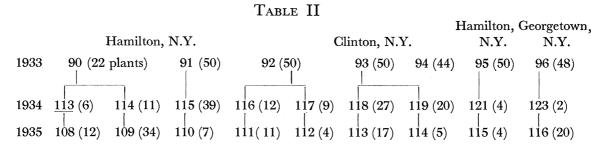


Fig. 1—O. paralamarckiana, culture 19.35.

that of the specimen in question, and in fact agrees with it in leaf shape more closely than does the Lamarckiana of DE VRIES because of the more pointed leaves of O. paralamarckiana, but the MICHAUX specimen has long petioles. There is, however, a great difference between O. Lamarckiana and O. paralamarckiana in flower-size, which almost certainly involves more than one factor for petal-length. Investigations of its trisomic mutations, which are much more frequent than in O. Lamarckiana, are being continued. Mr. C. E. Ford determined the chromosome catenation as a ring of 14, from a normal plant in culture 1.33.

O. pycnocarpa ATK. and BARTL. varieties

From seeds collected by Dr. G. L. Stebbin, jr., in September, 1932, at three neighbouring localities in New York State. They were at first regarded as belonging to an undescribed species, some strains of which are strictly cleistogamic while others are chasmogamic, and still others intermediate in this character. Marked variations in several other features are found, and several of these may be due to single genes. The following 25 cultures have been studied:



The plant from which culture 90.33 was derived grew on gravelly soil in a railway yard, the plant for culture 91.33 in loamy soil on the border of a field, that for culture 96.33 on a shady bank. These are all characteristic habitats for Oenothera, though sandy soils appear to be generally preferred. The plants and their descendants all clearly belong to one species, but the cultures differ markedly in such features as (1) flower size, (2) cleistogamy or chasmogamy, (3) red or green midribs, (4) upper rosette leaves and lowest stem leaves strongly pinnatifid or not.

Although these cultures are now regarded as all belonging to *O. pycnocarpa* ATK. and BARTL., yet it appears desirable to give a detailed description of the type culture (113.34) for comparative purposes, on account of the striking range of variations they show in different strains.

Description—Rosette leaves dull greyish-green, number of rosette leaves ca. 11, narrowly elliptic or elliptic-oblanceolate, apex acute or shortly acuminate, reaching 18–22 cm. × 35–49 mm. (petiole 4–5 cm.), flattish or slightly concave, crinkling none or slight, usually conspicuously undulate, margin repand-dentate to subpinnatifid below, repand-denticulate above, teeth green, midrib pale pinkish-mauve, surface finely erect-pubescent on both surfaces and crispulous appressed-pubescent on midrib (fig. 2).

Stem erect, ca. 108–112 cm., basal branches decumbent at base then widely arcuate-ascending, long, but shorter than central stem, which is scarcely ribbed, except very thinly so in upper part, green or tinged brownish- or purplish-red, rather sparsely patulous-hirsute with reddish papillae and rather sparsely arcute sub-appressed-pubescent. Stem leaves \pm deflexed or patulous-deflexed, lanceolate to elliptic-lanceolate, flattish, not wavy or crinkled, 15–17 cm. \times 40 mm., margin sparingly repand-dentate near base, repand-denticulate above, teeth green, both surfaces suberect-pubescent, midrib pinkish-mauve or nearly white, on lower leaves

quite white, \pm appressed-crisped-puberulous above, sparsely suberect-pilose and fairly densely subappressed-pubescent below. Lower bracts \pm spreading, concave, wavy at base, lanceolate, 8–14 cm. \times 30–40 mm., tips upcurved. Upper bracts \pm spreading with upcurved tips, very concave, wavy in lower half, ca. 12–30 mm. long.

Apex of inflorescence very narrow, \pm flat, overtopped by higher developed buds and flowers, spike not dense. Ovary 8-11 \times 2.5 mm., fairly densely patulous- or

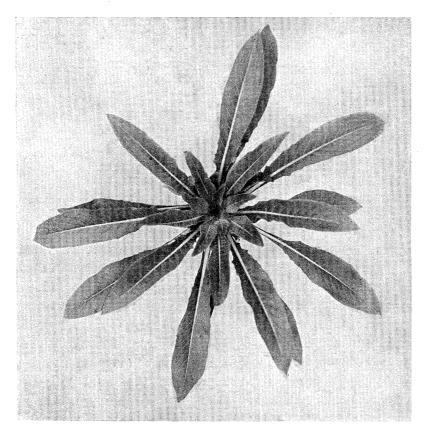


Fig. 2—O. pycnocarpa var. parviflora. Rosette, culture 115.34.

spreading-hirsute from red papillae, and spreading glandular-pubescent. Hypanthium $25-28 \times 2$ mm., sparsely patulous-hirsute from white base and sparsely glandular-pubescent. Bud-cone greenish-yellow, \pm subcylindric, $9-10 \times 5-55$. mm., indumentum as on ovary, but papillae white. Sepal tips 2-3 mm., somewhat divergent, reddish in upper quarter. Petals ca. $9-13 \times 10-13$ mm., truncate or with shallow sinus, opening to 45° , not contiguous. Filaments ca. 7-8 mm., anthers ca. 4.5 mm., reaching nearly to top of stigma in bud, stigma lobes ca. 3 mm. long, divergent, base of stigma ca. 7 mm. above hypanthium. Inflorescence elongated, fruits 31×7 mm., green with short pubescence and few long hairs.

In the 1933 cultures particularly there was a very marked distinction between "early" and "late" plants. Early ones formed no persistent rosette but became

bushy and flowered early, having curled bracts. Late plants formed a rosette of large leaves, came into flower much later, and had larger leaves and bracts. In some cultures these two types could be scored easily, as shown in Table III; in others this was difficult or impossible owing to the presence of intermediates. In one culture the plants were all late and in another they were all early. This difference appears to be a direct response to the conditions of culture, and shows no signs of being inherited in later generations, except in cultures 116.34 and 117.34. These were derived respectively from selfing a late and an early plant in culture 92.33. The plants in 116.34 were all mainly cleistogamic; those of 117.34 were earlier in development and were all chasmogamic. In the following generation the latter difference was completely maintained, but there was no difference in the rate of development.

TABLE III

Culture	Early	Late	Intermediate	
90.33	9	13	0	distinct (scored)
91.33	0	50	0	`
$92 \cdot 33$	6	44	0	distinct
93.33	50	0	0	 .
$94 \cdot 33$	6	29	9?	not distinct
$95 \cdot 33$	not classified			
96.33	15	33	0	very distinct

Other variations in these cultures may now be considered. Culture 90.33 was uniform, and cultures 113.34 and 114.34, each derived by selfing a different plant of this culture, were alike, as were their descendants 108.35 and 109.35. These cultures differed from the original O. pycnocarpa from Ithaca, N.Y., grown in the Gardens at the same time, in the following points: (1) plants smaller, (2) flowers smaller (petals 11 × 12 mm.), (3) red papillae on stem. This Hamilton, N.Y., strain may therefore be known as O. pycnocarpa var. parviflora, n. var.

Diagnosis—A specie differt planta minore, floribus minoribus (petalis 10–12 mm. longis), tuberculis rubris mediocris mensurae in caule.

Culture 91.33, from the same locality, differed from the above in (1) white midribs and narrower stem-leaves (35 mm. against 42 mm.), (2) slightly larger flowers (petals 12–15 mm. against 9–11 mm.), (3) appressed sepal tips. These differences remained constant in the 1935 cultures, and it was observed that the F_3 descendants of 91.33 differed in addition in (4) having no red papillae on the stems and (5) leaves longer and \pm crinkled.

The three cultures from Clinton, N.Y., showed marked differences. In culture 92.33, of the 44 (late) plants which produced rosettes, 33 had pink and 1 white midribs. The flowers were larger (petals 18–19 mm.), and all plants had open (chasmogamic) flowers. Two plants (I.2 and II.2) were selfed to produce cultures 116.34 and 117.34. No. I.2 had pink midribs and belonged to the late type. Its offspring were uniform, with rosettes, pink midribs, and some flowers cleistogamic

on each plant. No. II.2 was early. Its offspring differed from those of I.2 in that all the flowers were chasmogamous. The Clinton, N.Y., plants may be called var. cleistogama n. var. (fig. 3), since the three strains from this locality all showed the condition to some extent in the original or in descendant cultures. The condition is somewhat variable even in the same plants at different times, depending probably on temperature and other factors. The cleistogamic condition is caused by a failure of



Fig. 3—0. pycnocarpa var. cleistogama, in flower, culture 118.34.

the growth force at the base of the petals, which normally forces the sepals apart and so opens the flower. This may be completely absent or may be only sufficient to force the sepals apart at their base. Occasionally the sepals are burst apart or even turned back, but the petals do not unroll or separate. Flowers which never open are self-pollinated and produce seeds exactly like chasmogamous flowers; but the buds droop, turn yellow, fade, and finally fall off after fertilization without opening. Notwithstanding the variability of the condition, it is clearly inherited and probably is a

simple Mendelian difference. There is insufficient evidence as to which is dominant, but probably cleistogamy is recessive, and it is probable that it has arisen from the type through a single mutation.

Diagnosis—A specie differt floribus cleistogamis, petalis grandioribus (circa 15–18 mm. longis), costis albis vel rubris, foliis caulinis inferioribus pinnatifidis, tuberculis rubris in caule valde magnis.

Cultures 92.33 and 93.33 differed in that no cleistogamic flowers were observed in the former, while nearly all the flowers were cleistogamic in the latter. As already mentioned, the R and r factors (red and white midribs) were present in different plants of 92.33, and some plants evidently contained the factor for cleistogamy, while others did not, for of the two daughter cultures, in 116.34 all the plants had some cleistogamic and some chasmogamic flowers, while in 117.34 all the flowers opened properly. Culture 93.33 seldom opened a flower, and the same was true of its two descendant cultures in 1934. The F₃ cultures in 1935 were similar but with some variation. Thus 113.35, when beginning to flower on 27 July, had 105 cleistogamic and 39 chasmogamic flowers (21 of the latter on side branches), while on 5 August the flowers were nearly all cleistogamic and there were only 6 open flowers in the whole culture. In 114.35, on the other hand, all flowers were cleistogamic except some on the side branches. As shown elsewhere, (GATES 1932), the petals on side branches are always 2–3 mm. shorter than on the main stem, and this may be why such flowers open more easily. The results as regards cleistanthy are summarized in Table IV. In culture 94.33 some plants produced a mixture of open and closed flowers, some had only a few closed flowers, while in 18 plants the flowers were nearly or quite all open, and in the remainder the flowers were mostly closed. Hence while they could not all be scored, some plants were chasmogamic but the majority were cleistogamic. From the table it will be seen that cleistogamic plants produced only cleistogamic offspring, with some environmentally produced variation in the expression of the character, while pure chasmogamic plants also bred true, but there remains some doubt about the exact behaviour of heterozygous plants.

TABLE IV
O. pycnocarpa var. cleistogama from Clinton, N.Y.

1933	92 chasmogamic		93 cleistogamic	94 some plants cleisto.
				-
1934	116 ± cleistogamic	117 chasmo.	118 cleistogamic	119 cleistogamic
1935	111 cleistogamic	112 chasmo.	$113 \pm ext{cleisto}$.	114 cleistogamic

Culture 95.33, also from Hamilton, N.Y., agreed with the other cultures from that locality in having chasmogamous flowers, but this strain differed in having larger flowers, the petals being 20 mm. long (22 mm. in the descendant culture 121.34 and $18-22 \times 20-30$ mm. in 115.35). It therefore agrees with the type of the species

but has flowers of maximum size. The strain has therefore lost a dominant factor (or perhaps two or more linked factors) which has the effect of subtracting ca. 10 mm from the petal length. Several times it has been found that strains of a species occupying adjacent areas differ only or mainly in flower size. That the difference is genetic has been shown by growing them side by side for successive generations when, as in the present case, the difference remains constant.

Culture 96.33, from Georgetown, N.Y., belonged to var. parviflora (petals 10 mm.) but differed from the others in the presence of several marked subpinnatifid lobes and jags at the base of the last rosette leaves (fig. 4) and the lowest stem leaves,

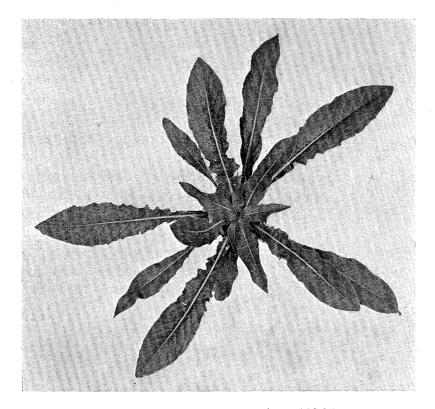


Fig. 4—O. pyncocarpa, rosette, culture 116.35.

a character of the species at Ithaca, N.Y. (BARTLETT, 1913, ATKINSON, 1918). Many of the rosette leaves were also conspicuously margined with a yellowish colour, the midribs were white, and in culture 116.35 it was noted that there were no red papillae on the stem. These features were perpetuated in culture 123.34 (petals 9 mm.) and 116.35 (petals 11 mm.). They were chasmogamic.

Summarizing this series of 25 cultures in three generations, all belonging to O. pycnocarpa, as observed especially in the nine cultures of 1935 (see Table II, p. 248); cultures 108 and 109 were identical, representing var. parviflora and differing from the type in (1) smaller flowers (petals 10–12 mm.), (2) red papillae of medium size on stem, (3) smaller plants. Culture 110, also from Hamilton, differed from 108 and 109 in

having (1) somewhat larger flowers (petals 13–14 mm.), (2) no red papillae on stem, (3) white midribs, (4) leaves longer and \pm crinkled. Culture 115, from the same locality, agreed with the previous in being chasmogamic, but differed in having (1) much longer petals (18–22 mm.), (2) no red papillae on the stem or very small ones, (3) pink midribs. Of the Clinton cultures, 111 differed from 108 and 109 in having (1) the lower stem leaves pinnatifid, (2) very large red papillae, (3) leaves slightly darker green, (4) cleistogamic, (5) petals 15×16 mm. Culture 113 was also cleistogamic, differing from 111 only in having (1) lower leaves more pinnatifid, (2) midribs pink (as in 108), (3) leaves lighter green and somewhat broader (as in 108). Culture 112 (also from Clinton) was chasmogamic and differed from 108 and 109 in having (1) larger flowers (petals 19 mm.), (2) large red papillae, (3) leaves somewhat lighter green. Culture 114, from Clinton, was essentially the same as 111 and 113, being cleistogamic and having petals 16-18 mm. long. The Georgetown culture, 116, differed from the Clinton cultures 111, 113, 114 in having (1) no red papillae on the stem, (2) midribs white, (3) many leaves having yellowish coloured edges, (4) flowers smaller (petals 11×10 mm.), (5) chasmogamic.

It will thus be seen that some of the original cultures showed segregation for certain characters in their offspring, but this was probably due to mixed pollination of certain wild plants from which the seeds for the 1933 cultures were obtained. The characters involved, each of which except flower-size is probably due to a single pair of genes, are (1) pink or white midribs, (2) lower leaves pinnatifid at base, (3) presence or absence of red in the papillae on stem, (4) large or small red papillae, (5) leaves lighter or darker green, (6) cleistogamy or chasmogamy, (7) flowers larger or smaller. Differences in flower-size were only noted when they could be readily seen by observing adjacent rows of plants. One or two measurements of typical flowers from the main stem were then made. On this basis the flower-size of the various strains can be classified as follows:

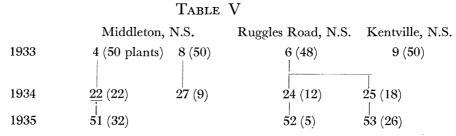
Flowers	s larger	Cultures	112, 115	Petals	18–22 mm.
,,	intermediate	,,	111, 113, 114	,,	15–18 mm.
,,	smaller	,,	110	,,,	13–14 mm.
,,	smallest	,,	108, 109, 116	,,	10-12 mm.

Cleistogamy has already been described in O. cleistantha Sh. and Bart. (Bartlett, 1915) from Huntingdon, Long Island, N.Y., but that species is very different, having cruciate petals, very leafy and dense branching, also long hairs on the calyx and around the top of the hypanthium. Cleistogamy has therefore probably originated as an independent mutation in O. pycnocarpa. O. stenomeres Bartl., from Maryland, also has flowers which are both cruciate and cleistogamic. De Vries (1913) has also figured a new (undescribed) species with small flowers (p. 34, fig. 9) from Manhattan, Kansas, which he collected in 1904 and in which the flowers, as a rule, do not open. Boedijn (1924) describes O. disjuncta, another cleistogamic species collected by De Vries in 1904 at North Town Junction, near Minneapolis. O. Bauri Boedijn, collected by Baur at Friedrichshagen near Berlin in 1918, rarely opens a

flower. This species is presumably related to O. biennis L. It therefore appears that cleistogamy has arisen at least five times in Oenothera through independent mutations—a striking instance of parallel mutations; but the relationship of O. stenomeres and O. cleistantha needs closer examination. It is also significant that in the Onagraceous genus Boisduvalia, B. cleistogama Curran, from California, never opens its earlier flowers although the later ones expand.

O. novae-scotiae Gates

This species, first described from near Middleton, Annapolis Co., Nova Scotia, in 1916, has been collected from a number of localities, and a large number of cultures belonging to this species has been grown. They show characteristic minor differences which will be briefly described. The native home of this species is the Annapolis Valley. A strain from Charny, Quebec, resembles this species, but its characters have not yet been fully elucidated; another strain, from Cap Tourmente, Quebec, is in the same condition. The thirteen cultures shown in Table V have been studied.



As the original description (GATES, 1916) was less complete, it is desirable to give a full account for purposes of comparison.

Description—Rosette leaves dull green, ca. 12–21, narrowly elliptic or oblanceolate, apex acute or shortly acutely acuminate, reaching $17-34 \times 45-50$ mm. (petiole 3–6 cm.). Undulation usually conspicuous, crinkling more or less marked, especially towards base of developing leaves, margin subentire, repand-dentate or pinnatifid at base, repand-denticulate above; midrib pink, shortly subappressed-crispate-pubescent with some suberect hairs, mesophyll suberect-arcuate-pubescent, with more erect hairs on lower surface (fig. 5).

Stem erect, 60–75 cm., numerous basal branches, decumbent at base, then widely arcuate-spreading-ascending, as long as or somewhat longer than central stem. Cauline branches numerous, ascending, flowering. Stem broadly ribbed, green or red, patulous-hirsute from red papillae and subappressed-crispate-puberulous. Stem leaves arcuate-spreading or arcuate-deflexed, slightly concave, lower elliptic-lanceolate, 13–17 cm. × 30–35 mm., acute with brownish-red tip, upper lanceolate, margin repand-dentate below, repand-denticulate above, teeth green; midrib pink in lower half; upper surface arcuate-suberect-pubescent, and midrib also minutely appressed-crispulous-puberulous, on lower surface hairs somewhat longer and more conspicuous. Inflorescence 26 cm. long, spike dense, many flowered;

lower bracts lanceolate, spreading, \pm concave, 9–11 cm. \times 30–35 mm.; upper bracts spreading 18–32 \times 5–8 mm. Apex of inflorescence somewhat depressed, about 2 cm. diameter, outer buds overtopping central, not comose.

Ovary 11–13 mm., $2\cdot5$ – $2\cdot7$ mm. diameter, ascending-hirsute with simple hairs from red papillae and spreading-pubescent with short gland-tipped hairs. Hypanthium 30– $32\times2\cdot5$ mm., indumentum as ovary but sparse and longer hairs spreading or patulous. Bud-cone yellow, subcylindrical, 14– 15×6 mm., with

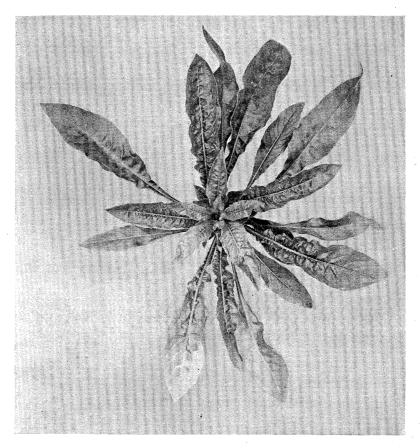


Fig. 5—O. novae-scotiae, rosette, culture 51.35.

long patulous hairs from white papillae and sparse, short spreading gland-tipped hairs. Sepal tips 4–5 mm., erect, appressed and parallel or slightly divergent at apex, green and yellow, pinkish at apex. Petals $18-23 \times 20-30$ mm.,* opening to ca. 60° , much overlapping, truncate or toothed, very obscurely, widely and shallowly emarginate. Filaments 10 mm., anthers ca. 7 mm., overtopping stigmas by 2–3 mm. Stigma lobes 4–5 mm., 7–8 mm. above hypanthium, widely divaricating in anthesis, and protruding from flower buds towards end of season. Fruits green, 18×5 mm., tapered only at apex, no long hairs nor papillae, few short hairs (fig. 6).

^{*} In the next generation (culture 51.35) the petals measured 25×29 mm.

Culture 8.33 was derived from a wild plant having distinctly larger flowers and the habit of later flowering on the cauline branches after all the fruits of the main stem were shedding their seeds. These features were equally marked in the offspring (fig. 7), the petals being $32-34\times32$ mm., ovary 15 mm., hypanthium 35×3 mm., fruits 20×6 mm. The catenation of this large-flowered strain was determined by

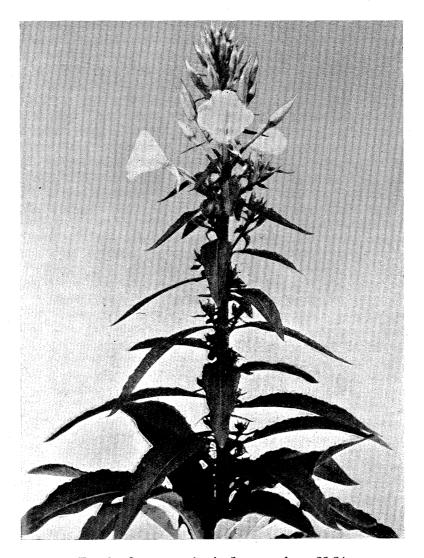


Fig. 6—O. novae-scotiae, in flower, culture 22.34.

Mr. C. E. Ford as a ring of 14. The type of the species had previously been shown to have a ring of 14 (Sheffield, 1927). In the next generation, culture 27.34, the petals were shorter though still exceptionally wide $(22 \times 29 \text{ mm.})$,* hypanthium

^{*} As this was the first flower to open on the plant, and as first flowers are sometimes abnormally small, like pullets' eggs, it is probable that the mean size of flower in this culture was considerably larger, but no further measurements were taken.

 30×3 mm., and ovary 12×3.5 mm. Whether a single gene is responsible for this difference in flower-size of the two strains is not yet known. The complexes of O. novae-scotiae were named grandiflorens and parviflorens, the smaller petal being dominant, but this difference in petal-length did not always appear in crosses with homozygous forms (Gates and Catcheside, 1932). Forms with equally large

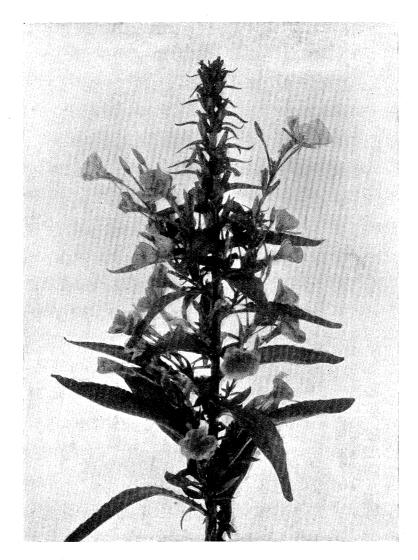


Fig. 7—O. novae-scotiae, strain with large flowers, culture 8.33.

flowers have since been observed in other areas adjacent to the Annapolis Valley. It appears probable that this large-flowered form is homozygous for one or more longer-petal genes for which the type of the species is heterozygous.

Culture 6.33 was derived from seeds of several plants in an orchard on the Ruggles Road, some two miles from Wilmot and about the same distance from Middleton, on 6 September, 1932. The plants were very numerous in this orchard, where

they were a serious weed. Some plants were noted as having crinkled stem leaves alternating with smooth ones. This culture belonged to *O. novae-scotiae*, but yielded two slightly different types which could be scored as rosettes. A selfed plant of each type yielded cultures 24 and 25 respectively in 1934, in which the constant differences shown in Table VI were observed.

Table VI

	Culture 24.34	Culture 25.34
Rosette leaves, 1933	23 cm. \times 58 mm.	$24 \text{ cm.} \times 42 \text{ mm.}$
Rosette leaves, 1934	44 cm. \times 82 mm.	$38 \text{ cm.} \times 60 \text{ mm.}$
Midribs	White or light pink	Red
Middle stem-leaf, 1934	19–20 cm. \times 43–49 mm.	$20 \text{ cm.} \times 38 \text{ mm.}$
Stem	Green, no red papillae	Red, with red papillae
Ovary	$14-16 \times 3.5 \text{ mm}.$	16×3.5 mm.
Hypanthium	$28-38 \times 3 \text{ mm}.$	$3034 \times 3 \text{ mm}$.
Bud cone	18×6 mm.	20×7 mm.
Sepal tips	7 mm.	9 mm.
Petals	20 – 22×26 – 27 mm.	26×34 mm.

From the observations and measurements it was clear that Type I had wider rosette and stem leaves, less red on the midribs, and smaller flowers. The sepal tips were long and strongly appressed as usual in O. novae-scotiae, in contrast to O. comosa, O. intermedia, and O. Hazelae var. parviflora (vide infra) in which they are more or less markedly subterminal. Unlike the type of O. novae-scotiae, both these cultures had green teeth on the leaf margins. The broad petals were exceptionally firm, usually remaining erect on the day following anthesis. Each petal generally opened out flat and erect, the petals being folded around each other to make a cupshaped flower.

Culture 9.33, from near Kentville, King's Co., N.S., represents a markedly distinct variety of O. novae-scotiae which may be called var. serratifolia n. var. It agrees with the species in such features as pink midribs, erect stem with red papillae, and in habit and general flower characters. But it differs in (1) narrower rosette leaves (20–21 cm. \times 32–34 mm.) tending to be acuminate and crinkled when young (fig. 8), (2) stem leaves markedly repand-dentate, (3) flowers much smaller (petals $10-11 \times 12$ mm.), sepal tips short (2–3 mm.), (5) inflorescence short and compact (fig. 9). In the F_2 of this strain the seeds failed to germinate and it has not been grown since, but its distinctness is clear.

Diagnosis—A specie sic differt: folia radicalia angustiora, folia caulina admodum repando-dentata, flores multo minores (petala 10–11 mm. longa), apices sepalorum breviores, inflorescentia brevis et compacta.

O. novae-scotiae var. distantifolia n. var.

Seeds of this variety were collected at Newport, Hants Co., Nova Scotia, on 27 September, 1932, the plants being noted as tall, with small flowers. The following cultures were grown:—

Description—Rosette leaves rather dull green, lustrous along midribs, reaching 19-25 cm. \times 41-62 mm., oblanceolate, apex acute, obtuse or shortly broadly

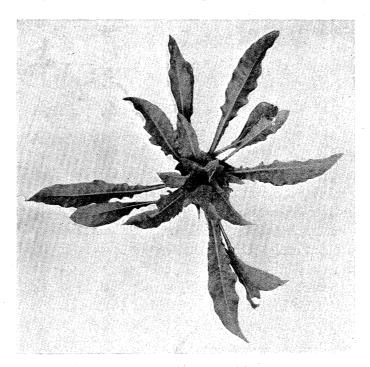


Fig. 8—O. novae-scotiae var. serratifolia, rosette, culture 9.33.

acuminate, flattish, crinkling usually conspicuous near midrib, margin repand-dentate (strongly) below, finely repand-denticulate above, teeth green, midrib white to pale pink, both surfaces regularly, not densely, subappressed-pubescent (fig. 10).

Stem erect, ca. 66 cm., several basal branches decumbent then widely ascending, numerous short ascending cauline branches; stem ribbed except above, green with reddish tinge, rather sparsely patulous and arcuate-ascending hispid in two series of different length, with conspicuous red papillae and arcuate-subappressed-puberulous, branches deep red in upper half. Stem leaves arcuate-deflexed, narrowly elliptic-lanceolate, 10–17.5 cm. × 17–34 mm., margin conspicuously wavy, conspicuously

repand-dentate below, obscurely repand-denticulate above, teeth green, midrib pinkish, both surfaces suberect-pubescent, midrib appressed crisped-puberulous above, with longer \pm erect hairs below. Inflorescence lax, 21.5 cm. long. Lower bracts arcuate-spreading to deflexed, lanceolate, 4.5–6 cm. \times 8–17 mm. Upper



Fig. 9—O. novae-scotiae var. serratifolia, in flower, culture 9.33.

bracts spreading with upturned tips, ca. 15-20 mm. long. Apex of inflorescence overtopping highest developed buds and flowers (fig. 11).

Ovary 13×3 mm., sparsely patulous-hispid with dark red papillae and densely spreading glandular-pubescent. Hypanthium $29-31 \times 2$ mm., indumentum as ovary but sparse and papillae green. Bud-cone greenish-yellow, subcylindric, \pm 4-angled, 14×5.7 mm., indumentum as ovary but sparser, from green papillae or with reddish tinge, sepal tips 2-3.5 mm. long, reddish in upper third, appressed

or somewhat divergent. Petals opening to ca. 60 deg., widely overlapping, 19 \times 19 mm., usually rather widely deeply emarginate. Filaments 10–11 mm., anthers 7–8 mm., overtopping stigmas by at least 2 mm. Stigma lobes 5 mm. long, divergent, 12–13 mm. above hypanthium. Fruits green, slender, 23 \times 4 mm., bearing dense short hairs and sparse long ones.

Diagnosis—A specie sic differt: longa spatia inter nodos, folia angusta, apices sepalorum breves.

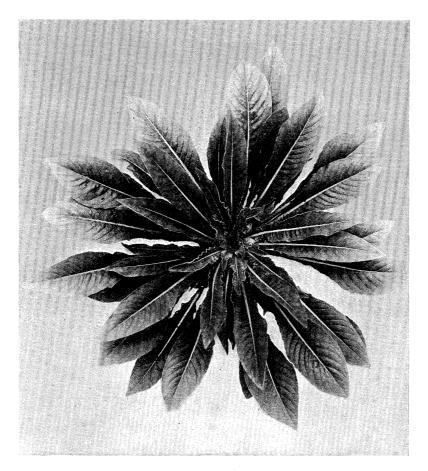


Fig. 10—O. novae-scotiae var. distantifolia, rosette, culture 29.34.

This variety differs from the type mainly in having (1) long internodes, (2) narrow leaves. In the narrow leaves and short sepal tips it agrees with var. serratifolia, but the latter differs markedly in the repand-dentate margins of the stem leaves and in the much smaller flowers.

O. comosa n. sp.

This species is described from seeds collected at Wilmot, N.S., in an apple orchard about two miles from Middleton, on 6 September, 1932. The following two

cultures were grown and yielded a uniform strain with numerous distinctions from O. novae-scotiae. Its relationships will be discussed later.

1933 5 (50 plants)
$$\begin{vmatrix} 5 & (50 & 23) \\ 23 & (32) \end{vmatrix}$$

Description—Rosette leaves dark green, narrowly elliptic, acute, reaching 23 cm.



Fig. 11—O. novae-scotiae var. distantifolia, in flower, culture 29.34.

 \times 39 mm. total length, smooth or nearly so; midrib broad, bright red (green below) surface with many small liver-coloured spots (fig. 12).

Stem erect or very slightly bent at tip, 120–125 cm., numerous basal branches widely decumbent then arcuate-ascending, about as long as central stem, cauline branches few and short. Stem conspicuously ribbed, bright deep red, very finely appressed-puberulous, with very sparse long hairs from papillae which are red where exposed to light. Lower stem leaves deflexed, upper spreading, shape

narrowly oblong-lanceolate or elliptic-lanceolate, 14–17 cm. \times 28–33 mm., \pm concave, margin finely reddish-denticulate, scarcely wavy, surface sparingly purple-blotched, usually smooth, midrib deep red; upper surface extremely finely, lower surface very finely, appressed-puberulous. Lower bracts long and leafy, spreading or spreading deflexed, reaching 10 cm. \times 24 mm. Upper bracts much shorter, spreading or patulous, ca. 40– 45×10 mm. Apex of inflorescence flat or slightly concave, wide, conspicuously comose, overtopping developed buds.

Ovary 13–15 \times 3–3·2 mm., ascending erect hispid from green papillae and densely spreading glandular-pubescent. Hypanthium 27–40 \times ca. 2.5 mm., sparsely ascending hispid and rather sparsely glandular-pubescent. Bud-cone yellowish-green,

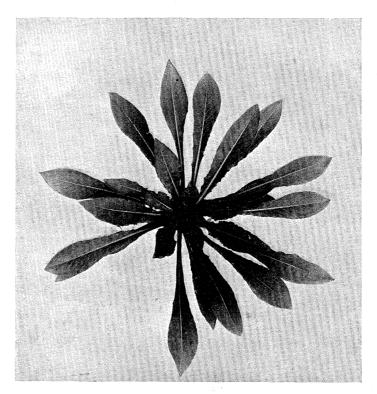


Fig. 12—O. comosa, rosette, culture 23.34.

quadrangular, 12×5 –5·5 mm., rather abruptly attenuate, very sparsely ascending hispid, shortly finely subappressed-pubescent, and rather densely spreading glandular-pubescent. Sepal tips definitely subterminal, rigid, stout, erect, and separate, 4–5 mm. long, subulate, green (fig. 13). Petals 16×15 –16 mm., expanding to ca. 60° , overlapping, widely not deeply emarginate. Filaments ca. 10 mm., anthers 7 mm., overtopping stigma by 2–3 mm. or overtopped by stigma. Stigma lobes 4–6 mm., nearly parallel or opening out flat, base of stigma ca. 10 mm. above hypanthium. Fruits green, tapering from base to apex, \pm arcuate, 28×5 mm., reaching 50 mm. long \times 8 mm. diameter near base, 3 mm. at apex which is strongly cupped, nearly glabrous below.

Diagnosis—Folia radicalia atroviridia, anguste elliptica, acuta; costa lata, clara rubra; superficies multibus parvis maculis purpuris. Caulis erectus aut suberectus clarus ruber, inflorescentiae apex comosus. Ovarium viridotuberculatum, petala 16 mm. longa, apices sepalorum robusti rigidi, subterminalis, erecti disjuncti.

It was at first intended to include this species as a variety of O. novae-scotiae, but the differences were too marked. This species shows evident relationships not

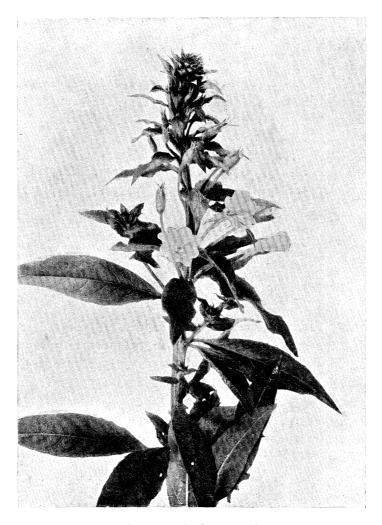


Fig. 13—O. comosa, in flower, culture 23.34.

only with O. novae-scotiae but also with O. intermedia and O. Hazelae var. parviflora. O. comosa is similar to O. novae-scotiae in general habit and in stem colouring, but it differs in (1) narrower dark green rosette leaves bearing many small liver-coloured spots, a few occurring also on the stem leaves. These leaf spots are found in a number of Oenotheras and may be due to a single gene; (2) rosette leaves much smaller, \pm shining, midribs dark red; (3) stems tall, sometimes very slightly bent at the tip; very few short cauline branches; (4) apex of inflorescence comose;

- (5) ovary bearing green papillae; (6) sepal tips stout, rigid, subterminal, erect, and separate.
- O. comosa resembles O. intermedia and O. Hazelae var. parviflora in having rosette leaves rather dark green and shining (but with more numerous liver-coloured spots) and in having the stem tip somewhat bent. They also all (as well as O. novae-scotiae) agree in having red or pink midribs. O. Hazelae var. parviflora differs from O. comosa in having much smaller flowers (petals 8×10 mm.), in habit, in the stouter, subterminal, separate sepal tips, different terminal bracts, etc. O. comosa resembles O. intermedia in the subterminal sepal tips, but differs from it in (1) narrower rosette and stem leaves, (2) very slightly bent stem tip, (3) almost complete absence of long hairs from papillae, (4) larger flowers and longer style. From culture 5.33 the catenation was determined by Mr. C. E. Ford as a ring of 14.

O. intermedia, n. sp.

This species is derived from seeds collected at Bear River, Digby Co., Nova Scotia, on 22 September, 1932. The following cultures were grown and were quite uniform:

Description—Rosette leaves green, rather bright and shining, oblanceolate to elliptic-oblanceolate, apex acute, or obtuse with an acute point, reaching 15–35 cm. \times 35–60 mm. (petiole 5–9 cm.), \pm crinkled and undulate, margin subentire, repanddentate or even pinnatifid below, repand-denticulate above, with reddish teeth; midrib wide, conspicuously, often rather deep, pink; both surfaces finely appressed-pubescent, upper leaves usually with sparse liver-coloured spots (fig. 14).

Stem erect or stem tip (9 cm.) bent, ca. 60 cm., ribbed, green (generally no red papillae), with diffuse red in lower part, hirsute from mostly green papillae and patulous-pubescent, a ring of basal branches coming into flower before the main stem and becoming bright red above. Lowest stem leaves \pm pinnatifid below, middle leaves 21 cm. \times 42 mm., petiolate, red below at stem attachment, midribs pink, \pm horizontal, \pm troughed, indumentum as rosette, but midrib has also scattered, patulous pubescence below. Lower bracts lanceolate, acute, 10 cm. \times 29 mm. Upper bracts 25×9 mm., erect, slightly tipped with red. Inflorescence dense, flat-topped, bracts exceeding the developing buds (fig. 15).

Ovary $10\text{--}14 \times 3$ mm., numerous long ascending hairs with scarcely developed papillae, short erect and \pm appressed pubescence. Hypanthium $22\text{--}29 \times 2$ mm., with sparse long hairs and scattered short pubescence. Bud-cone $9\text{--}11 \times 5$ mm., greenish-yellow, squarish, not tapering, indumentum as ovary but long hairs more spreading, from green papillae. Sepal tips 2--5 mm., markedly subterminal, arcuate,

erect or \pm spreading, green tipped with red. Petals $10\text{--}14 \times 10\text{--}18 \,\mathrm{mm.}$, emarginate, opening to 45° , overlapping. Filaments 7–9 mm., straight, anthers 6–7 mm., reaching nearly to top of stigma. Stigma lobes 4–5 mm., separating in anthesis, base of stigma 3 mm. above hypanthium. Fruits $25 \times 6 \,\mathrm{mm.}$, green, tapering from base to apex, sparsely hirsute without papillae, and with scattered pubescence.

Diagnosis—Folia radicalia viridia, aliquantum clara et nitentia, oblanceolata aut elliptico-lanceolata, acuta aut obtusa cum apice acute, \pm bullata et undulata, margine subintegro, repando-dentato aut pinnatifido ad basim, repando-denticulato

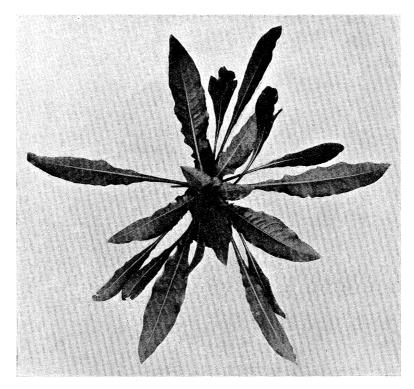


Fig. 14—O. intermedia, rosette, culture 3.33.

supra, dentibus rubescentibus; costa lata, manifesto rubicunda. Caulis erectus aut apex declinatus, viridis cum diffuso rubro colore ad basim. Folia caulina infima \pm pinnatifida ad basim, folia petiolata, rubra infra ad nodum, \pm horizontalia, concava. Inflorescentia spissa, bractae alabastrae excedentes. Ovarium multis pilis longis ascendentibus ex tuberculis vix formatis, apices sepalorum admodum subterminales, arcuati, erecti vel \pm expansi, petala 10 mm. longa, basis stigmatis 3 mm. supra hypanthium.

This species shows such marked differences from O. novae-scotiae and O. Hazelae, to both of which it is clearly related, that it has been necessary to describe it as a separate species. It agrees with O. novae-scotiae in having the lowest stem leaves pinnatifid below, and it resembles that species in many of its characters. The differences, however, are marked and extend to all parts of the plants. They include (1) the

narrower, shiny rosette leaves, (2) the weakly bent stem tips, O. novae-scotiae always having an erect stem, (3) the smaller flowers, (4) the much later development, (5) the subterminal sepal tips, (6) the very short style. It resembles O. Hazelae var. parviflora, which also occurs in adjacent areas, perhaps more nearly, especially in flower-size, in habit (short stems with long basal branches coming into flower first), in its shining rosette leaves with purplish spots; but it agrees with the much more distinct O. Hazelae from eastern Nova Scotia rather than the var. parviflora



Fig. 15—O. intermedia, in flower, culture 50.35.

in (1) the bent stem tip, (2) the short style just above the mouth of the hypanthium, (3) the longer, erect, subterminal sepal tips.

This species thus combines features of both the species mentioned, while disagreeing with both. It has perhaps originated through crossing, though not as a simple hybrid between these species, but it breeds true owing to the catenation of its chromosomes, and it cannot logically be treated as a mere variety of either O. novae-scotiae or O. Hazelae. On the other hand, the three forms cannot be merged into one variable species because O. novae-scotiae and O. Hazelae maintain their separate identity when growing in the same areas, as at Middleton, N.S. The name O. intermedia is used in default of a more appropriate one.

O. flecticaulis n. sp.

From seeds collected on a point of land and shingle beach near the mouth of the Lahave River, Lunenburg Co., N.S., on October, 1932, by Mrs. Winthrop Bell. The following cultures of this striking species were grown:

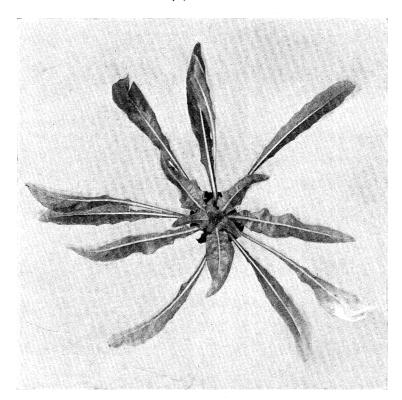


Fig. 16—O. flecticaulis, rosette, culture 78.33.

Description—Rosette leaves rather shining, greyish-green, narrowly elliptic-oblanceolate, apex acute or shortly cuspidate, reaching 15–19 cm. \times 23–32 mm. (in 1935, 19–26 cm. \times 45–50 mm.), including petiole 5–7 cm. long, flattish or slightly concave, crinkling slight, or definite near midrib, wavy or not, midrib white to pink, margin subentire to repand-dentate below, repand-denticulate above, teeth reddish, both surfaces very finely closely appressed-puberulous (fig. 16).

Stem short, very strongly bent (fig. 17), very red, with many red papillae, strongly ribbed, basal branches as long as main stem, many cauline branches. Stem leaves narrow (midleaf 10 cm. × 19 mm.), crinkled, troughed, pendant, margin wavy, repand-denticulate below, subentire above. Bracts narrow but long, troughed, \pm curled. Inflorescence compact, apex flat, comose. Ovary 9 mm., hirsute

from small papillae which are red on exposed side of ovary, and glandular-pubescent. Hypanthium 29×2 mm., may be streaked with red where exposed, scanty long hairs. Bud-cone 12×6 mm., squarish, yellowish, tapering from base to apex, with red papillae in streaks, especially along the midveins, covered with exceptionally long hairs from papillae, some of which are red. Sepal tips terminal, green, appressed, 4–5 mm. Petals $9-12 \times 8-11$ mm., overlapping, not opening out flat, with broad shallow sinus. Filaments 9-10 mm., anthers 4 mm. Stigma lobes



Fig. 17—0. flecticaulis, in flower, culture 103.34.

6–7 mm., appressed, style about 1 mm. above hypanthium. Fruits 30×8 mm., green, many short and scattered long hairs especially towards apex.

Diagnosis—Folia radicalia aliquantum nitentia, canoviridia, anguste ellipticooblanceolata, acuta aut breviter cuspidata, leviter bullata, undulata aut non, costa alba ad rubicunda, margine subintegro ad repando-dentata ad basim. Caulis brevis, apex admodum flexus, valde ruber, rubropapillatus. Folia caulina angusta, bullata, pendentia. Inflorescentia compacta, apex planus, comosus. Ovarium 9 mm. longum, hirsutum cum papillis parvis rubescentibus ubi lucem accipit, glandulariter pubescens. Hypanthium rubrolineatum ubi lucem accipit. Alabastra flavescentia cum rubris papillis lineatis, apices sepalorum terminales, virides, appressi, 4–5 mm. longi. Petala 9–12 mm. longa, 8–11 mm. lata.

This species belongs to the series of forms with strongly bent stem tip and numerous red papillae sensitive to light, which appear to extend around the eastern coast of Canada. They include O. ammophiloides from Guysborough Co., N.S., its var. laurensis from Westmoreland Co., N.B., and O. Hazelae var. parviflora from

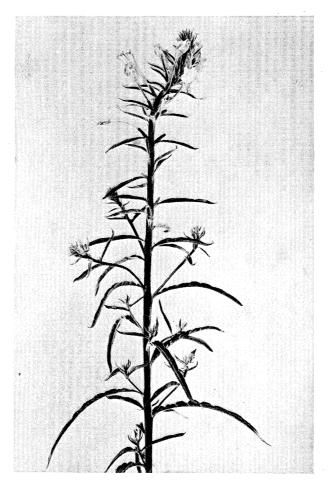


Fig. 18—0. flecticaulis mut. linearis, in flower, culture 79.33.

Shelburne and Lunenburg Counties, N.S. O. flecticaulis agrees in flower-size with its nearest coastal neighbour, the last of these forms, while O. ammophiloides and its variety have petals of about twice the length. The present species differs from O. Hazelae and its variety in a number of significant points, including (1) the strongly bent stems, (2) pale pink to white midribs, (3) red papillae on stem, (4) stem leaves narrower, crinkled, and troughed, (5) bud-cone tapering throughout and continued in the terminal, appressed sepal tips.

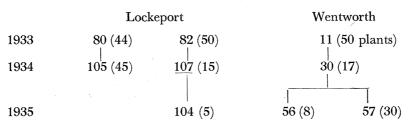
Culture 79.33 contained one mut. *linearis* (fig. 18) which was significantly similar to that from *O. ammophiloides* var. *laurensis* (fig. 39, p. 295), and was also doubtless

trisomic. The rosette leaves were $27 \text{ cm.} \times 15 \text{ mm.}$, the stem leaves linear, one leaf $22 \text{ cm.} \times 4 \text{ mm.}$, and the flowers much smaller with widely divaricating sepal-tips.

O. Hazelae n. sp.

From seeds collected in October, 1932, by Mrs. Winthrop Bell, (a) by the railway on the mainland near Lockeport, Shelburne Co., N.S., and (b) by the railway track on an islet between Lockeport and the mainland. Seeds of the same species were collected by me at Wentworth, Cumberland Co., N.S., by the railway tracks near the station, on 28 September, 1932. The Wentworth strain agrees closely with that from Lockeport, but differs in certain minor particulars. This species is named after Mrs. Winthrop Bell, of Chester, N.S., whose activity in collecting and obtaining seeds from various localities has been a great help in these investigations. It, with its var. parviflora, appears to be the most widely distributed species in Nova Scotia, being known already in five widely separated counties. It is a handsome species of small stature but with many distinctive features, and is described from culture 107.34 as the type. The following cultures (Table VII) have been grown and compared:—

Table VII



Description—Rosette leaves pale greyish-green, ca. 14–15, oblanceolate or narrowly elliptic-oblanceolate, apex acute, obtuse, or apiculate, 16–24 cm. \times 26–56 mm. (petiole 3·5–5 cm.), flattish, no crinkling or undulation, except in younger leaves, sparse liver-coloured blotches, margin subentire, repand-dentate or pinnatifid below, repand-denticulate above, teeth red; midrib pale pink above and below; surface finely appressed-pubescent on both surfaces (fig. 19).

Stem erect or slightly bent, short, $ca.\,66-74$ cm., numerous basal branches developing early and coming into flower before the central stem, decumbent at base then widely arcuate-ascending, equalling or exceeding the central stem, cauline branches none or few. Stem stout, very strongly broadly ribbed from leaf bases, red at base, paler above, green towards apex, branches dark red except upper third; stem spreading- or patulous-ascending-hirsute in two series of different length, from pale red or almost colourless papillae. Stem leaves spreading, lanceolate, or elliptic-lanceolate (lower \pm oblanceolate), $11-15 \times 30-38$ mm., acute with reddish tip, conspicuously concave, not wavy, rather obscurely crinkled, margin strongly repand-dentate below in lower leaves, upper very sparsely and shallowly so, \pm

repand-denticulate throughout, teeth green or reddish, midrib \pm pink above, leaves sparsely and very finely appressed-puberulous on both surfaces, midrib with a few longer appressed or patulous hairs. Lower bracts spreading, very concave, lanceolate, 8–10 cm. \times 28–33 mm. Upper bracts large, spreading, or patulous, very concave, 2.5–4 cm. \times 6–13 mm., with bright red tips, forming a characteristic terminal rosette. Inflorescence compact, up to 25 cm. long apex flat, very slightly depressed, comose, exceeding the highest developed bud-cones, broad and dense (fig. 20).

Ovary $11-12 \times 3.5-5$ mm., densely ascending-hirsute with white or small red papillae and green glandular pubescent. Hypanthium $28-34 \times ca$. 1.8 mm.,

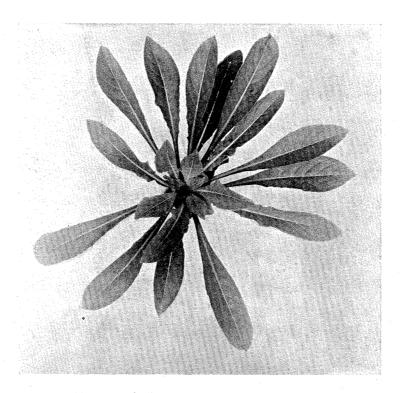


Fig. 19—O. Hazelae, rosette, culture 30.34.

sparsely patulous-hirsute and spreading glandular-pubescent. Bud-cone yellowish, squarish $12\text{--}14 \times 5\text{--}55$ mm., rather densely patulous-hirsute with white papillae, and densely spreading-glandular-pubescent. Narrowed abruptly to sepal tips 4--4-5 mm., green throughout or slightly tipped with red, hooded inside, erect or somewhat divergent. Petals ca. $14\text{--}16 \times 18\text{--}20$ mm., scarcely or slightly overlapping, thin and delicate, opening nearly flat, deeply widely emarginate with sinus ca. 2 mm. deep. Filaments 10 mm., slightly arcuate, anthers 6--8 mm., reaching top of stigma in bud, base of stigma 1--8 mm. above hypanthium tube, stigma lobes 3--6 mm., appressed or spreading. Flowers very fragrant. Fruits 26×7 mm., tapering above, square, green, with few short and sparse longer hairs.

Diagnosis—Folia radicalia pallida cano-viridia, oblanceolata aut anguste ellipticooblanceolata, acuta, obtusa aut apiculata, plana, sparse purpureo-maculata; costa pallida rubicunda supra et infra. Caulis brevis, erectus vel leviter declinatus, multis ramis radicalibus longis instructus qui ante caulem proprium florescunt. Bractae superiores grandes, patulae, valde concavae, singularem rosulam terminalem efficientes. Inflorescentia compacta, apex admodum leviter depressus comosus



Fig. 20—O. Hazelae, in flower, culture 105.34.

latus, densus. Ovarium dense hirsutum, albopapillatum, alabastra flavescentia, albopapillata, subito angusta ad apices sepalorum quae sunt virides, intus scapulati, erecti aut aliquantum divergentes. Petala 14–16 mm. longa.

This distinct species bears some resemblance to *O. novae-scotiae* in its marked red colouring but is by no means nearly related to it, and no other species is at all like it. The outstanding specific characters are (1) the habit, with very neat rosettes, basal branches often exceeding the short stem and coming into flower first, (2) the terminal

rosettes of stem and branches with relatively large, smooth bracts, (3) the fragrance was very marked in cultures 80.33, 82.33 and 107.34, but the third generation (104.35) showed no fragrance.

The cultures of this species were very uniform but culture 104.35 contained one probable mutant, smaller with shorter leaves, and paler midribs. In culture 80.33 one flower was tripartite, with 3 petals, 3 sepals, 6 anthers symmetrically



Fig. 21—O. Hazelae, in flower, culture 30.34.

arranged, and stigma lobes which might be counted as 3 or 4. The Wentworth strain differed in (1) tips of stem and branches strongly bent, (2) flower smaller (petals $10-11 \times 10-14$ mm.), (3) sepal tips shorter (2 mm.), markedly subterminal (fig. 21).

O. Hazelae var. parviflora n. var.

From seeds collected by Mrs. WINTHROP BELL at Port Mouton, Queen's Co., N.S., and Chester, Lunenburg Co., N.S., in October 1932. The first two plants showed

many basal branches and were growing on the sand dunes at Port Mouton, the third also growing on the coast. The Middleton strain was collected by me on 26 September, 1932. It was noted that some rosettes in the small colony had bright red midribs and some green. The sepal tips were also noticed to be "sprung" and red inside at the base.

		Γable VIII		
	Port Mouton	Port Mouton	Chester	Middleton
1933	87 (50 plants)	88 (50)	89 (50)	7 (50)
1934	$\frac{110}{1}$ (59)	111 (47)	112 (25)	26 (6)
1935	105 (32)	106 (5)	107 (32)	54 (18)

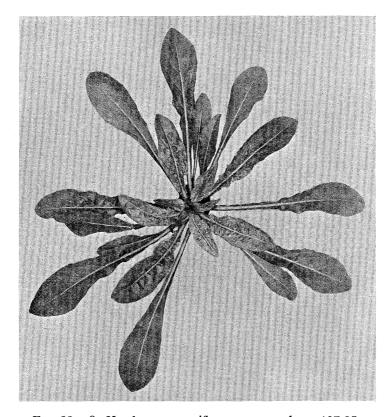


Fig. 22—O. Hazelae var. parviflora, rosette, culture 107.35.

The two sets of cultures from Port Mouton are practically identical, while those from Chester differ in certain particulars to be mentioned. They all agree with the species in habit (short stem and a ring of longer basal branches coming into flower first), rosette leaves elliptic-oblanceolate, midribs pink, sparse liver-coloured blotches, and in general flower characters. They differ, however, in having longer, narrower rosette leaves (19–26 cm. \times 30–42 mm.) \pm crinkled, dark green, shining, midribs brighter pink, wider leaves (19 cm. \times 49 mm. against 14 cm. \times 34 mm.), stems and midribs much redder. The stem tip is sometimes distinctly bent but sometimes erect. The petals are smaller, 8×10 mm., opening out flat, almost

truncate, stigma lobes 1–2 mm., sepal tips shorter (1–2 mm.). These measurements are from cultures 110.34 and 105.35. In comparing cultures 88.33 and 89.33, the Chester plants were found to differ in the following particulars: (1) Leaves somewhat larger and rosette leaves lighter green, less crinkled, more spatulate (fig. 22), (2) stem green, basal branches weakly red, no red papillae, (3) flowers somewhat larger, petals 10×12 mm. These locality differences have been maintained in two later generations of cultures. This is an example of the way in which small but constant differences are frequently found when the same species or variety is grown from adjacent geographic areas.

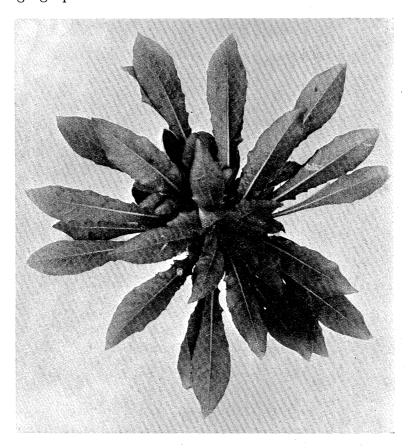


Fig. 23—O. Hazelae var. parviflora, rosette, culture 26.34.

Diagnosis—A specie sic differt: folia radicalia longiora, angustiora, \pm bullata, atroviridia, nitentia, costae latiores, clariores rubicundae; caulis rubrior; petala minora (8 mm. longa, 10 mm. lata); apices sepalorum breviores.

The Middleton strain agreed with the variety in having dark green, shiny leaves with bright red midribs (fig. 23), but was in some respects intermediate between species and variety. The flower-size varied, petals $8-13 \times 10-15$ mm. The habit, with basal branches longer than the central stem and coming into flower first (fig. 24), is the same as that of the species. This strain was observed in 1935 to differ from the Wentworth cultures 56.35 and 57.35 in the following characters:

(1) stem erect, (2) foliage somewhat darker green, more crinkled, and with more liver-coloured spots, (3) last rosette leaves not spatulate, (4) stigma higher above hypanthium (at mouth of tube in the Wentworth strain), (5) sepal tips longer, subterminal but tips in contact (shorter and erect in Wentworth strain), (6) seedling has leaves less wide. Fig. 25 shows the central stem in flower (cf. fig. 20). From culture 87.33 Mr. C. E. Ford determined the catenation as a ring of 14.

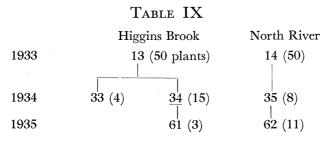
It appears probable that if all the strains from intermediate areas could be assembled they might fill the gaps so as to give an appearance of essential continuity between the species and variety. Nevertheless, it is convenient at present to recognize the variety as distinct from the species. The seedlings, at least of the Middleton strain, have narrower leaves than in the species.



Fig. 24—O. Hazelae var. parviflora, habit, culture 54.35.

O. subterminalis n. sp.

From seeds collected from one plant in a colony by the roadside at Higgins Brook, near Wentworth and at North River, Colchester Co., Nova Scotia, 28 September, 1932. The plants at Higgins Brook were observed to have rather narrow, crinkled leaves, red midribs and stems, buds green. The cultures grown are shown in Table IX.



The original culture of 50 plants was uniform except for one rosette which was much larger and with broader leaves. This rosette was chimaeral, having some leaves which were pale green on one side of the midrib and normal green on the other. Open pollinated seeds from this plant yielded 4 rosettes in culture 33.34, which were uniform and narrower-leaved than the type, but may have been hybrids. The description is from culture 34.34.

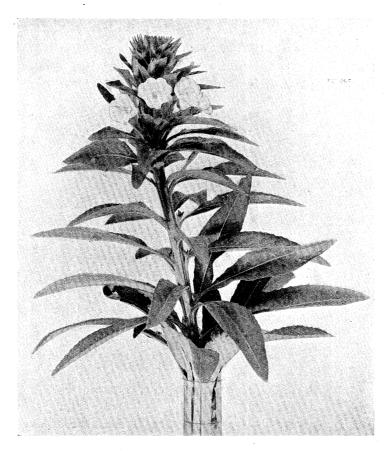


Fig. 25—O. Hazelae var. parviflora, in flower, culture 26.34.

Description—Rosette leaves dull, rather deep greyish-green, oblanceolate, apex acute and shortly acutely cuspidate, reaching 11-14 cm. \times 27-40 mm. (petiole 3-4·5 cm. long), usually strongly concave, crinkling very conspicuous becoming bullate, midrib conspicuously pinkish, margin strongly repand-dentate to pinnatifid below, repand-denticulate above, teeth, margin, and apex reddish-purple, leaves finely appressed-pubescent on both surfaces, very sparsely purple-blotched (fig. 26).

Stem ca. 56-67 cm., tip bent, ring of basal branches red, decumbent then widely ascending, nearly as long as the central stem, tips bent. Stem ribbed, dark red, patulous-hirsute with red papillae, and appressed crispulous-puberulous, collar green. Stem leaves arcuate, deflexed, narrowly elliptic-lanceolate, upper lanceolate, acute with red tip, concave, crinkled, midrib deep pink, margin strongly repand-

denticulate below (lower sub-pinnatifid below), repand-denticulate above, teeth reddish or green, appressed-puberulous above and subappressed-puberulous below. Upper bracts 1.7-2.5 cm. \times 5-10 mm., spreading arcuate, red tips often recurved (fig. 27).

Inflorescence very compact, apex flat when young, convex when mature. Ovary 12×3 mm., densely patulous-hirsute and short spreading-glandular-pubescent, small pale, reddish papillae. Hypanthium $25\text{--}30 \times 2$ mm., indumentum as on ovary, long hairs sparse from scarcely visible papillae. Bud-cone yellowish with reddish marginal streaks, squarish, slightly tapering, $14\text{--}15 \times 5$ mm., indumentum as ovary but short glandular hairs sparse and obscure. Sepal tips 5 mm., slender, erect, markedly subterminal (distinctly hooded inside) erect, neither appressed nor

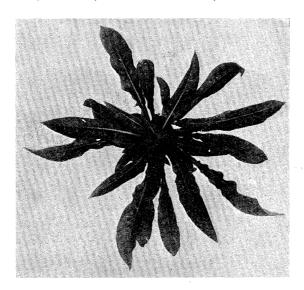


Fig. 26—O. subterminalis, rosette, culture 13.33.

spreading, greenish or tipped with red on inner face. Petals 20×24 mm. (12×15 mm. in 1933),* truncate and very obscurely emarginate, overlapping at base, opening out flat and not wilting quickly. Filaments 12 mm., anthers 8 mm., overtopping stigma by at least 4 mm. Stigma lobes 2–4 mm., gradually spreading or appressed, base of stigmas 8 mm. above hypanthium. Fruits somewhat tapered, \pm red in upper part, ca. 22×5 mm., base nearly glabrous, many long and short hairs on upper part.

Diagnosis—Folia radicalia surda satis plena cano-viridia, oblanceolata, acuta et breviter acute cuspidata, insigniter bullata, costa manifesto rubicundescens. Caulis brevis, atroviridis, apice declinato, ramis radicalibus longis instructus. Folia caulina arcuata, deflexa, anguste elliptico-lanceolata, acuta, apicibus rubris, concava,

* All the flower measurements in this culture were larger in 1934 than in 1933. This may have been because the plant selected as parent of culture 34.34 happened to have genes for somewhat larger flowers.

bullata, costa atrorubicunda. Ovarium 12 mm. longum, 3 mm. latum, tubercula parva rubescentia ; alabastra flavescentia rubrolineata. Apices sepalorum manifesto subterminales, erecti. Petala circa 20 mm. longa.

This species is well characterized by its somewhat narrow, crinkled leaves, with red midribs, red stem, and flowers of moderate size with markedly subterminal sepal tips, the latter feature almost as marked as in O. angustissima, to which it is, however, not nearly related except in this character. It resembles O. Hazelae in the



Fig. 27—O. subterminalis, in flower, culture 34.34.

short \pm red stem slightly bent at tip, but differs in the narrower, crinkled, acute-pointed leaves and smaller bracts. It does not appear to be closely allied to any other species. From culture 13.33, Mr. C. E. Ford determined the catenation to be a ring of 14.

The North River strain, observed in three generations, showed certain minor constant differences: (1) somewhat smaller plants with narrower less crinkled leaves, (2) bright pink midribs, (3) smaller, conspicuously emarginate-notched petals (14×14 mm.), withering more quickly. The two strains agree in all other characters.

O. grandifolia n. sp.

From seeds collected at Wentworth Station and Port Howe, Cumberland Co., N.S., and Waugh's River, near Tatamagouche, Colchester Co., N.S., on 28 September and at Point de Bute, Westmoreland Co., N.B., on 30 September, 1932. This species forms very large rosettes and evidently occupies a considerable area in eastern Nova Scotia and the adjacent portion of New Brunswick. It has been studied in the cultures shown in Table X.

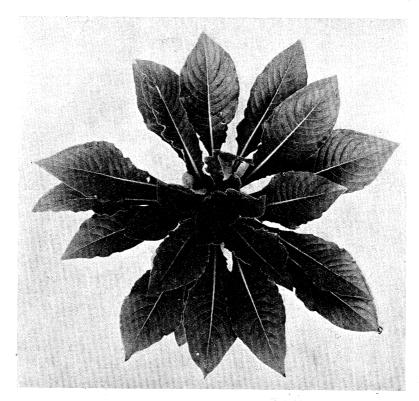


Fig. 28—O. grandiflora, rosette, culture 31.34.

			Table X		
	Went	worth	Waugh's River	Port Howe	Point de Bute
1933	12 (50	plants)	15 (50)	16 (50)	21 (50)
1934	31 (15)	32 (14)	<u>36</u> (5)	37 (15)	44 (26)
1935	<u>58</u> (22)	59 (13)	•	63 (21)	

Description—Rosette leaves light green, 11–21 in number, elliptic to obovate-elliptic, apex acute or shortly acutely cuspidate, very large, reaching 22·5 cm. \times 65 mm. (petiole 2·5–4 cm. long), flattish, \pm crinkled, conspicuously undulate, margin repand-dentate or almost runcinate below to repand-denticulate above.

teeth green, except near apex which is usually purplish, midrib white with occasional faint tinge of pink, lamina usually very sparsely purplish-blotched, indumentum on both surfaces subappressed-pubescent (fig. 28).

Stem erect, short, ca. 75 cm., strongly ribbed above, ascending hirsute from green papillae and patulous- or appressed-puberulous. Usually a ring of basal branches. Stem leaves broadly lanceolate, dentate-pinnatifid below, then repand-dentate,



Fig. 29—O. grandiflora, in flower, culture 15.33.

repand-denticulate, apical third subentire, lowermost 28 cm. \times 72 mm., margin wavy, teeth green, midribs white, both surfaces patulous-puberulous, denser on midrib and scattered hirsute on midrib below. Lower bracts 10 cm. \times 26 mm., lanceolate, concave, margin undulate, distantly repand-denticulate. Upper bracts ca. 22 \times 5 mm. (fig. 29).

Inflorescence dense, apex flat, somewhat comose. Ovary $10\text{--}16 \times 3\text{--}5$ mm., patulous-hirsute from green papillae and patulous-pubescent. Hypanthium $23\text{--}32 \times 2\text{--}5$ mm., stout, greenish, scattered patulous-pubescent and erect short glandular-pubescent. Bud-cone greenish, 22×5 cm., squarish, scarcely tapering, bearing long patulous hairs from colourless papillae and short suberect glandular

pubescence. Sepal tips 2–4 mm., terminal, appressed, apices spreading. Petals 22×21 mm., opening to 45°, overlapping, truncate, fading red at base only. Stigma lobes 8 mm., widely spreading. Anthers 10 mm., filaments arcuate, 14 mm., base of stigma lobes 10–11 mm. above mouth of hypanthium. Fruits long and slender, 39×5 mm., green, with many long and few short hairs.

Diagnosis—Folia radicalia ingentia, leucoviridia, elliptica ad obovato-elliptica, acuta aut breviter acute cuspidata, ad 22·5 cm. longa, 65 mm. lata, manifesto undulata, margine paene runcinata ad basim, dentes virides, costa alba, lamina plerumque rarissime purpura maculata, pubescentia subappressa. Caulis brevis, viridi-tuberculatus, folia caulina late lanceolata, dentata-pinnatifida ad basim. Inflorescentia densa, apex planus aliquantum comosus. Ovarium 10–16 mm. longum, 3·5–5 mm. latum, viridi-tuberculatum, hypanthium robustum, alabastra sub-viridia, apices sepalorum 2–4 mm. longi, terminales, appressi, apicibus extensis. Petala 15–24 mm. longa, truncata, in marcescendo rubra ad basim.

This species is most sharply characterized by its huge rosettes and very broad leaves. It shows certain resemblances to O. pycnocarpa and O. novae-scotiae, but differs from both in its short stems as well as in leaf and flower characters. The subruncinate leaves of the rosettes show some similarity to those of O. pycnocarpa. It is further distinguished from O. novae-scotiae by the almost complete absence of red pigment from stems and buds. The species shows marked resemblance to O. biennis L., from which it differs mainly in (1) much larger rosettes with broader leaves, (2) short stems. The Point de Bute strain (culture 21.33) was found, however, by Mr. C. E. FORD to have a ring of 14 chromosomes whereas the European O. biennis has a ring of 6. O. grandifolia appears to be nearer to O. biennis than to any other species. They agree in having no red papillae on the stem.

The seeds for the Wentworth cultures were collected 465 feet above sea level near the Railway Station, where there were clusters of small plants with broad leaves. From the seeds for culture 12.33 50 plants were grown, 34 of which were typical O. grandifolia while the remaining 16 differed in having narrower, paler green leaves, with bright pink midribs, and were earlier in development. This is probably a case of segregation, because it is repeated in other cultures belonging to O. grandifolia. The second type apparently belongs to O. novae-scotiae, which is found in the Annapolis Valley. A plant of this type was selfed to produce culture 32.34, in which the plants which flowered early were very much like O. novae-scotiae, while the persistent rosettes forming short stems were very much like O. grandifolia. Openpollinated seeds from one plant produced culture 59.35 which again showed "segregation", 11 plants having narrower leaves and pink midribs while 2 had broad leaves and white midribs. The genetical relationship of O. novae-scotiae to grandifolia requires further investigation. Phenotypically they are very unlike.

The Waugh's River strain of O. grandifolia differs from the Wentworth strain in having the leaves much crinkled, as in O. Lamarckiana, and flowers slightly smaller (petals 18×18 mm. as against 21×21 mm. at end of 1934 season, but still smaller,

 14×12 mm., in the previous year) with red papillae on the ovary, the rosette leaves reaching 27 cm. \times 80 mm. Culture 15.33, like 12.33, contained plants of two types, three plants with pink midribs being classed definitely with O. novae-scotiae, the remainder being a much crinkled O. grandifolia. The Port Howe strain was uniform with somewhat crinkled leaves and pink midribs. The plants were strikingly like the type of O. biennis L., differing mainly in the crinkling, and the short stems. In this strain also the flower-size increased from petals 15×14 mm. in 1933 to 24×24 mm. in 1934 and 21×29 mm. in 1935. This species appears to show quite exceptional fluctuations in flower-size, one plant of culture 16.33 having petals 20×25 mm. The Port Howe and Point de Bute strains agree with O. grandifolia in having no red papillae on stem or ovaries, the latter agreeing with the type in every particular.

Striking features of this species are (1) its similarity to O. biennis L., (2) its "segregation" of a type resembling O. novae-scotiae, (3) its similarity in certain respects to O. pycnocarpa, although there is not a close relationship and the species is very distinct.

O. Royfraseri n. sp.

From seeds collected at Sackville, New Brunswick, by Professor Roy Fraser, in 1933. The cultures, grown at Regent's Park, are shown in Table XI.

	Table X	I	
1934	1 (12 plants)	2 (11)	3 (43)
1935	38 (6)	•	39 (22)

Description—Rosette leaves dull greyish-green, elliptic-lanceolate or oblanceolate, apex obtuse to acute or shortly acuminate, reaching 11–14 cm. × 30–40 mm., somewhat crinkled in lower part, margin repand-dentate below, repand-denticulate above, last rosette leaves sinuately pinnatifid below, midribs reddish; upper surface pubescent with suberect hairs, on lower surface midrib and lateral nerves coarsely, mesophyll finely pubescent (fig. 30).

Stem erect, 56–65 cm. high, no basal branches, few ascending cauline branches. Stem obscurely angular and ribbed from leaf bases, pale green, hirsute from red papillae and finely crispulous pubescent. Stem leaves arcuate-spreading or spreading-ascending, elliptic-lanceolate, acute, margin often incurved, strongly repanddentate, or subpinnatifid below, repand-denticulate above, teeth green, measuring 9–14·5 cm. \times 23–40 mm., midrib pinkish, upper surface suberect-pubescent, lower surface densely \pm erect pubescent, the prominent midrib and nerves green, with hairs of unequal length, one series longer than that of the mesophyll. Lower bracts spreading, lanceolate, upper bracts arcuate or ascending, tips recurved.

Apex of inflorescence nearly flat, but lower buds slightly longer than central. Ovary $12-13\times 3$ mm., sparsely hirsute with very small red papillae and arcuate-subappressed-pubescent. Hypanthium $25-30\times 1\cdot 5-2$ mm., with long scattered

ascending-patulous hairs and short, spreading gland-tipped hairs. Bud-cone 14×5 mm., squarish, yellowish-green, with sparse, spreading long hairs, and short, spreading gland-tipped hairs. Sepal tips 3–4 mm., green, slender, appressed, apices spreading, terminal, subulate, hooded inside. Petals $13-18 \times 13-17$ mm., cuneate, \pm widely emarginate, with narrow spaces between, opening at $45-60^{\circ}$. Filaments arcuate, 10.5 mm. long, anthers 7–8 mm. Stigma lobes 4.5-6 mm. long, spreading, base 3–4 mm. above hypanthium, exceeded by anthers (fig. 31). Fruits green, nearly smooth.

Diagnosis—Folia radicalia surda canoviridia, elliptico-lanceolata aut oblanceolata, apex obtusus vel acutus vel breviter acuminatus, extrema folia sinuato-pinnatifida

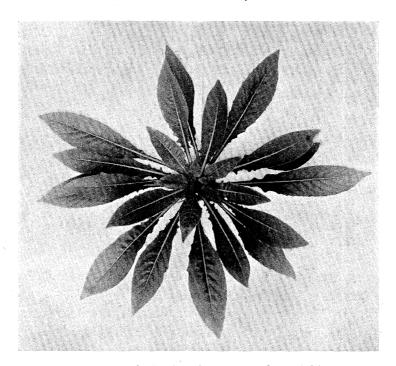


Fig. 30—O. Royfraseri, rosette, culture 1.34.

ad basim, costa rubescens. Caulis erectus, pallidoviridis, rubropapillatus, folia caulina arcuato-extensa, elliptico-lanceolata, repando-dentata ad subpinnatifida ad basim. Petala 11–18 mm., apices sepalorum viridia, attenuata, terminalia, apicibus extensis.

This species is markedly distinct from the other species, O. sackvillensis, found in the same locality. It differs from the latter in the following points: (1) reddish midribs, (2) O. sackvillensis has much smaller, sharper, more pointed and numerous basal teeth on all lower stem leaves, while in O. Royfraseri the last rosette leaves are sinuately pinnatifid below, (3) red papillae on stem, (4) sepal tips appressed, only the tips spreading, (5) petals smaller, 11–18 mm., (6) plants smaller, but this may be due to the 1934 cultures being somewhat shaded.

Culture 3.34 was grown in the partial shade of high trees, with the result that most of the plants were biennial, flowering in 1935, while the selfed seeds of one plant which flowered were grown in full sunlight as annuals (culture 39.35). The phenotypic effects of partial shade could thus be determined. The shade plants were somewhat smaller with somewhat narrower darker green leaves and paler red midribs. The petal-size does not appear to have been affected.

Culture 38.35 and 39.35 differed slightly, the former having many large red papillae on the stem and somewhat lighter green leaves, while the latter had few

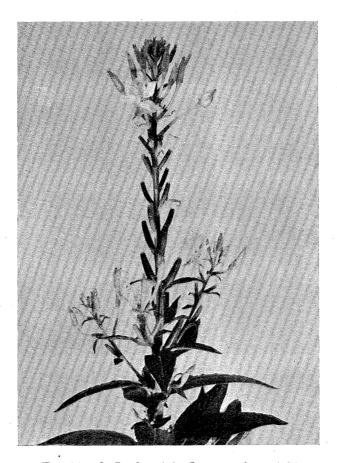


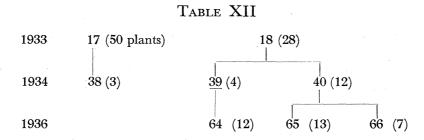
Fig. 31—O. Royfraseri, in flower, culture 1.34.

small papillae. The former culture contained two plants which differed in having smaller petals (10–11 mm. instead of 15–17 mm.), redder stems and white midribs, while the latter culture contained one plant with equally small petals and no red papillae on the stem. These differences are presumably due to gene changes.

O. sackvillensis n. sp.

At Sackville, N.B., large colonies of Oenothera having uniform appearance were growing behind the power house of the University and in the adjacent vegetable

garden. Cultures from seeds collected 29 September, 1932, have been grown from this source, and are shown in Table XII.



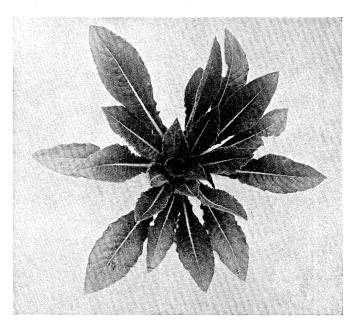


Fig. 32—O. sackvillensis, rosette, culture 38.34.

Description—Rosette leaves light rather greyish-green, oblanceolate or elliptic-oblanceolate, apex acute or shortly cuspidate, blade reaching 18 cm. \times 55 mm. (one late rosette 28 cm. \times 64 mm.), petiole 4–6 cm. long, midrib white, slightly concave, considerably crinkled and undulate, margin repand-dentate or pinnatifid below, repand-denticulate above, teeth green, both surfaces of blade erect-pubescent, rare liver-coloured patches (fig. 32).

Stem erect (fig. 33), ca. 80 cm., basal branches long-decumbent or almost prostrate then widely arcuate-ascending, equalling or exceeding central stem; latter stout, ribbed below, green, no red papillae, sparsely shaggy, patulous-hirsute with hairs of varying length, densely \pm appressed crisped-pubescent. Middle stem leaves elliptic-lanceolate, smooth, somewhat wavy, strongly repand-dentate or subpinnatifid below, repand-denticulate above, teeth green, 17 cm. \times 44 mm., midrib white, hirsute below, blade suberect-pubescent both surfaces. Lower bracts spreading,

concave and wavy, narrowly lanceolate, ca. 4 cm. long, 9-10 mm. wide. Upper bracts ascending, flattish, ca. 2-2.5 cm. long.

Apex of inflorescence flattish, slightly depressed, far overtopping highest developed buds and flowers. Spike not dense. Ovary $13-17 \times 3.5$ mm., rather densely patulous-hirsute from green papillae, and shortly spreading glandular-pubescent. Hypanthium 27×3 mm., indumentum very sparse. Bud-cone greenish, squarish, tapering at apex, 16×5.5 mm., indumentum as ovary. Sepal tips 3-4 mm.,

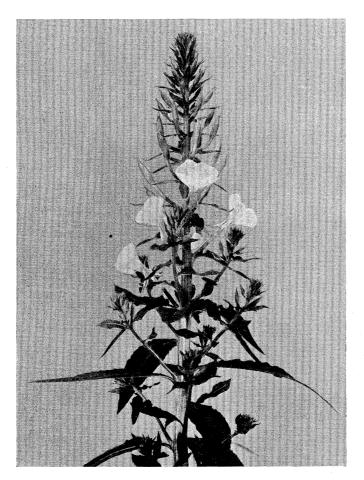


Fig. 33—O. sackvillensis, in flowers, culture 40.34.

green, terminal, appressed. Petals $21-25 \times 22-23$ mm., opening widely, truncate and irregularly toothed, or obscurely retuse at apex. Filaments 13 mm., anthers 9 mm., about level with top of stigmas, lobes 6-7 mm. becoming widely divergent or remaining appressed, 7-9 mm. above hypanthium. Fruits green, ca. 30 \times 5 mm., bearing many long hairs, few short.

Diagnosis—Folia radicalia lucida subcanoviridia, oblanceolata aut ellipticooblanceolata, acuta vel cuspidata, leviter concava, insigniter bullata et undulata, raris maculis purpureis, costa alba, margine repando-dentata aut pinnatifida ad basim, dentibus viridibus. Caulis robustus, erectus, viridis, non rubropapillatus; inflorescentiae apex leviter depressus, flores longe superans. Ovarium robustum, 13–17 mm. longum, hirsutum, viridipapillatum; alabastra viridia, apices sepalorum 3–4 mm. longi, virides, terminales appressi. Petala 21–25 mm. longa.

This species is marked by its stout, erect stems, absence of red from papillae and midribs, and the medium sized flowers. In general leaf shape and flower-size and in the absence of red papillae from the stem it resembles O. biennis. It has shown striking variability, which may be briefly described. The culture 18.33 from wild



Fig. 34—O. sackvillensis, seg. albiviridia, rosette, culture 40.34.

seeds, which numbered 28 plants, included one dwarf mutation, which reached a height of ca. 60 cm. but remained unbranched, with small, curled bracts and smaller flowers (petals 17 mm.). This plant was selfed and produced culture 40.34, which included one dwarf exactly like the parent, 4 normal talls and 7 of a striking new type which may be called *albiviridia* n. var. (figs. 34 and 35) and which differs from the type as follows: the leaves are light green, rather conspicuously troughed, narrower (rosette leaves 10-17 cm. \times 25-33 mm.), conspicuously crinkled and undulate, with no liver-coloured spots, and the flowers appear to be somewhat deeper yellow.

Diagnosis—A specie sic differt: folia manifesto concava, alboviridia, angustiora, manifesto bullata et undulata, non rubromaculata.

Open-pollinated seeds of the dwarf in culture 40.34 yielded culture 65.35, thirteen plants, of which three were typical dwarfs (fig. 36), the rest being tall. This dwarf type proves on cytological examination by Mr. C. E. FORD to be a trisomic mutation, as its genetic behaviour suggests. A normal plant from culture 40.34 was selfed and gave seven plants, two of which were the light green type. Hence some normal



Fig. 35—O. sackvillensis var. albiviridia, in flower, culture 40.34.

plants segregate a high frequency of this type in each generation. Its chromosomes have not yet been examined. Culture 39.34 contained certain plants in which the green papillae on the sepals were elongated and cylindrical. One of these plants was selfed to produce culture 64.35, all of which were uniformly of the light green type. Hence it would appear that this segregate breeds true, and that the true character of the parent plant of this culture was overlooked.

O. ammophiloides var. laurensis n. var.

From seeds collected at Port Elgin, Westmoreland Co., N.B., near the railway station, on 30 September, 1932, and grown in Regent's Park. Cultures 19 and 20 were both from Port Elgin, while culture 22 was from the shore at Cape Tormentine

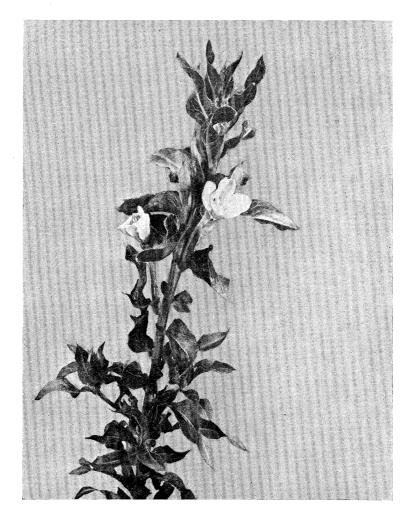


Fig. 36—O. sackvillensis, trisomic dwarf mutation, in culture 65.35.

and culture 23 was from seeds of a plant near C. Tormentine on the road to Port Elgin.

		1 ABLE	AIII		
1933	$\frac{19}{ }$ (50 plants)	20	<u>20</u> (22)		23 (50)
1934	41 (48)	 42 (50)	43 (3)	45 (24)	46 (13)
1935	67 (35)		68 (6)		

Description—Rosette leaves thick, greyish-green, narrowly elliptic, later ones oblanceolate, apex acute or obtuse, reaching 34.5 cm. × 52 mm. (petiole 4–7 cm.), margin repand-denticulate below, obscurely so above, with reddish glands, midrib white, both surfaces very finely appressed-pubescent (fig. 37).

Stem ca. 85–100 cm., tip bent (ca. 5 cm.), ring of basal branches shorter than central stem, tips bent, later becoming erect or suberect. Stem ribbed, ribs very thick above, thin below, stem pale green, or pinkish near base, patulous-ascending-hispid with bright red papillae, and finely arcuate-appressed puberulous.

Lower stem leaves deflexed, upper spreading, lower narrowly oblanceolate, upper \pm elliptic-lanceolate, 19–27 cm. \times 30–38 mm., acute, red-tipped, margin irregularly

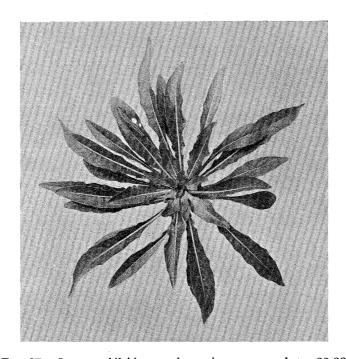


Fig. 37—O. ammophiloides var. laurensis, rosette, culture 22.33.

repand-dentate below, obscurely repand-denticulate above, upper half subentire, glands obscure, green, midrib white, with some longer \pm suberect hairs below, both leaf surfaces finely appressed-pubescent. Lower bracts lanceolate, concave, $12-13 \times 36-40$ mm., spreading, uppermost ascending ca. 2·5 cm. \times 5 mm., red on under surface (fig. 38).

Apex of inflorescence flat or rather slightly depressed, comose. Ovary $10-13 \times 3$ mm., rather shortly ascending-hirsute with many bright red papillae and shortly spreading glandular-pubescent. Hypanthium $28-33 \times ca$. $2\cdot 5$ mm., sparsely ascending-or patulous-hirsute from red papillae (papilla often forming a streak by extension of pigment longitudinally from its base) and sparsely spreading glandular-pubescent; hypanthium greenish, often tinged with deep red. Bud-cone squarish, scarcely tapering, yellowish, covered with conspicuous red papillae where exposed to light,

 $14-19 \times 5.5-6$ mm., densely ascending-hirsute from red papillae and spreading glandular-pubescent, sepal tips 3-4 mm., subterminal, appressed or diverging, constricted at base, green with a red spot at the base inside. Petals 16×16 mm.- 22×26 mm., emarginate, widely overlapping, opening to 45° , turning orange. Filaments 13 mm., anthers 7-8 mm., stigma lobes 8-11 mm., widely divergent, base of stigma lobes 4-6 mm. above hypanthium, anthers overtopping stigmas ca. 5 mm. Fruits 35×7 mm., green with touches of red at apex, nearly glabrous

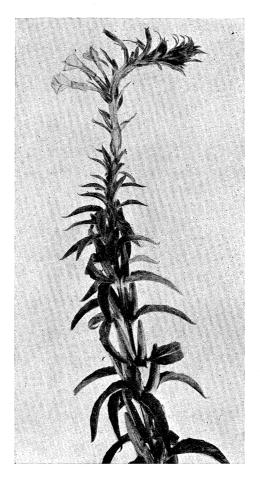


Fig. 38—O. ammophiloides var. laurensis, in flower, culture 19.33.

below, numerous mostly short hairs above. Mr. C. E. Ford examined a normal plant in culture 20.33 and found a ring of 14 chromosomes.

Diagnosis—A specie sic differt: flores grandiores (petala 16–22 mm. longa), stigmata longiora, fructus brevior, rubrae papillae, pauciores et minores, maxime in caule et hypanthio, caulis et alabastra minus pubescentia.

This form is clearly related to *O. ammophiloides* Gates and Catcheside, which is also a coastal species, described from Guysborough Co., N.S. (Gates 1933, p. 180). It differs mainly from the latter species in (1) larger flowers, (2) longer stigma lobes,

(3) shorter fruits, (4) plant less hairy, (5) fewer and smaller red papillae, especially on system and hypanthium. It may therefore be regarded as a variety having larger flowers, fewer red papillae, less pubescence, and shorter fruits. Cultures 22 and 23 and their descendants differed from the type cultures 19 and 20 in the nearly complete absence of red papillae from stem and buds. This is a good example of the way in which minor differences appear in strains of the same species from different localities.

Culture 20.34, numbering 22 plants from wild seeds, produced one striking mutant *linearis* with extremely narrow, almost linear, subentire leaves (rosette leaves

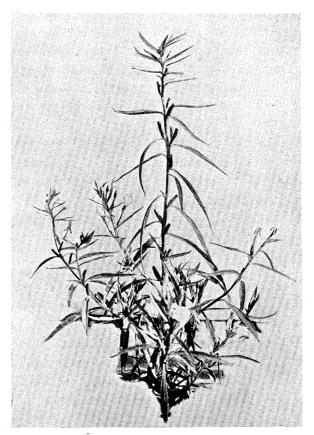


Fig. 39—O. ammophiloides var. laurensis mut. linearis, culture 43.34.

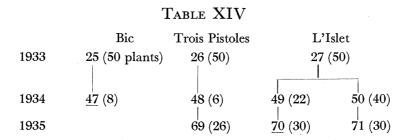
30 cm. \times 35 mm.) and smaller flowers (petals 13 \times 12 mm.). Otherwise it agreed with the type. Open-pollinated seed produced 3 plants (culture 43.34, two having very narrow leaves, one with white and the other with red midribs, showing that the latter was a hybrid, while the third, which flowered, had rosette and stem leaves only 5–8 mm. wide and empty anthers (fig. 39). This plant had even narrower leaves than the original parent mutant from which it was descended. The chromosomes were examined by Mr. C. E. FORD and it was found to be trisomic, having 15 chromosomes. Mut. *linearis* produces very few seeds, and from open-pollinated seeds of this plant only four offspring were obtained, two of which were

typical and two mut. *linearis*. Although not strongly viable, this linear-leaved trisomic has therefore reappeared in three successive generations with a frequency which is in accord with the 50 per cent expected, but it is not clear why the later specimens should have been so much more extreme than the original mutant.

This trisomic mutant is very similar to the mut. graminifolia obtained by RUDLOFF and Stubbe (1935) in the offspring of O. Hookeri after X-raying the pollen. It also had smaller flowers and mostly bad pollen. They class it with a number of others as a gene mutation. This conclusion is based on an examination of the pollen grains and the fact that when selfed they breed almost true, no count of the chromosomes being made. These reasons are, however, inadequate, and it appears more probable that mut. graminifolia was a trisomic. It is unfortunate that no cytological examination was made. MICHAELIS (1930) obtained 60 per cent heteroploid offspring from O. Hookeri by subjecting the plants to high temperature. These included plants with 15 and 13 chromosomes and others with a fragment, but unfortunately there is in this case no description of the phenotypic characters. By X-raying the pollen of O. blandina, CATCHESIDE (1935) obtained a number of F₁ variants. Four of these were called "willow leaf" and one "bootlace". The latter had rolled leaves about 1 cm. in diameter. Both types showed seven pairs of chromosomes and were probably due to deletions. On selfing or back-crossing to normal they gave all normal offspring. It thus appears that very narrow-leaved mutations may be (1) trisomic, (2) due to deletions, or (3) perhaps due to gene mutation.

O. parva n. sp.

This species is in a sense a continuation of the coastal species O. ammophiloides, which is found on the southern coast of Nova Scotia and continued on the gulf shore as var. laurensis. It occurs on the south shore of the St. Lawrence river and is represented by seeds collected on 2 October, 1932, from Bic, Rimouski Co., Quebec, by an old wharf; Trois Pistoles, Temiscouata Co., on the beach by the Biological Laboratory of Laval University; and at L'Islet, L'Islet Co., by the roadside near the river shore. The resulting cultures are closely similar, but they differ so markedly and constantly from the Port Elgin, N.B., cultures as to require separate specific recognition. The cultures grown are shown in Table XIV.



The relationship of this species to O. ammophiloides var. laurensis is confirmed by the seedling stage, which is very similar, the only detectable difference being the

constantly smaller size. It remains markedly smaller in the rosette and flowering stages. The L'Islet strain differed in certain features from the other two in the flowering stage, but as the rosettes were indistinguishable the description of this stage has been taken from culture 70.35 and that of the flowering plants from culture 47.34. The latter culture remained rosettes in 1934 and only flowered as (biennials) the following year. Minor differences between these strains will be pointed out later.

Description—Rosette leaves pale greyish-green, narrowly oblanceolate, acute, reaching $18 \text{ cm.} \times 30 \text{ mm.}$, smooth, concave, margin repand-dentate below, finely

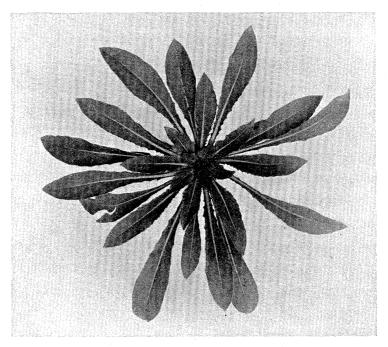


Fig. 40—O. parva, rosette, culture 47.34.

repand-denticulate above, teeth reddish, midrib white, indumentum on both surfaces of lamina extremely finely appressed-puberulous (fig. 40).

Stem reaching 140 cm. (in partial shade), 10 cm. at tip bent horizontal when developing, red from papillae, especially where exposed to light; basal branches decumbent then widely ascending, cauline branches numerous, arcuate-ascending. Stem thinly ribbed below, more conspicuously in upper half, usually red below, pale green and reddish above, softly conspicuously patulous-hirsute from crimson papillae and inconspicuously subappressed-crisped-puberulous.

Stem leaves arcuate-deflexed, narrowly lanceolate or elliptical-lanceolate, flattish, margin dentate below with 1–3 coarse teeth, otherwise extremely finely denticulate with green or red teeth, 12·5–13·5 cm. \times 22–24 mm., midrib white, lamina very sparsely irregularly subcrect-pilose and very finely densely \pm appressed-pubescent. Inflorescence with long internodes below, more densely flowered above, with few

flowers. Lower bracts patulous or deflexed, lanceolate, concave, wavy near base, ca. 5.5-8 cm. $\times 14-20$ mm. Upper bracts spreading with arcuate-upcurved apices ca. 2-2.5 cm. $\times 5-6$ mm. Apex of inflorescence flattish or slightly depressed, comose, ca. 1.5-2 cm. across, slightly overtopped by highest developed buds, straight (fig. 41).

Ovary 13×4 mm., copiously ascending and patulous pilose from papillae which are crimson, especially on side exposed to light, densely shortly spreading, glandular-pubescent. Hypanthium $21-25 \times 2\cdot 5$ mm., greenish, sparsely ascending pilose



Fig. 41—O. parva, in flower, culture 70.35.

from papilla bases which form \pm conspicuous red lines where exposed, copiously spreading glandular-pubescent. Bud-cone yellowish-green, red where exposed, quadrangular, ca. 10×5 mm., densely ascending-pilose from numerous red papillae and shortly spreading gland-tipped-pubescent. Late buds and stem apex deep red, but uppermost bracts with little red on their lower surface. Sepal tips 4 mm., subterminal, green tipped with red, \pm divergent. Corolla cup-like, petals 16×15 mm. (rapidly diminishing to $8-9 \times 6$ mm.), emarginate, opening to ca. 60° , scarcely overlapping in early flowers, widely overlapping in later. Base of stigma

5–6 mm. above mouth of hypanthium, stigma lobes 7–2 mm. long, generally tipped with red, reaching 3 mm. above anthers, appressed or spreading. Anthers 7 mm., filaments 9 mm.? Fruits 30×7 mm., red at tip when maturing.

Diagnosis—Folia radicalia pallida canoviridia, anguste oblanceolata, acuta, plana, costa alba, lamina magnopere tenuiter appresso-puberula. Apex caulis horizontaliter flectus, sanguineopapillatus. Folia caulina arcuato-deflexa, anguste lanceolata vel elliptico-lanceolata, plana. Inflorescentia paucis floribus; ovarium 13 mm. longum, 4 mm. latum, abundanter pilosum de papillis sanguineis, maxime ubi lacum accipit. Hypanthium viridescens, manifesto rubrolineatum, sepala flavescentia-viridia, rubra ubi lucem accipiunt. Petala 16–19 mm. longa, apices sepalorum 4 mm. longi, subterminales, virides, acuminibus rubris, ± deflectentes.

The Bic culture 47.34 showed one interesting mutant. In the rosette stage the plants were uniform and differed from the Cape Tormentine strain (O. ammophiloides var. laurensis) only in having leaves narrower and smoother. Having wintered over, and formed stems about 6 inches high, in one plant the stem and leaf margins were seen (26 April, 1935) to be bright yellow, lacking chlorophyll except in the middle portion of the leaves. This periclinal chimera, unlike all other plants in the culture, was severely affected by a heavy spring frost. It managed to survive in a weak state, but all the yellow tissue disappeared, and it produced a few flowers as a green plant with narrow leaves and no trace of yellow tissue. Whether its seeds will germinate remains to be seen.

The strain from Trois Pistoles differs but slightly from the Bic strain in having the stem tips more strongly bent, the stems and buds somewhat redder. A plant from the Bic strain (culture 25.33) was examined by Mr. C. E. Ford and found to have a ring of 14 chromosomes. The L'Islet strain stands apart from the other two in several features: (1) rosette leaves less grey-green, margin of leaves redder, rosettes less persistent, (2) stem leaves shorter and narrower, less dentate below, stem suberect, short (reaching ca. 71 cm.), and slender, (3) plants earlier to finish flowering, producing only about 15 (as against 30) flowers on the main stem, (4) stems pale diffuse red, (5) flowers smaller (petals $8-12 \times 8-10$ mm.), (6) fruits short, $23-28 \times 5-7$ mm. It might be treated as a separate variety or even species, but it clearly falls into the coastal series which stretches from the south coast of Nova Scotia up the estuary of the St. Lawrence.

The original culture 27.33 contained one aberrant plant, which may be called mut. hebetifolia, whose open-pollinated seeds produced culture 50.34. This plant differed from the type in being smaller, with blunt leaf tips and very short fruits. The offspring were of the two types, showing respectively blunt and pointed leaves in the ratio 13:27. Fig. 42 shows a rosette (cf. fig. 40), and fig. 43 the flowering stage (cf. fig. 41). The blunt-leaved type was also later in flowering and the leaves are more or less blotched with pale green. One of these plants, which survived the winter as a rosette and flowered in 1935, had extremely small flowers, rounded, yellowish-green buds, petals only 6 mm. long, ovary 7–8 mm., sepal tips 1–2 mm.,

slender, sub-terminal, green tipped with red. Culture 71.35 was derived by selfing a pointed-leaved plant of 50.34. The offspring were all identical with 70.35.

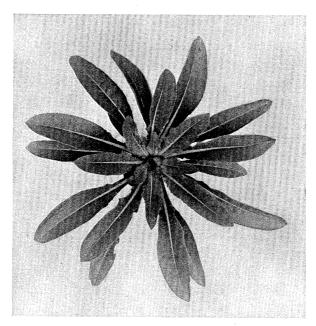


Fig. 42—O. parva mut. hebetifolia, rosette, culture 50.34.



Fig. 43—O. parva mut. hebetifolia, in flower, culture 50.34.

Hence the unut. hebetifolia segregates the type, which later breeds true. This behaviour is characteristic of a trisomic, but its cytology has not yet been investigated. A plant of the blunt type in culture 50.34 was selfed, but its seeds failed to germinate.

O. leucophylla n. sp.

From seeds collected at St. Valier, Bellechasse Co., Quebec, on 30 September, 1932. This extremely uniform and distinct species has been studied in the cultures shown in Table XV, all of which were derived from St. Valier, except cultures

		TABLE X	ΚV		
1933	33 (50 plants)	36 (50)	42 (50)		
1934	56 (3)	<u>59</u> (13)	65 (28)		
1935			76 (33)	133 (31)	134 (31)
			135(26)	136 (32)	137 (25)

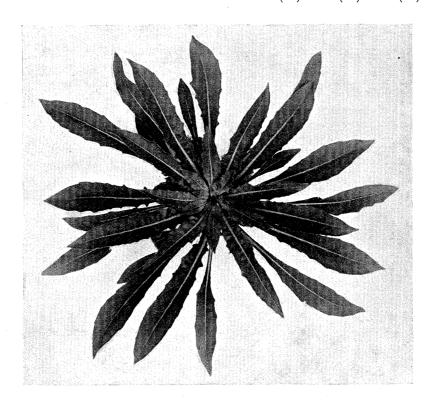


Fig. 44—O. leucophylla, rosette, culture 59.34.

133-137, which were from seeds collected by Miss Marie Rousseau at Berthieren-bas, Montmagny Co., Quebec, on 1 September, 1934.

Description—Rosette leaves small, light pale green, narrowly oblanceolate or elliptic-oblanceolate, apex acute or obtuse, reaching 11-18 cm. \times 23-32 mm. (petiole 3-5 cm.), flat, smooth, or somewhat crinkled, margin repand-dentate or subpinnatifid below, repand-denticulate above, midrib white, finely-appressed pubescence on both surfaces (fig. 44).

Apical 8–10 cm. of stem strongly bent, height ca. 60–75 cm., broadly, thickly ribbed throughout, very pale green, with copious red papillae, sparsely ascending- or patulous-hirsute from red papillae and densely finely appressed-crispate-puberulous; sometimes forming basal branches bent at tips, but more usually many short, widely spreading cauline branches, especially from upper part of stem.

Stem leaves usually arcuate-spreading, very narrowly elliptic-lanceolate, wavy, somewhat crinkled, pale green, margin pinnatifid or sub-pinnatifid near base, then much repand-dentate, then repand-denticulate, with numerous green teeth (glands), 8–17 cm. × 12–32 mm., midrib white above and below, surface appressed or subappressed-pubescent, midrib below pubescent and puberulous in two series. Lower bracts spreading, convex, narrowly lanceolate, ca. 5 cm. × 10–12 mm., upper bracts arcuate-ascending, 1·5–2 cm. long.

Apex of inflorescence flat or convex, conspicuously comose, easily overtopping highest developed bud cones and flowers. Ovary $10\text{--}12 \times 2\text{-}5$ mm., ascending-hirsute from dense red papillae and densely shortly spreading glandular-pubescent. Hypanthium $ca.\ 26 \times 2$ mm., sparsely patulous hirsute from red papilla (papillae forming streaks) and rather densely spreading glandular-pubescent. Bud-cone dark red (from papillae) where exposed to light, \pm quadrangular, $13 \times 4\text{--}5$ mm., indumentum as on ovary, sepal tips 4–6 mm. long, divergent, reddish at or near apex. Petal $ca.\ 8\text{--}10 \times 9\text{--}11$ mm., not contiguous, opening to 45° , never wide-spreading, widely shallowly emarginate and toothed in sinus. Filaments $ca.\ 11$ mm., anthers 6 mm., overtopping stigmas by 1–3 mm., base of stigma $ca.\ 4\text{--}7$ mm. above hypanthium, stigma lobes 4–6 mm. long, not or slightly separating (fig. 45).

Diagnosis—Folia radicalia parva, pallida alboviridia, anguste oblanceolata ad elliptico-lanceolata, acuta vel obtusa, plana aut aliquantulum bullata, costa alba. Apex caulis valde declinatus, caulis pallidissime viridis, copiosus rubropapillatus, multis ramis caulinis. Folio caulina angustissime elliptico-lanceolata, undulata, aliquantum bullata, arcuato-extensa. Apex inflorescentiae manifesto comosus. Ovarium dense hirsutum, rubropapillatum, hypanthium rubrolineatum; alabastra papillata, atrorubra ubi lucem accipiunt. Petala circa 8–10 mm. longa.

This species is easily characterized by the small, pale green, rather narrow stem leaves and rosette leaves, and the red papillae on the sepals where exposed to light. The latter character relates the species to O. ammophiloides, but it differs markedly from that species in the smaller pale rosettes, in foliage, and in the smaller size of the flowers. O. leucophylla also resembles O. eriensis in having narrow leaves; but they are pale green, not grey-green and the rosettes are semi-persistent; the flowers are of approximately the same size, but the light-sensitive red papillae of the buds are like those of O. ammophiloides and are very different from those of O. eriensis, which also differs in having no red papillae on its stems and in dropping its early buds. O. leucophylla differs from O. muricata L. markedly in the more strongly bent stem tips and in having red papillae on the sepals, as well as in the narrower pale green leaves. It is perhaps most nearly related to O. eriensis among earlier species. It has

some features of O. eriensis among earlier species. It has some features of O. eriensis and of O. ammophiloides and it stands between them in its geographical distribution.

No differences were discovered between the cultures from St. Valier and those from Berthier-en-bas except that the latter were distinctly larger, those from St. Valier (76.35) having a height of ca. 76 cm. while from Berthier-en-bas ranged

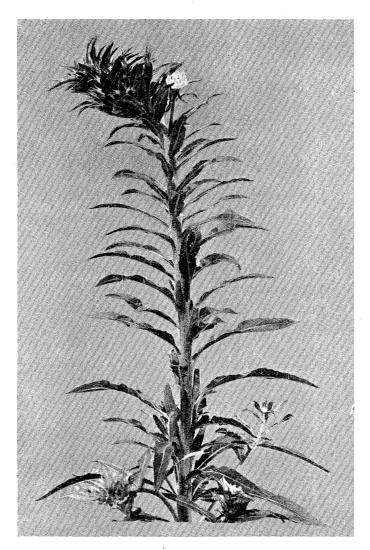


Fig. 45—O. leucophylla, in flower, culture 36.33.

from 102–110 cm. Plants from the three original cultures, 33.33, 36.33, and 42.33, from St. Valier, were examined by Mr. Ford and found to have a ring of 14 chromosomes in each case.

O. biformiflora n. sp.

From seeds collected at St. Valier, Quebec, by Messrs. VICTORIN and ROUSSEAU. 1 October, 1932, and myself at Charny, Que., on 3 October, 1932. The large colony

at St. Valier is now known to contain several well-marked species. The colony at Charny was on both sides of the road at the south end of the Quebec bridge. The 17 cultures grown of this species are shown in Table XVI.

Table XVI St. Valier St. Valier St. Antoine Charny Charny (cruciate) (broad (cruciate) (broad) les Fonds (broad and petals) cruciate) 1933 37 (50 plants) 38 (50) 48 (50) 47 (50) 46 (50) 71 (14) 72 (10) 1934 60 (15) 61 (4) 70 (6) 68 (4) 69 (6) 81 (6) 74 (7) 79 (2) 80 (3) 73 (14) 35 (10) 1935

The same species has been obtained from all three localities in both the broadpetalled and the cruciate form. The inheritance of this difference will be recorded below.

Description—Rosette leaves dull green, early leaves elliptic or obovate-elliptic, apex obtuse, later leaves oblanceolate, acute or shortly cuspidate, rarely subobtuse, blade reaching 10--36 cm. \times 35--67 mm., petiole 4--5 cm., slightly concave, often conspicuously crinkled near base, midrib pale pink or nearly white, margin repanddentate below, repand-denticulate above, teeth green, surface rather sparsely appressed-pubescent above, subappressed-pubescent below (fig. 46).

Stem erect, ca. 60–90 cm., basal branches decumbent at base or simply ascending. shorter than central stem which is broadly ribbed, ± red below, green in upper part, densely patulous-hirsute from conspicuous dark red or colourless papillae and arcuate-subappressed puberulous. Stem leaves spreading or deflexed, ± concave, middle elliptic, lower elliptic-oblanceolate, upper ovate-lanceolate, acute with purple apex, 7.5-12 cm. \times 29-32 mm., midrib white or faintly tinted with pink in lower leaves. Lower bracts ovate-lanceolate or lanceolate, deflexed or arcuate-deflexed, 4.5-6 cm. × 19-26 mm. Upper bracts arcuate spreading or ascending, $15-20 \times 4-7$ mm. Apex of inflorescence flattish, slightly depressed, less than 1 cm. across, easily overtopped by developed buds, spike dense. Ovary 8–10 imes2-3 mm., rather sparsely patulous or ascending hirsute with few small red papillae. and densely shortly glandular-spreading-pubescent. Hypanthium $16-29 \times$ 1.7-2 mm., very sparsely patulous-hirsute, rather densely glandular-pubescent. Bud-cone greenish or yellowish, squarish, $9-13 \times 4.5$ mm., scarcely tapering, sparsely patulous-hirsute, densely glandular-pubescent, no red papillae on bud visible to naked eye. Sepal tips green, 1-2 mm., very slender, terminal, appressed. Petals $12-15 \times 12-23$ mm. (cruciate, $12-14 \times 3-5$ mm.), broad (or roughly linear with blunt apex), yellow (cruciate petals irregularly marked with green), (fig. 48), spreading. Filaments 7 mm., anthers 5–6 mm., about level with summit of stigma, lobes 3–5 mm., appressed or spreading, base of stigmas ca. 3–5 mm. above hypanthium. Fruits green, 30×7 mm., tapered only at apex, surface rough with tuberculations, no red papillae, few short hairs (fig. 47).

Diagnosis—Folia radicalia surda-viridia, obovato-elliptica ad oblanceolata, obtuse ad acuta, costa pallida rubicunda ad paene alba, dentibus margine viridibus. Caulis erectus, folia caulina elliptica ad ovato-lanceolata, acuta, apicibus purpureis,

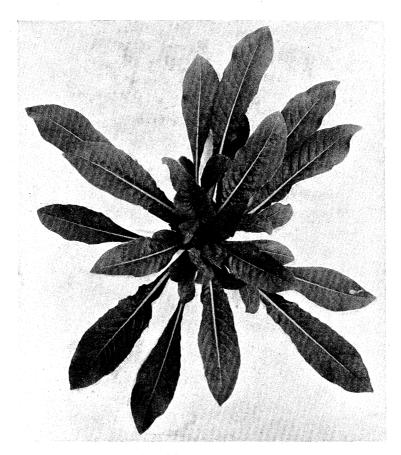


Fig. 46—O. biformiflora, rosette, culture 71.34.

costa alba aut languide rubicunda colorata. Ovarium 8-10 mm. longum, hirsutum, paucis parvis rubris papillis; alabastra vix attenuata, viridescens vel flavescens, apices sepalorum 1-2 mm., gracilimi, terminales, appressi, virides. Petala circa 12-15 mm. longa, lata vel cruciata.

This species has both broad-petalled and cruciate plants in all areas where it has been found, but no intermediates appeared except in artificial crosses between the two types. The form with narrow petals may be known as var. cruciata n. var. In culture 37.33, the 38 plants which flowered all had cruciate petals. Culture 38.33 had only broad petals, ca. 15×23 mm., notched, slightly overlapping at base. It

also differed in having (1) white midribs, (2) white papillae on stem and ovaries, (3) rosette leaves strongly repand-dentate to pinnatifid below, with a few purplish blotches. Each of these characters may be controlled by a single gene. The pubescence was also erect rather than subappressed. The same differences could be observed between their descendant cultures 73.35 and 74.35.

Culture 38.33 included one plant which was not observed to differ phenotypically from the rest, but which was shown by Mr. C. E. FORD to be triploid, having 21



Fig. 47—O. biformiflora var. cruciata, in flower, culture 71.34

chromosomes. The plants from Charny in culture 46.33 all had broad petals, but no red papillae on the stem. This culture was derived from the seeds of four wild plants but was uniform except for one plant, which evidently belonged to a different species. It showed some resemblances to O. novae-scotiae, having a red stem, and was selfed to produce culture 69.34. This proved to be a distinct type having pale green, narrowly elliptic or oblanceolate rosette leaves, apex acute or obtuse and apiculate, reaching 18 cm. \times 38 mm., but its flowering stage has not yet been described. In culture 47.33 the single wild parent plant from which seeds were

taken probably had cruciate flowers, since the buds were noted as peculiar, giving the appearance of having been touched with frost, but in the first season only ten offspring flowered, 7 with broad petals and 3 cruciate. One row of 22 rosettes were wintered over and flowered in 1934. The flowers were uniform, markedly smaller than in the St. Valier plants, broad petals uniformly $7-9 \times 7$ mm., obcordate, emarginate. They mostly failed to open, although the plants which were annuals appear to have opened their flowers normally. In the biennial plants the sepals were pushed apart at the base but remained adherent at the apices.



Fig. 48—O. biformiflora var. cruciata, near view of flowers showing the cruciate character.

A broad-petalled plant gave culture 70.34 with broad petals, measuring 12×12 mm., while a cruciate-flowered sister plant gave culture 71.34, all with cruciate flowers and precisely like 60.34 from St. Valier. Similarly culture 37.33 produced only cruciate offspring in two generations and 38.33 produced only broad petals. Cultures 34.35 and 35.35, both from different broad-petalled plants of 47.33, gave only broad petals. These two cultures were also devoid of red papillae on the stem.

Culture 48.33, from St. Antoine les Fonds, was derived from mingled seeds of two wild plants. Of those which flowered, 25 had cruciate and 8 had broad petals.

They agreed exactly with the other cultures of this series, having midribs and red papillae on the stem. On cruciate plants the petals were not only narrower but considerably longer than on broad-petalled plants. Thus in the latter they measured 7×6 –7 mm., while in the former they were 10– 14×3 –6 mm., but in one cruciate plant only 7×2 mm.

Each type thus breeds true when selfed, but seeds of one wild plant gave some broad-petalled and some cruciate-flowered offspring. The broad-petalled and cruciate forms grow intermingled in all three localities. At St. Valier they differ in several features besides the petals, as already pointed out. The broad-petalled strain from Charny differed from the cruciate strain of that locality only in petal width, whereas at St. Antoine the cruciate form had longer as well as narrower petals.

In 1934, reciprocal crosses were made between the broad-petalled and cruciate strains of this species from St. Valier. Culture 60.34 had midribs white or faintly tinged with pink, while in culture 61.35 the midribs were white and the latest rosette leaves were pinnatifid, with basal lobes reaching 7 mm. in length. x broad 18 plants were grown, and 3 plants from the reciprocal. There were no constant differences, the rosettes having faintly pink midribs, later leaves scarcely pinnatifid. In cruciate × broad the stems bore red papillae, which were absent in the reciprocal. Of the 18 plants from cruciate × broad, 10 had cruciate flowers, 6 had broad petals, and 2 had petals of intermediate shape or mixed character. The broad petals were ca. 17 \times 18 mm., cruciate petals were 12-14 \times 2-4 mm., while intermediate flowers had petals $15 \times 5-7$ mm. One of the intermediate plants had broad petals on the main stem, intermediate petals on one basal branch, cruciate petals on two other basal branches, and a mixture of petal types on the fourth. The other intermediate plant had both broad and intermediate petals on the main stem, two side branches with intermediate petals, and three with cruciate petals. This behaviour, with both parental types of petal appearing in different F₁ plants, and even in the same plant, as well as intermediate petals, is in accord with earlier studies by DE VRIES (1902) of the inheritance of the cruciate condition. reciprocal, broad × cruciate, from the same two parental plants, gave only three offspring, all with broad petals $11-12 \times 14$ mm.

One further cross was made, between two members of the cruciate strain from Charny (71.34 \times 47.33). This cross was made possible by the fact that many plants from the 1933 culture only flowered in 1934. The seed parent had cruciate and the pollen parent broad petals. It yielded 14 uniform plants having the bright red midribs of the Charny strain, 5 of which had cruciate flowers, 5 had broad petals, and 4 were intermediate. The broad petals were 13-14 mm. long. One of the plants had on 6 August broad petals on its main stem, cruciate on 4 basal branches, and broad on one basal branch. The same plants continued flowering and on 17 August had broad petals and one cruciate flower on the main stem, the side branches having some cruciate and some intermediate flowers. Some of the broad-petalled plants also showed later some intermediate flowers. No full explanation of these phenomena need be attempted at the present time.

The absence from all 17 of the cultures of O. biformiflora of plants having intermediate petals or a mixture of broad- and narrow-petalled flowers, indicates that natural crossing is rare, or that plants with intermediate or mixed petals are eliminated in nature, each type being stable. There appears to be no difference in size or vigour between plants of the cruciate or latipetalous types, so it appears improbable that hybrids with intermediate petals would be eliminated in nature. On the other hand, experiments to be described below indicate that once a cross is made a mixed and variable condition of the petals continues indefinitely in some of the offspring of later generations.

Cruciate petals furnish one of the most interesting and significant cases of BARTLETT (1914a), in a study of parallel mutations in wild *Oenothera* species. cruciate types, cites the following cruciate forms which are most reasonably interpretated as derived or descended from independent mutations: (1) O. cruciata NUTT. described from Massachusetts by Don in 1824, and also apparently found in Vermont; (2) O. biennis mut. cruciata DE V. = O. biennis var. leptomeres BARTL., a single plant found at Santpoort, Holland, in 1900; specimens were afterwards obtained from several other localities in Holland, and also from the Lunenburger Heide (Klebahn, 1914), and elsewhere in Germany, indicating that the cruciate form arises repeatedly from O. biennis;* (3) one branch with cruciate flowers in a culture of an undetermined species from Springfield, Missouri; (4) a form from Mobile, Alabama; (5) O. atrovirens Sh. and BARTL. from Hudson Falls, N.Y., near Lake George; (7) O. stenomeres BARTL. from Maryland, allied to O. gauroides HORNEM. from the same area, and practically cleistogamic; (8) O. stenopetala BICKN. from Nantucket Id., Massachusetts, related to O. Oakesiana (ROBB.) S. WATSON; (9) O. cleistantha Sh. and Bartl. (1915) from Long Island, N.Y., cultivated by SHULL; (10) O. Robinsonii BARTL. (1915) from Jaffrey, New Hampshire. In addition, specimens with cruciate petals in the Gray Herbarium are cited from Nova Scotia (Sable Island), Maine, Cumberland, New Hampshire, Vermont, the Adirondaks, and three localities in Massachusetts. The O. cruciata of Gruppenweise Artbildung (DE VRIES, 1913) is one of three cruciate forms which DE VRIES cultivated (1913, p. 58). One of these, from Jaffrey, N.H., was afterwards described as O. Robinsonii BARTL. The other two came from Hudson Falls, near Lake George, N.Y., via MacDougal and others (1905) (who described some of their characters under the name O. cruciata), and differed mainly in the thickness of the buds. with thicker buds DE VRIES (1913) used in his later experiments. He found it constant through several generations and used it in many crosses. He briefly characterized it as follows (1913, p. 58): small linear petals, very dense and generally short spike, very small leaves, dark red-brown in nearly all parts, numerous cauline branches, fruits short, young stems strongly nutating. This was described as O. atrovirens Sh. and Bartl. (Bartlett, 1913), the other from the same locality as O. venosa SH. and BARTL.

^{*} DE VRIES (1913, p. 299) afterwards obtained from it a dwarf mutation, O. biennis cruciata nanella, which came true from seed.

The present record shows that O. biformiflora occurs commonly in three localities on the south bank of the St. Lawrence in both the cruciate and the broad-petalled form. The large number of records of cruciate forms belonging to various species in eastern North America indicates that this is a mutation which occurs with a high rate of frequency and has arisen independently many times as parallel mutations from different species. Not only is the genus Oenothera prone to this mutation, but it has also been described in Epilobium (Stomps, 1913). From a single cruciate plant of E. hirsutum found wild in England, he showed by crossing that E. hirsutum cruciatum is a simple Mendelian recessive to the type, and that it segregates cleanly without intermediates. Oehlkers (1935) has recently repeated these crosses, using strains of E. hirsutum from three different parts of Germany, and confirming the results of Stomps. When the crosses were repeated on a larger scale, however, he began to obtain more or less defective, i.e., intermediate, petals.

DE VRIES (1902) originally described the variable behaviour of the petals in O. biennis cruciata varia, a strain which he regarded as having arisen in gardens through crosses between O. cruciata Nutt. and some other species in Europe. From crosses which he made between it and the three species he recognized as naturalized in Europe, namely, O. biennis, O. muricata, and O. Lamarckiana, DE VRIES concluded that it had been crossed with O. muricata. He devoted a section of "Die Mutationstheorie" (II, pp. 593–633) to the study of its hybrids. (This section is omitted from the English translation.) He called O. cruciata varia a Mittelrasse because of its continuous variability in petal width, but he failed to reach a decision whether this inconstancy had resulted from crossing or from mutation.

The O. cruciata of the Gruppenweise Artbildung (vide supra) agrees in many features with O. cruciata varia DE V., and hence probably with O. cruciata NUTT. It apparently differs, however, at least in having strongly bent stem tips.

Oehlkers (1930a, b, 1935) has made an extended study of the variation and inheritance of cruciate petals or sepalody in Oenothera. Only a limited number of the results can be referred to here. The forms used in his crosses included O. biennis cruciata (apetala) from Leiden Botanical Garden, which was constant, O. biennis cruciata sulfurea from Hanover, and O. Lamarckiana cruciata from Tübingen Botanical Garden, and O. biennis cruciata gigas from Stomps, which were inconstant. Crosses were made with broad-petalled strains of O. biennis, O. suaveolens, O. Lamarckiana and O. Hookeri. Among other things it was shown that when broad and cruciate flowers on the same plant are selfed there is a true somatic segregation, since the offspring follow in general the condition of the parent flower. Oehlkers used the length-breadth index as a measure of the condition of each petal. He concludes that the cruciata from O. Lamarckiana and from O. biennis are both in a labile condition, and postulates a series of *cruciata* genes of different strength, so that in O. Lamarckiana a state could be reached in which cruciate was dominant to broad petals. O. Lamk. × "weak" O. Lamk. cruc. gave 15 plants all with broad petals, while the "strong" cruciata produced in F₁ 4 plants with broad petals, 1 with cruciate, and 1 with strongly affected petals. This agrees with results for the

Quebec strains, mentioned above. The F_2 from selfing a strongly cruciate plant contained 27 cruciate and 6 normal, while the F_2 from a normal contained 20 normal, 2 cruciate, and 2 subcruciate. Back crosses were also made. The reciprocal cross Lamk. cruc. \times Lamk. gave 11 with normal, 2 with cruciate petals, and 2 with strongly affected petals. The conclusion is reached that both the velans and the gaudens complex of O. Lamarckiana contain a cruciata factor (cr_4 and cr_3 respectively), but the cr_4 is not strong enough to be dominant to Cr (broad petals). The tetraploid O. biennis gigas cruciata was also crossed with O. biennis gigas, O. biennis cruciata, O. biennis, and other forms, the analysis being in terms of the complexes, albicans and rubens, of O. biennis. O. biennis gigas cruciata \times biennis gigas and the reciprocal gave, in 9 offspring, every condition between purely cruciate and fully normal petals, the plants being otherwise uniform. Both the relative dominance of the cruciate condition and its variability were greater than in the diploid crosses.

It thus appears that many cr genes are present in the Oenothera germplasm, and if, for instance, the velans and gaudens complexes of O. Lamarckiana each contain such a factor, then the cruciate mutation may arise through crossing-over between the two complexes, in such fashion that the assemblage of cr genes overbalances the genes making for broad petals. Similarly, the phenotypic expression of the cruciate mutation may only be reached in other species when Cr genes already present are rearranged so that in the zygote they dominate the Cr genes. To determine whether this is an adequate interpretation of the various cruciate mutations and their inheritance requires still further investigations. The fact that there is generally no other difference between the cruciate and broad-petalled races of a particular species makes it difficult to believe that crossing-over of the ordinary type can be involved.

The occurrence of broad, narrow, and intermediate petals on the same plant, as well as in different plants of the F₁ in crosses between wide and narrow petals, is similar to the hereditary behaviour as regards longer and shorter petals in certain Oenothera crosses (Gates 1917, 1923). Hybrids of O. biennis \times rubricalyx and its reciprocal were made, O. biennis having petals ca. 20 mm. and O. rubricalyx ca. 40 mm. in length. The F_1 were uniform, but they were few in number and larger numbers might have shown variation in flower-size. In F₂-F₄, however, three forms of segregation took place; (1) genetic segregation of plants having longer or shorter mean petal-length and various ranges of variability in this feature. That the segregation was genetic was shown by breeding from large-flowered and small-flowered segregates; (2) segregation between larger and smaller flowers on the same plant, some at least of such plants having a bimodal curve of variability; (3) somatic segregation between longer and shorter petals in the same flower. These three types of segregation also occur as regards the cruciate gene, where the results of Oehlkers indicate that Cr genes are cumulative in their effects. Other results, mostly unpublished, indicate that small-flowered species of Oenothera have several dominant cumulative genes for short petals, some of which produce a larger decrement in the petals than others. It is therefore probable that petal-length and petal-breadth follow the same rather peculiar laws of inheritance, peculiar in combining genetic with various degrees of somatic segregation.

The present species, O. biformiflora, appears to be rather nearly related to O. cruciata Nutt., which was grown and described by Don in 1824 from Massachusetts, and has probably been grown in European gardens ever since. The original very general description by Don, a photograph of the type specimen at Geneva, and a description of an apparently identical specimen in Herb. Phila. Acad. by Bartlett (1914a) indicate similarities to O. biformiflora in stem colour and pubescence, in the slender hypanthia, and in bud-size, and perhaps shape. The leaves of O. biformiflora are, however, markedly wider, approaching the ovate condition, and the sepal tips are terminal and appressed, whereas in O. cruciata, according to BARTLETT, they are "distinctly infra-terminal and well separated in the bud". The O. cruciata varia of DE VRIES (1902) has very narrow leaves, as shown by his fig. 136, p. 603. This may have been accentuated by crossing with O. muricata as DE VRIES suggests has taken place, but O. cruciata varia could not have derived the brown-red colour on the stem-leaves, sepals, and fruits from this source. characters, together with its short and slender stem, small narrow leaves, small flowers (petals 12 × 2-4 mm.), and fruits longer and thinner than O. biennis, probably belonged to the original O. cruciata Nutt. Since O. biformiflora has greenish or yellowish buds and green fruits of good size, these are additional distinctions from the brownred sepals and (small) fruits of O. cruciata varia and hence apparently of O. cruciata NUTT. How close the relationship between the latter and O. biformiflora may be can only be determined by obtaining O. cruciata afresh from Massachusetts, or Vermont. At present it appears preferable to regard them as distinct, especially as O. biformiflora is the only species yet known to occur wild with both broad-petalled and cruciate plants intermingled in the same localities. Since O. stenomeres BARTL. is allied to O. gauroides HORNEM., and O. stenopetala BICKN. is similarly related to O. Oakesiana S. Wats., each pair has probably diverged from a common ancestor in which the cruciate mutation appeared, followed by an accumulation of other mutational differences under conditions of inbreeding combined with physiological or geographical isolation.

O. laevigata BARTL. var. similis n. var.

From seeds collected at St. Valier, at the mouth of the River Boyer, on the south shore of the St. Lawrence, Quebec, on 31 September, 1932, by Messrs. VICTORIN and ROUSSEAU and on 2 October, 1932, by myself. The plant which supplied the seeds for culture 28.33 was noted as tall with bunched fruits, and was preserved by Professor VICTORIN as specimen A in his herbarium. The parent plant of culture 29.33 (specimen B) resembled O. angustissima in its long subterminal, spreading sepal tips, red inside, the stem top being dark red with much red on the bracts below. The parent plant of culture 31 was observed to have much red on the under surface of the bracts and fruits with a rather broad attachment. In 1933 the cultures put out long side-shoots, many of which flowered. The plants grown in 1934 from

selfed seeds produced a few flowering side-shoots but wintered over as rosettes and formed tall flowering stems in 1935. An account of the extensive and remarkable *Oenothera* colonies at St. Valier will be found elsewhere in this paper. The cultures of this variety grown are shown in Table XVII.

Table XVII				
29 (50)	31 (50)	34 (50)	4	

1933 28 (100 plants) 29 (50) 31 (50) 34 (50) 44 (10) 45 (50) 1934 51 (46) 52 (45) 54 (48) 57 (49)

The description here given is fuller than that of Bartlett (1914b).

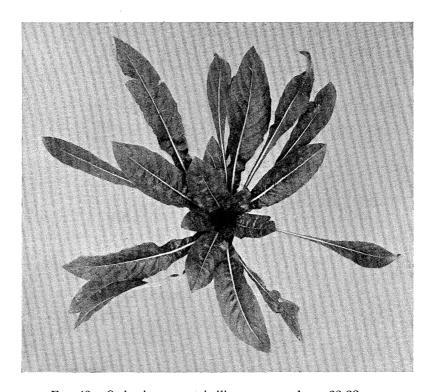


Fig. 49—O. laevigata var. similis, rosette, culture 28.33.

Description—Rosette leaves dull green, ca. 16-20, oblanceolate to lanceolate' apex acute or shortly cuspidate, reaching 24-39 cm. × 55-70 mm. (petiole 3-5 cm. long), flattish, with sparse liver-coloured spots on a few leaves of each rosette, crinkled only when young, young leaves conspicuously undulate below and very pale reddish at base, margin subentire or repand-denticulate with obscure reddish teeth; midrib white; upper surface finely sparsely appressed-pubescent and minutely puberulous; lower surface glabrescent to the naked eye, very sparsely appressed-pubescent and very minutely puberulous (fig. 49); rosettes very persistent, forming very long, decumbent, and widely ascending side branches or a central stem generally leaning from the base and strongly bent at the tip.

Stem tall, 138–143 cm., very brittle, tip strongly bent, very leafy, with numerous ascending cauline branches, very strongly ribbed, pale green and deep peach bloom red, rather sparsely suberect or ascending-hirsute from small greenish or reddish papillae, some in the form of red patches with roughened surface, otherwise practically glabrous. Stem leaves deflexed or arcuate-deflexed, elliptic-lanceolate or elliptic-oblanceolate, somewhat crinkled, margin not wavy, denticulate, sometimes dentate below with 1–2 teeth, 12–17 cm. \times 24–50 mm.; upper surface \pm flecked and margined with red-purple, glabrescent to the naked eye, very finely subappressed-puberulous and scurfy-puberulent, midrib white; lower surface glabrescent, sparsely suberect-puberulous.

Inflorescence dense, not elongating much in fruit; lower bracts spreading, leafy, ca. 5-7 cm. × 15-22 mm.; upper bracts arcuate-spreading, narrowly oblonglanceolate, ca. 1-2 cm. × 24-40 mm., red at base, terminal bracts very small, red on lower surface. Apex of inflorescence bent, narrow, comose, usually tinged with red. Ovary 7-13 \times 2 mm., green or with small red protuberances without a hair, glabrous or very sparsely spreading glandular pubescent in upper half; hypanthium $27-37 \times$ 1.5-2 mm., pale green, glabrous; bud-cone $11-16 \times 4-5$ mm., sharply quadrangular, greenish-yellow, or ± reddish, especially on shoulder and base, slightly tapering, sepal tips rigid, erect, slender, subterminal, hooded within, scarcely divergent, 3-4 mm., green with reddish tips and a touch of red at the base, not densely but distinctly ascending pubescent and puberulous. Petals $10-15 \times 11-16$ mm., truncate or shallowly widely emarginate, opening to 45°, slightly overlapping. ca. 7 mm., anthers 5-6 mm. Stigma lobes 1-4 mm., surrounded by anthers in bud; in anthesis the lobes become slightly divergent, but owing to elongation of the hypanthium, they are drawn down nearly or quite into the mouth of the tube although occasionally they may be as much as 6 mm. above. Fruits green, glabrous, tapering, 36×7 mm., \pm curved, according to position of stem (fig. 50). Plants from the three cultures, 28.33, 29.33, and 31.33, were found by Mr. FORD to have a ring of 14 chromosomes in each case.

Diagnosis—Folia radicalia surda viridia, oblanceolata ad lanceolata, acuta aut breviter cuspidata, subplana, sparse purpureomaculata; costa alba; dentes marginales rubescentes; rosulae valde permanentes instructae ramis radicalibus longis aut caule medio declinante, apex valde flexus. Caulis et rami radicales foliosi cum ramis caulinis ascendentibus, pallidis viridibus et atrorubris. Folia caulina ellipticolanceolata, marmorata et marginata purpura, oculis nudis subglabra. Inflorescentia densa in fructus, apex angustus, comosus, rubrotinctus. Apices sepalorum rigidi, erecto tenuiter, subterminales. Petala 10–15 mm. longa, stigmata 1–4 mm. longa, ad aut prope os hypanthii in floribus apertis.

In culture 29.33 the petals reached 17×20 mm., and remained slightly larger in the F_2 . The position of the stigma varies greatly in this species. In one plant of culture 34.33 the stigma lobes in all the flowers were "drawn down" some distance into the hypanthium tube by its growth, the lobes being only 1 mm. in length. They

were already pollinated, as the anthers surround the stigma in the bud and are ruptured the day before the flower opens. In some plants of this culture the stigmas reached above the top of the anthers in bud and were just above the mouth of the hypanthium in flower. The hypanthium increases in length during the intervening period, from ca. 26 mm. to 30–34 mm. The stigmas in the open flower may be as much as one-third of the way down the length of the hypanthium tube, and they may even be in the tube at the bud stage, so that self-pollination cannot take place and cross-pollination is also made almost impossible.

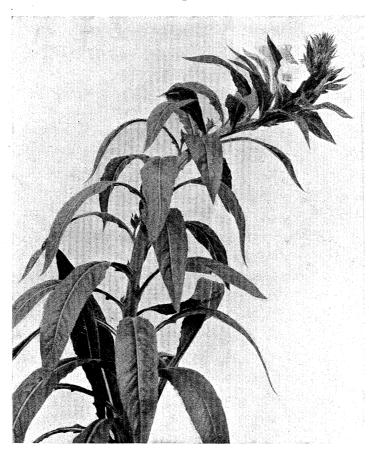


Fig. 50—O. laevigata var. similis, in flower, culture 28.33.

Bartlett (1914b) described O. laevigata from White Sulphur Springs, W. Virginia, having the striking feature that the rapid elongation of the hypanthium pulls the stigma down into its mouth. He states that allies of this species are widespread in the Alleghanian region. Var. similis is evidently a still more northerly representative of the same species, occurring on the St. Lawrence. These strands of descent, as it were, running north and south, probably represent a line of migration northwards following the retreat of the ice. On the Pacific coast a similar line representing O. Hookeri Torr. and Gray, and its descendants, can be traced from California into British Columbia.

Var. similis agrees with O. laevigata especially (1) in being glabrescent, and (2) in having the stigma drawn down into the hypanthium in anthesis, (3) quadrangular buds. There are, however, a number of differences in var. similis, which has (1) wider, dull green rosette leaves with sparse liver-coloured spots and white midribs, (2) somewhat smaller flowers, (3) inflorescence dense, (4) the drawing down of the stigma appears to be more extreme. It may be that a fuller comparison of these forms will result in raising the variety to specific rank, but it appears preferable to recognize the close relationship by retaining the St. Lawrence form as a variety.

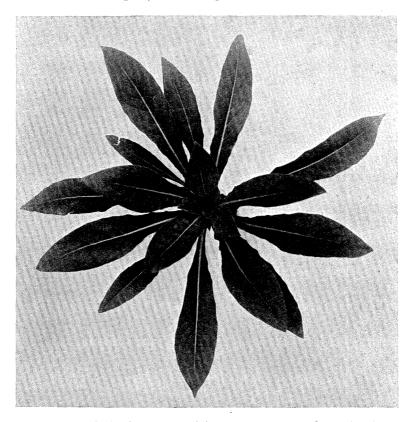


Fig. 51—O. laevigata var. rubripunctata, rosette, culture 53.34.

O. laevigata BARTL. var. rubripunctata n. var.

From seeds collected at St. Valier, Quebec, on 30 September, 1932, by Professor Victoria and M. Rousseau, and by myself on 2 October, 1932, from the same colony. The wild plant from which seeds for culture 30.33 were taken showed resemblances to O. ammophiloides, having a leaning stem, large fruits bending upwards, and red blotches. It was pressed by Professor Victoria as specimen E. The cultures grown are shown in Table XVIII.

TABLE XVIII					
1933	30 (50 plants)	32 (50)	35 (50)		
1934	53 (49)	1 55 (50)	58 (30)		

This strain is nearly related to O. laevigata var. similis from the same locality, but differs markedly and constantly in several features. It also shows marked similarity to O. ammophiloides var. laurensis from Port Elgin, and Cape Tormentine, N.B., especially in the leaning or strongly bent stems and the hairy buds with numerous red papillae on the exposed side of the sepals. It differs from O. laevigata var. similis in (1) smaller, narrower, smooth rosette leaves, duller green, with no red



Fig. 52—O. laevigata var. rubripunctata, in flower, culture 30.33.

spots (fig. 51), reaching 29 cm. \times 42 mm., (2) ovary covered with red papillae bearing long hairs, (3) bud-cone studded with conspicuous red papillae where exposed to light, (4) stigmas from just above to well above hypanthium, less variable in position, (5) fruits large, 40×10 mm., tapering, straight or curved at the tip (fig. 52). A plant of culture 30.33 was found by Mr. Ford to have a ring of 14 chromosomes.

This strain shows remarkable relationships to the glabrate O. laevigata from W. Virginia, on the one hand, and to the hairy budded O. ammophiloides from Nova

Scotia on the other. It should perhaps be raised to specific rank, but for its striking resemblances in habit and foliage to O. laevigata var. similis.

Diagnosis—A varietate simili sic differt: folia radicalia angustiora, surdiora viridia, non purpureo-maculata. Ovarium multirubropapillatum, sepala etiam rubropunctata ubi lucem accipiunt, stigmata supra hypanthium; fructus magni, 40 mm. longi, 10 mm. lata ad basim, attenuati.

Differs from O. laevigata and var. similis in (1) narrower rosette leaves, duller

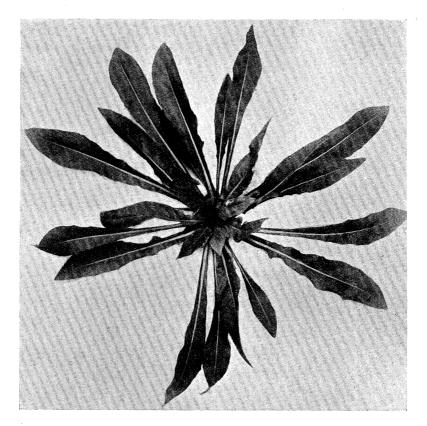
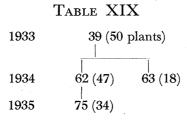


Fig. 53—O. laevigata between var. similis and var. rubripunctata, rosette, culture 62.34.

green, with no red spots, (2) ovary red punctate, (3) bud cone red punctate where exposed, (4) stigmas above hypanthium.

The cultures shown in Table XIX represent a strain from St. Valier which combines features of var. *similis* and var. *rubripunctata*.



It may represent a hybrid between them. The rosettes were, however, narrower-leaved than either (fig. 53), they were less grey-green than var. rubripunctata, and nearly glabrous like var. similis. The stem tips were strongly bent and bore a few red papillae (fig. 54); the buds had many red papillae, as in rubripunctata, petals 18×24 mm., hypanthium 41×2.5 mm., arcuate, stigma above the tube in anthesis. This condition was, however, not constant, because plant I.1 (the parent of culture 62.34) had so short a style that in certain open flowers the stigma reached only half-way up the hypanthium tube, the stigma being very tiny. In late flowers of



Fig. 54—O. laevigata between var. similis and var. rubripunctata, in flower, culture 62.34.

this plant the style appears to have aborted and dried up. Cultures 62.34 and 63.34, however, showed no differences at all, both breeding true to the conditions above described for this strain, and retaining certain features of both varieties. Mr. C. E. Ford examined a plant in culture 39.33 and found a ring of 14 chromosomes.

O. Victorini Gates and Catcheside

This species, described from St. Hubert near Montreal (1933), is nearly related to O. pycnocarpa Atk. and Bartl. which is widespread in New York State. O. Victorini is found roughly from the St. Lawrence below Quebec to Montreal and Toronto.

Several varieties of both species are here described. The two species differ mainly as shown in Table XX.

TABLE XX

	O. pycnocarpa	O. Victorini
Rosette leaves	Smooth or ± crinkled, oblanceolate	Smooth, elliptical.
Upper rosette leaves	Deeply pinnatifid	Not pinnatifid.
Stem	Red papillae on stem	Green papillae on stem.
Petals	16–20 mm.	26 imes 30 mm.
Fruits	25 – 33×5 mm.	Reaching 45×7 mm.

O. Victorini may therefore be looked upon as a more northern ally of O. pycnocarpa, having differences in leaf-shape, especially in the absence of pinnatifid lobing, absence of red papillae from the stem, larger flowers and fruits. They agree in general habit, and in having petals which are firm and resistant to wilting, but O. pycnocarpa is generally a more luxuriant plant with more basal branches. Both species cover a wide area and show several varieties. The following three varieties of O. Victorini are here described.

In 1932 and the following year cultures were grown from seeds collected at West Wittering, Sussex, where an *Oenothera* is naturalized. They proved to be the same as *O. Victorini*, differing from the type cultures only in having a somewhat shorter stem bearing red papillae. How the introduction took place is quite unknown, but it was presumably unintentional, and probably from somewhere in the area between Montreal and Quebec.

O. Victorini var. parviflora n. var.

Seeds sent by Professor Marie-Victorian were collected on 12 October, 1931, from four different plants among a colony growing on dry gravelly or sandy soil on waste ground at St. Anne, Kamouraska Co., Quebec. The resulting cultures (Table XXI) were uniform, except for slight variation in petal length. The cultures from St. Antoine les Fonds differ in having slightly larger petals (13–14 × 12 mm.).

TABLE XXI

		St. Anne,	Kam. Co.		St. Antoine
1933	56 (40 plants)	57 (50)	58 (22)	59 (50)	49 (13)
1934	$\frac{80}{1}$ (5)	81 (3)	82 (11)	83 (4)	73 (4)
1935	88 (6)	89 (11)	90 (6)		82 (8)

Description—Rosette leaves pale green, elliptic, obovate-elliptic or oblanceolate, apex shortly cuspidate or acute, reaching 24 cm. × 55 mm. (petiole 4–5 cm.), flattish and smooth, midrib whitish with pinkish tinge, margin repand-dentate or denticulate below, repand-denticulate above, teeth green, both surfaces finely rather sparsely ± erect-pubescent, also densely minutely crispulous-appressed-pubescent on midrib, leaves with liver-coloured blotches.

Stem erect, ca. 83 cm., basal branches decumbent at base, then widely arcuate-ascending, shorter than central stem. Stem rather thickly ribbed throughout, pale green, sparsely patulous-hirsute with white papillae, arcuate-ascending-pubescent and subappressed-crispate-puberulous. Stem leaves deflexed or uppermost spreading, elliptic-lanceolate (uppermost lanceolate), $11-15\cdot 5$ cm. \times 32–49 mm., flattish, not wavy or crinkled, margin repand-dentate below, repand-denticulate above, teeth usually green, midrib nearly white but faintly pinkish-mauve in lower half, \pm appressed-puberulous and with some longer hairs below. Both surfaces rather sparsely suberect-pubescent. Lower bracts arcuate-spreading, concave, 4–5 cm. \times 12–17 mm. Upper bracts arcuate-spreading, or patulous-ascending with upcurved tips, 1·5–2 cm. \times 3–7 mm. Apex of inflorescence narrow (ca. 1 cm.), flat, not comose, easily overtopped by upper developed buds and flowers, spike dense.

Ovary 9–11 \times 2·5–3 mm., sparsely patulous-hirsute from colourless papillae, and densely spreading glandular-pubescent. Hypanthium 20–26 \times 1·7–2·2 mm., very sparsely patulous-ascending-hirsute and rather sparsely glandular-pubescent. Bud-cone \pm cylindric, pale green, 11 \times 5 mm., extremely sparsely patulous-hirsute from colourless papillae and rather densely spreading glandular-pubescent. Sepal tips ca. 2 mm., slightly divergent and reddish. Petals 7–11 \times 6–10 mm., truncate and irregularly toothed, opening to 45°, not overlapping. Filaments 7–9 mm., anthers 3·5–5 mm., overtopping stigmas in bud, base of stigma ca. 3 mm. above hypanthium, stigma lobes 4–6 mm., widely divergent, soon arcuate-divaricate.

Diagnosis—A specie sic differt: Flores minores, petala 7-14 mm. longa.

This variety differs from the species mainly in having smaller flowers (petals 7–14 mm. instead of 26 mm.). There is also evidence of minor differences in flower-size within this variety, in cultures 80.34 to 83.34. Another collection of seeds of O. Victorini from the original locality, St. Hubert near Montreal, by Miss Marcelle Sauvreau on 19 September, 1931, differs from the type (see Gates, 1933, p. 182) in having petals of intermediate size (11–14 mm. long), as shown by cultures 55.33, 79.34, and 87.35. The variety parviflora therefore exists with the type at St. Hubert. From much statistical work it is shown that in some species of Oenothera a series of genes for petal-size are present, but the range in O. Victorini (7–26 mm.) is exceptionally wide. Observations show that in O. novae-scotiae there is a large-flowered segregate, so that the range is 15–26 mm. The St. Antoine strain agrees with O. Victorini in having no red papillae on the stem, but it differs in having white midribs.

O. Victorini var. intermedia n. var.

Three lots of seeds have been collected which belong to this variety: (1) from St. Valier on 30 September, 1932, by Professor Victoria and M. Rousseau, (2) from the railway embankment near Ste. Anne de Bellevue, Jacques Cartier Co., Que., 5 November, 1933, by Mr. W. G. Dore, received through the courtesy of Dr. R. Ingalls, (3) from Cap Tourmente, Montmorency Co., Que., on 12 October, 1933,

by Messrs F. Michel and M. L. Chollet. The cultures grown are shown in Table XXII.

TABLE XXII

	St. Valier	St	e. Anne de	Bellevue		Cap T	ourmente
1933	43 (50 plants)						
1934	66 (7)	4 (5)	<u>5</u> (97)	6 (9	98)	9 (7)	10 (4)
1935	77 (27)		40 (9)	41 (17)	42 (26)		45 (21)

A plant culture 43.33, examined by Mr. C. E. FORD, showed a ring of 14 chromosomes.

This variety of O. Victorini from both shores of the St. Lawrence is intermediate in flower-size between the species and its var. parviflora. The rosette leaves agree with var. parviflora, but the stem leaves are narrower (8.5–18 cm. × 17–34 mm.). The petals are 15–19 × 11–17 mm., the upper half spreading flat in anthesis (see fig. 55). The plants continue flowering very late, producing numerous flowers from cauline branches at the end of the season. The Cap Tourmente strain differs in certain particulars, having narrower rosette leaves (25–40 mm. wide) with finely appressed pubescence. The petals remain stiffly erect, but the plants have the same habit of producing numerous late flowers from cauline branches. In culture 45.35 the midribs ranged from white to pink and all the plants except four had red papillae on their stem, but neither character could be sharply scored.

Diagnosis—A specie sic differt: folia radicalia et caulina angustiora, petala media longitudine, 15–19 mm. longa, diutissime florescentia in ramis caulinis.

O. Victorini var. undulata n. var.

From seeds collected on York Mills Road, near Toronto, Ont., 7 October, 1932. While belonging to *O. Victorini* they form a well-marked variety with small flowers, but culture 63.33 and its descendants differ from var. *parviflora* in other characters. The cultures grown and studied are shown in Table XXIII.

	TABLE XXIII	
1933	62 (100 plants)	63 (50)
1934		85 (13)
1935		91 (16)

Agrees with the St. Anne (Kamouraska) cultures (i.e., var. parviflora) in having small flowers (petals 10–12 mm.) but differs in having leaves with white midribs, \pm crinkled, margin markedly undulate, lower stem leaves broader (12–21 cm. \times

25–60 mm.), deeply pinnatifid at base, margin serrate. The leaves, buds, and stems are also less sparsely pubescent and the teeth green or reddish. The stems are taller (85–95 cm.) and the bracts somewhat smaller. The fruits are short and stout in this variety, 24×7 mm., as against 45×7 mm. in the species. This description applies especially to culture 63.33 and its descendants. Culture 62.33 differed in being almost devoid of the crinkling, undulation, and serration of foliage found in var. parviflora. This Eastern Ontario form stands rather apart from the rest of the



Fig. 55—O. Victorini var. intermedia, in flower, culture 5.34.

species and its relationships will be clearer when other *Oenotheras* from this region have been studied. A ring of 14 chromosomes was found by Mr. C. E. Ford in a plant from culture 63.33.

Diagnosis—A specie sic differt: folia, caules et sepala minus sparse pubescentia; costa alba; folia ± bullata, margo valde undulata, folia caulina inferiora latiora, valde pinnatifida ad basim; caules altiores, petala 10–12 mm. longa, fractus breves et robusti.

O. angustissima var. quebecensis n. var.

From seeds collected at Cap Tourmente, Montmorency Co., Quebec, on the north shore of the St. Lawrence on 12 October, 1933, by Messrs. F. Michel and M. L. Chollet and sent by Professor Marie-Victoria. The following cultures were grown:—

1934 <u>8</u> (42 plants) 11 .(84) 1935 44 (28)

O. angustissima was described from Ithaca, N.Y. (GATES, 1913). It stands apart from other species in eastern North America. It has been shown (GATES and

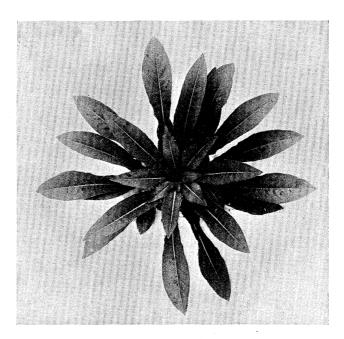


Fig. 56—O. angustissima var. quebecensis, rosette, culture 11.34.

CATCHESIDE, 1932) to be composed of two distinct complexes, which were called rubrans and divergens. Its full formula is divergens (rubrans) \$\varphi\$. divergens \$\varphi\$, only one pollen complex being functional and the large majority of the megaspores carrying the divergens complex owing, apparently, to its greater strength in competition with rubrans. These two complexes also differ in flower-size, rubrans carrying genes for larger flowers than divergens; the latter also has a factor for bent stem tip—a condition which is present phenotypically in var. quebecensis.

Marie-Victorin has seen my cultures, and in his "Flore Laurentienne" (1935) recognizes O. angustissima as a constituent of the Quebec flora. The present strain from north of the St. Lawrence represents a well-marked variety, but it could belong to no other species and it extends the distribution of O. angustissima to a distance of some 400 miles from the originally known locality. It agrees with the

species in all its main characters, being glabrate, with deep red stems and midribs, stem tips nutating, narrow leaves, and markedly subterminal sepal tips. It differs constantly, however, in having (1) wider rosette leaves (3–4 cm. against 25 mm.) and stem leaves (9–16 cm. \times 20–30 mm. against 25 cm. \times 15 mm.), (2) numerous small liver-coloured blotches on the leaves (fig. 56), (3) sepals pale yellow with faint red streaks, (4) ovary and hypanthium becoming red on exposed side, (5) sepals



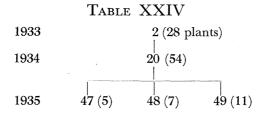
Fig. 57—O. angustissima var. quebecensis, in flower, culture 8.34.

bearing many long hairs from colourless papillae, (6) stigma lobes remaining appressed, (7) stem tip slightly bent, (8) fruits very tapering, reaching 40×7 mm. (fig. 57).

Diagnosis—A specie sic differt: folia latiora cum multis parvis purpureis maculisi sepala pallida flava, infirme rubrolineata; ovarium hypanthiumque rubrum ub, lucem accipiunt, sepala multas longas pilas de pellucidis papillis ferentia; fructus admodum attenuati.

O. niagarensis n. sp.

From seeds collected in the Niagara Gorge, on the American side, 28 August, 1932.



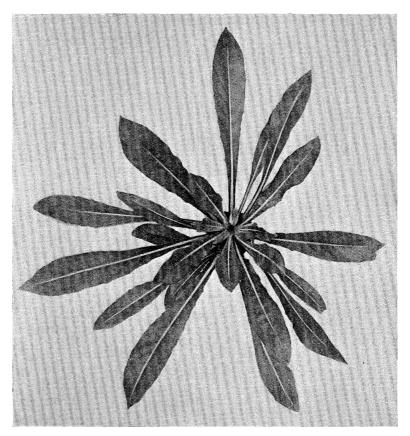


Fig. 58—O. niagarensis, rosette, culture 47.35.

Description—Rosette leaves dull, somewhat greyish-green, smooth, rather narrowly oblanceolate, apex acute to shortly cuspidate, reaching $25 \text{ cm.} \times 30\text{--}40 \text{ mm.}$ (petiole 6–8 cm.)., margin repand-dentate to subpinnatifid below, repand-denticulate above, midrib pink or white, both surfaces very finely appressed-pubescent. The young rosette leaves are margined with pink and also have diffuse pale red near the base, making the heart of the rosette brownish red (fig. 58).

Stem ca. 76-94 cm., stout, strongly ribbed, the terminal 4-10 cm. bent horizontal, stem pinkish at base, green above (no red papillae) or with tinges of pink and widely scattered small red papillae. Ring of basal branches, long-decumbent at base

then widely patulous-ascending, some exceeding the central stem; short cauline branches from the axil of nearly every leaf, widely ascending. Stem sparsely ascending or subappressed hirsute and densely, minutely appressed crispulous-puberulous. Stem leaves mostly deflexed, some of upper spreading, narrowly elliptic-lanceolate, somewhat greyish-green, acute, tips red, reaching 18 cm \times 33 mm., short petiole decurrent as ridge on stem, leaf margin scattered repanddentate, denticulate near apex, teeth reddish or green; finely, sparsely subappressed



Fig. 59—O. niagarensis, in flower, culture 47.35.

puberulous on both surfaces, base of young leaves tinged with red above. Midrib white, with some long patulous hairs below (a temporary touch of pale red at base of petiole on each side of midrib). Upper bracts heliotropic-spreading on bent apex, red-tipped, apex recurved, 2–3 cm. long (fig. 59).

Inflorescence lax, with long lower internodes, apex convex, very comose, innermost bracts pink with green tips, much longer than upper fully developed buds. Many of the buds drop when very young. Ovary $10-12 \text{ mm.} \times 2.5 \text{ mm.}$, steeply ascending

or subappressed short hirsute with small, mostly green papillae, and subappressed arcuate-pubescent. Hypanthium 23–30 mm. \times 1·5–2 mm., shortly ascending-hirsute and subappressed crispulous-puberulous, reddish on exposed side. Bud cone yellowish, sometimes with streaks of red, squarish, conspicuously attenuate, 12–14 mm. \times 4·5 mm., \pm ascending-hirsute and shortly ascending-arcuate-pubescent. Sepal tips very pointed, 3–4 mm. long, appressed, or spreading from base, green or pinkish in upper half. Petals 9–13 \times 10–12 mm., truncate or rather conspicuously widely emarginate, opening to 45°, with narrow spaces between, at cuneate base. Filaments 7–8 mm. long, anthers 4·5–5 mm. long. Stigma lobes 7–8 mm. long, base ca. 5 mm. above hypanthium, lobes widely separate from the first, reaching 3–4 mm. above anthers. Fruits green, short, and strongly tapering to slender apex, ca. 21 \times 6 mm., frequently somewhat curved, bearing scattered hairs without papillae.

Diagnosis—Folia radicalia surda aliquantum canoviridia, plana, aliquantum anguste oblanceolata, acuta aut breviter cuspidata, costa rubicunda ad alba, folia radicalia nova margine rubicundo, media rosula rubrofusca. Caulis robustus, apex horizontaliter flectens, viridi- et rubicundo-tinctus, non rubro-tuberculatus, rami caulini de axilla omnium foliorum. Bractae superiores extendentes, in apice flexo, rubro acumine apex recurvatus. Inflorescentia laxa, apex convexus, comosissimus; apices sepalorum 3–4 mm. longi, admodum acuti; appressi vel divergentes de basi; petala circa 9–13 mm. longa. Fructus breves, valde attenuati.

This species is clearly related to O. eriensis, with which it agrees in having narrow grey-green foliage, bent stem tips, in flower-size, and in dropping its buds. It differs constantly, however, in having (1) wider leaves, bearing red pigment when young, (2) a well-formed rosette, (3) a stouter stem straight except at tip, whereas O. eriensis has a more slender stem more or less irregularly bent, as though the gravitational response was variable. O. niagarensis has the habit of O. ammophiloides and the foliage is similar, but the midribs may be white or pink (white in O. ammophiloides). It differs also in having no red papillae on the stem, much smaller flowers, and much less hairy fruits. It has been constant in cultures. The touch of red which appears on the stem leaves at the base of the petiole on each side of the midrib below, completely disappears later. I classify this as an evanescent character. It appears regularly but temporarily on each leaf, and is therefore not a fluctuation but has a genetic basis.

O. repandodentata n. sp.

From seeds collected in the sandy bank on the north shore of Lake Erie, at Colchester, Essex Co., Ont., on 9 October, 1932. This was the original locality for O. eriensis (see Gates, 1927, 1928), and on account of the narrow grey-green leaves it was supposed, when collected, to be the same species, although it showed certain differences. The original plant from which seeds were collected was observed, however, to have strongly denticulate bracts, a compact inflorescence, red stripes

on the hypanthium and sepals, and small, narrow, notched petals with wide spaces between them. These are all distinctions from *O. eriensis*. The new species has bred perfectly true for three generations, as shown by the following cultures:

Description—Rosette leaves 14-18, "mat" pale greyish-green, narrowly oblance-olate or elliptic-oblanceolate, apex acute, reaching $16-19 \text{ cm.} \times 15-25 \text{ mm.}$ (petiole

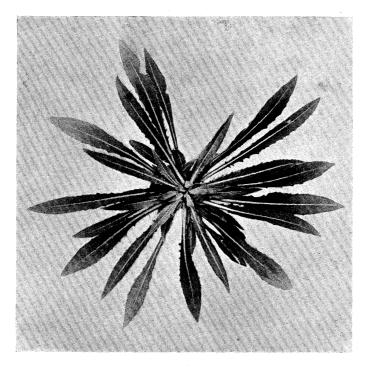


Fig. 60—O. repandodentata, rosette, culture 94.34.

5-5.5 cm.), flattish, without crinkling or undulation, margin rather finely and sparsely repand-dentate below, repand-denticulate above, teeth usually red, midrib faintly pinkish-mauve, both surfaces finely rather sparsely appressed-pubescent (fig. 60).

Stem ca. 78 cm., erect when growing or slightly bent at extreme tip, basal branches none or (usually) several slightly decumbent, then steeply ascending, shorter than central stem, bent at tip, many cauline branches, long, steeply ascending, \pm bent at tip (fig. 61). Stem strongly and thickly ribbed above, a beautiful deep peachbloom pink-mauve, except upper third which is greenish; sparsely patulous or ascending-subappressed hirsute from red papillae, and densely minutely appressed crispulous-puberulous; collar green or pink. Stem leaves arcuate-spreading or

lower arcuate-deflexed, elliptic-lanceolate, acute, red tips, convex, not wavy; margin regularly repand-dentate throughout, repand-denticulate only near apex, teeth green or reddish; size ca. 12 cm. \times 21–27 mm., midrib faintly pinkish-mauve in lower half and densely appressed-crispulous-puberulous above, also with some longer patulous hairs below, leaf surface subappressed-pubescent above, rather sparsely below. Lower bracts spreading or patulous-ascending, concave and toothed like leaves, lanceolate, 9–10 cm. \times ca. 25 mm. Upper bracts arcuate-patulous, crowded, 2–2·5 cm. long, uppermost 5 mm. or less in width. Apex of



Fig. 61—O. repandodentata, habit, culture 70.33.

inflorescence depressed, very comose, easily surpassing highest developed bud-cones. Spike with long internodes, not dense, few-flowered (fig. 62).

Ovary $10\text{--}13 \times 2\text{--}5\text{--}3$ mm., copiously ascending-hirsute from dark red or colourless papillae and densely crispulous \pm appressed-pubescent. Hypanthium $26\text{--}31 \times 2$ mm., indumentum as on ovary, but no red papillae and also sparsely spreading-glandular-pubescent. Bud-cone greyish-yellow, squarish, $12\text{--}15 \times 5$ mm., patulous or ascending sparsely short-hirsute from reddish or colourless papillae, and densely subappressed pubescent. Sepal tips 2--4 mm. long, slender, green or reddish at apex, \pm appressed. Petals opening to 45° , $14\text{--}18 \times 11\text{--}14$ mm., not at all

or slightly overlapping, conspicuously deeply emarginate (sinus 1.5–2 mm.). Filaments 10 mm., anthers ca. 6 mm., nearly reaching top of stigmas in bud, stigma lobes 4–9 mm. long, slightly or widely separating. Fruits very stout, 32×9 mm., tapering, green, few long and short hairs.

Diagnosis—Folia radicalia surda pallida canoviridia, anguste oblanceolata vel elliptico-oblanceolata, acuta, plana, margine repando-dentata ad basim. Caulis

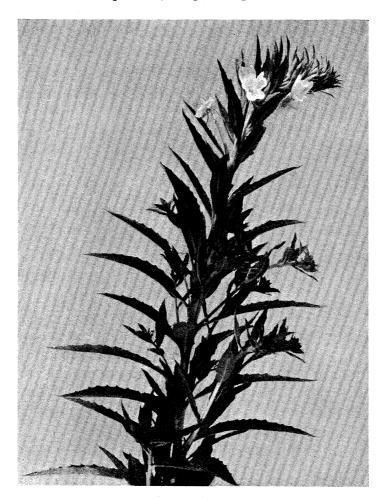


Fig. 62—O. repandodentata, in flower, culture 94.34.

erectus vel levissime declinatus, rubropapillatus, rubicundo-purpureus, triens supra viridescens, rami valde ascendentes. Folia caulina elliptico-lanceolata, acuta, apicibus rubris, tota margine constanter repando-dentata. Inflorescentia non densa, paucis floribus, apex depressus, multum comosus. Petala 14–18 mm. longa, valde emarginata. Fructus robustissimi et attenuati.

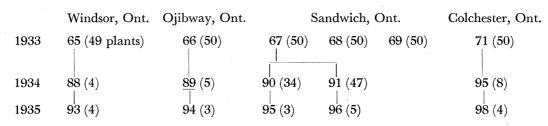
This species, while clearly related to *O. eriensis*, differs markedly in nearly all its characters. The most prominent differences are (1) rosette less evanescent, stem pinkish-mauve, nearly erect, (2) leaves wider, with faintly pinkish midrib, more

ascending and longer, margin regularly repand-dentate, (3) petals larger, with deep sinus. O. eriensis has not only bent tips but an irregularly bent stem. In O. repandodentata the stem is always erect except the extreme tip, and in some stages of growth or under some conditions, it may be entirely erect.

O. deflexa n. sp.

This very distinct species is common on waste ground in the vicinity of Windsor, Ontario. Seeds were collected from six localities on 9 October, 1932, from which many cultures have been derived. They show numerous minor but marked differences, which are constant in the cultures and will be described below. The cultures with their place of origin are as follows, the specific description being taken from culture 89.34. The plant from which these seeds were taken was on the grounds of the Canada Steel Corporation, and the following characters were noted on adjacent plants: rosettes dark green, leaves crinkled, stems red, flowers small, fruits smooth.

TABLE XXV



Description—Rosette leaves pale green, narrowly elliptic-oblanceolate, apex acute, reaching 19–23 cm. \times 32–40 mm. (petiole 4·5–6 cm.), flattish or slightly concave, slightly crinkled, usually undulate, margin repand-dentate below, repand-denticulate above, teeth usually green, midrib white with pinkish tinge, surface finely subappressed-pubescent above, subappressed to suberect pubescent below; rosette stage \pm evanescent (fig. 63).

Stem erect, tall, ca. 100–112 cm., basal branches none or short, cauline branches numerous, long and \pm arcuate-ascending. Stem weakly ribbed below, strongly ribbed above, excorticating at base, green streaked with red (branches frequently very red in parts), patulous or ascending-hirsute (two series) with reddish or \pm colourless papillae and appressed-crispate-puberulous. Stem leaves spreading or arcuate-deflexed, lanceolate or elliptico-lanceolate, acute, red-tipped, \pm concave, conspicuously wavy; lower subpinnatifid and strongly repand-dentate below; upper repand-dentate below, repand denticulate above, teeth green, size 11–22 cm. \times 25–45 mm.; midrib white or faintly tinged with pinkish mauve, green below with scattered long hairs; surface very sparsely suberect-pubescent and copiously subappressed-puberulous above, subappressed or suberect-pubescent with scattered longer hairs below. Lower bracts spreading or sometimes arcuate-deflexed, very concave and wavy, lanceolate, 6–8 cm. \times 20–28 mm. Upper bracts arcuate-deflexed

and very undulate and concave, uppermost deflexed or spreading, flat, not wavy, 13–23 mm. long, red-tipped. Apex of inflorescence flat or slightly depressed, exceeding or level with or slightly exceeded by outer developed bud-cones and flowers (fig. 64).

Ovary $10-11 \times 2-2.5$ mm., not densely ascending or patulous hirsute with green papillae, and rather densely spreading-glandular-pubescent. Hypanthium slender, $20-22 \times 1.5$ mm., very sparsely hirsute and not densely glandular-pubescent. Bud-cone yellowish, becoming reddish below, \pm cylindric, $14-15 \times 3-4$ mm., gradually long-attentuate, nearly glabrous, shining, sepals sparsely ascending-hirsute from white papillae and not densely spreading-glandular-pubescent. Sepal

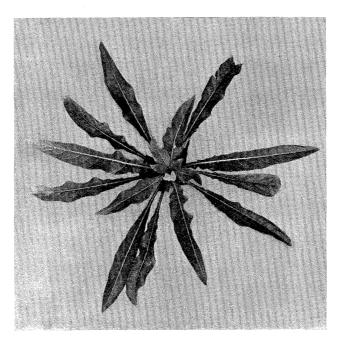


Fig. 63—O. deflexa, rosette, culture 65.33.

tips 1–2 mm., appressed, occasionally slightly divergent at apex, slightly hooded within, green tipped with red. Petals $10-12 \times 11-12$ mm., widely overlapping, never opening out flat, petals bending outwards at top, truncate, toothed, and scarcely retuse. Filaments 8 mm., anthers 4 mm., usually touching only base of stigma in bud, stigma lobes 3–5 mm., spreading, base of stigma 6–9 mm. above hypanthium.

Diagnosis—Folia radicalia pallida viridia, anguste elliptico-oblanceolata, acuta, leviter bullata, fere undulata; costa alba rubicundotincta, rosula \pm evanida. Caulis altus, erectus, multis ramis caulinis instructus, rubrolineatus. Folia caulina arcuata, deflexa, acuta, rubro acumine, \pm concava, undulata, inferiora subpinnatifida ad basim. Ovarium viridopapillatum; hypanthium graciles; alabastra subcylindrica, attenuata, paene glabra, nitida. Apices sepalorum 1–2 mm. longi, appressi. Petala 10–12 mm. longa, truncata, multum superjacentia.

This very small-flowered species is marked by many distinctions, including (1) the relatively evanescent rosettes and bushy habit, (2) the foliage, (3) the rounded, subglabrous buds, very short sepal tips, and very small flowers. It does not appear to be nearly related to any other *Oenothera* described, but it probably occupies a large area in the Niagara peninsula of Ontario. The six original cultures, each from seeds of a different plant, showed an exceptional range of variation, which will now be described.

The original plant of culture 65.33 was collected by the roadside between Windsor

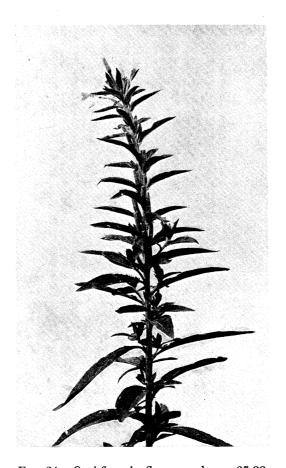


Fig. 64—O. deflexa, in flower, culture, 65.33.

and Amherstburg, Ont. It was noted as having small flowers, petals notched sepals nearly glabrous, sepal tips very short, leaves narrow. The resulting cultures showed the following constant differences from the form here described as the type: (1) smaller, narrower stem leaves (13 cm. \times 25 mm. as against 23 cm. \times 39 mm.), plants less tall, (2) midribs pale pink, (3) flowers larger (petals 15–18 \times 18–19 mm.), hypanthium 32 \times 2 mm., ovary 12 \times 3.5 mm., petals not spreading outwards at top, stigma lobes at or even below the mouth of hypanthium tube. The fruits were long and slender, 37 \times 5 mm.

Cultures 67.33 and 68.33 were alike. They showed marked differences from the type and may be characterized as var. bracteata n. var. Both were from plants on waste land of the Yawkey Estate at Sandwich, Ont. The former plant was observed to have extremely narrow, small, cuneate, notched petals, and narrow leaves turning reddish. Observations of these cultures and their descendants show the following constant peculiarities of var. bracteata: (1) Plants larger, with larger rosette leaves (fig. 65) and stem leaves (16–17.5 cm. \times 35–47 mm.) not subpinnatifid, pink midribs, (2) bracts very foliaceous (14.5 cm. \times 38 mm.), falcate-arcuate-deflexed, overshadowing the buds and flowers, not curled or appreciably crinkled (fig. 66), (3) petals very narrow but not cruciate (i.e., not linear), ranging from 13 \times 11 mm. to 8 \times 4 mm., bud-cone yellowish to pale red, rounded, 9 \times 5 mm., not tapering,

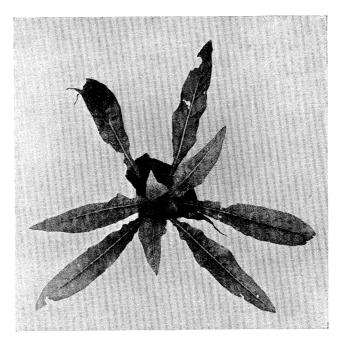


Fig. 65—O. deflexa var. bracteata, rosette, culture 68.33.

sepal tips 1-3 mm., terminal, subulate, spreading; stigma lobes long, 7-10 mm., spreading beyond petals.

Diagnosis—A specie sic differt: planta grandiora, folia ampliora, non subpinnatifida; bractae multum foliaceae, falcatae, arcuatae, deflexae; petala admodum angusta (11–13 mm. longa, 4–8 mm. lata), apices sepalorum terminales, subulati, extensi.

Culture 69.33 was derived from a very small plant on the same estate which had thin hypanthia and narrow leaves. The resulting culture had round liver-coloured spots on the leaves, which were not found in other strains. Culture 71.33 and its descendants, derived from a tall plant growing among grass in the village at Colchester, Ont., agreed with 65.33 and its descendants except in having smaller, narrow

petals ($12-14 \times 8-9$ mm.). All the differences mentioned are constant for each culture and thus represent inherited differences. They are probably due in certain cases to single genes, but more often to sets of linked genes. The most marked variations in this species are in size of flower, width of petal, size of bracts, and presence or absence of red on the midribs. The variation in petal-width is of quite a different kind from that seen in cruciate flowers, the latter being, in some cases at least, a single gene difference. In this species the petals never become linear,



Fig. 66—O. deflexa var. bracteata, in flower, late type, culture 67.33.

but narrowly cuneate, and the difference from broad petal is perhaps not due to a single gene.

The only other marked variation in this series of cultures was a plant in culture 63.33 which was a chimera having white leaf-margins and blotches of whitish tissue.

This species, like several others, tends to put up a stem early under the conditions of cultivation, so that the rosette may be almost omitted. Frequently in a culture

some plants are of this "early" type while others remain much longer in the rosette stage and belong to the "late" type. The evidence indicates, however, that this difference is not inherited but that it is purely a physiological reaction to the environmental conditions at a certain stage of development. The seeds tend to germinate badly in cultivation and so two of the strains were lost.

O. insignis BARTL.

From seeds collected by Professor W. P. Thompson on the golf course at Saskatoon, Sask., Canada, 18 September, 1933. Sixteen plants were grown as culture 14.34. They were uniform except for one typical *lata* mutation (fig. 69), and a full description is given, as it supplements the one already published (Bartlett, 1914b).

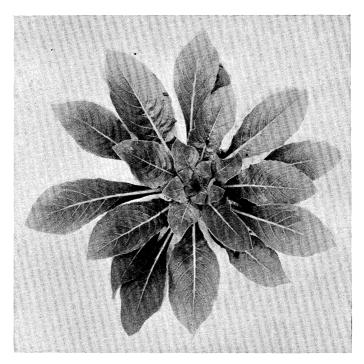


Fig. 67—O. insignis Bartl., from Saskatoon, rosette, culture 14.34.

Description—Rosette leaves pale grey-green, ca. 19–21, appressed to the soil, elliptic-obovate, apex apiculate from a rounded or obtuse apex, or merely acute, lamina 10–14 cm. \times 40–53 mm. (petiole $1\cdot5$ –3 cm. long), nearly flat, crinkling obscure, \pm slightly undulate below, margin repand-dentate or subpinnatifid below, repand-denticulate above, midribs white, finely appressed-pubescent on both surfaces (fig. 67).

Stem erect or slightly bent at tip, in annual plants reaching only 40 cm. and producing flowers and fruits from the base, and even in the axils of the later rosette leaves. This is probably its natural habit on the Canadian prairies. In Regent's Park only two plants flowered the first year. Eleven of the remainder survived the winter and in 1935 produced tall, erect stems ca. 120–130 cm. high, rather strongly

ribbed in the upper part and often fasciated.* Numerous basal branches, shortly or far decumbent and arcuate-ascending. Cauline branches numerous, arcuate-ascending. Stem very pale green, occasionally tinged with mauve, inconspicuously arcuate-ascending or patulous-pilose from scattered reddish papillae and finely subappressed-crisped-puberulous.

Stem leaves deflexed, flattish, or slightly concave, dull greyish-bluish-green, slightly crinkled, lanceolate to narrowly elliptic-lanceolate, margin finely denticulate,

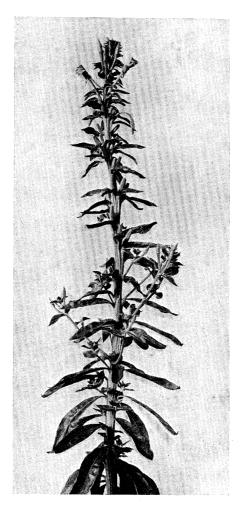


Fig. 68—O. insignis Bartl., from Saskatoon, in flower as biennial, culture, 14.34.

8-10 cm. \times 17-28 mm., midrib white, upper surface finely subappressed-puberulous with a few longer suberect hairs, lower surface similar but all hairs more suberect.

* A number of cultures remained rosettes in 1934 and produced fasciated stems in 1935 (fig. 68). O. purpurea Kleb., which can only be grown with us as a biennial, also always produces strongly fasciated stems. Fasciation in all these cases appears to be the result of the large persistent rosettes storing an excess of reserve material in the fleshy roots, this excess nourishment causing fasciation when the plant finally forms a stem in its second season.

Inflorescence not dense except towards apex. Lower bracts patulous or deflexed, concave, lanceolate, ovate-lanceolate or rarely ovate, rounded at base, 4-7 cm. \times 10-20 mm. Upper bracts spreading, ca. $15-30 \times 6-12$ mm. Apex of inflorescence flattish or slightly depressed, comose, easily overtopped by highest developed buds.

Ovary 9–10 \times ca. 3 mm., densely ascending or \pm subappressed softly hirsute from brownish-red or green papillae. Shortly spreading glandular-pubescent, but this pubescence is mostly hidden. Hypanthium $21-24\times2$ mm., rather sparsely ascending- or patulous-hirsute from green papillae and rather sparsely spreading glandular-pubescent. Bud-cone $11-12\times4\cdot5-5\cdot5$ mm., yellowish-green, \pm obscurely quadrangular, attenuate into sepal tips with reddish lines descending from sinuses between the tips. Indumentum as on ovary, but hairs longer, more spreading, papillae green. Sepal tips terminal but hooded within, appressed or divergent at apex, 2–3 mm. long, sometimes red at apex. Petals ca. $10\times8-9$ mm. (15–17 \times 15–20 mm. in annual plants), overlapping, truncate, flower cup-like, not opening widely, petals withering orange on margin.

Filaments 6-7 mm., anthers 6 mm., stigma lobes 3-4 mm., reaching nearly to top of anthers, appressed or spreading in anthesis. This strain from Saskatoon, Sask., nearly agrees with O. insignis, described by Bartlett (1914b) from the shore of Lake Superior near Duluth, Minnesota.

No other species is known with the habit of flowering from the lowest stem nodes and the leaf-axils of the rosette. The differences between the two strains can only be fully determined by growing them side by side, but the following minor differences from the species appear to exist: (1) rosette leaves elliptic-obovate (shape not described in O. insignis), (2) bracts narrower, not petiolate, (3) sepal tips shorter, appressed, or divergent. This record indicates that the species is essentially a prairie form, extending from Saskatchewan to Lake Superior. It is evidently on the way to becoming acaulescent in habit, like many prairie species, as Bartlett suggests, but when grown under English climatic conditions this sub-acaulescent habit is nearly suppressed.

The *lata* mutation (fig. 69) occurring in wild seeds is of particular interest. It, and other cases recorded in this paper, shows that, whether they survive or not, trisomic mutations must occur not infrequently in nature. This rosette was an exact parallel to *O. Lamarckiana* mut. *lata* in leaf-shape, but in other respects the leaves agreed with those of the species. This plant survived the winter, but was killed by the heavy frosts in the spring of 1935. Since all the other rosettes of the culture survived and flowered, it is evident that the *lata* mutant was less resistant than the type of the species.

O. albinervis, n. sp.

From seeds collected in the town of Fargo, N. Dakota, at Kindred, N.D., and on open ground near sand dunes at Barrie, Richland Co., N. Dakota, 40 miles from Fargo, 15 October, 1932. When growing under these somewhat arid sandy conditions the leaves were narrow, smooth, and covered with a conspicuous silky pubescence.

In the climate and soil of Regent's Park, the silky pubescence failed to appear and the leaves become strongly crinkled. In this species, as in several others, "early" and "late" types are strongly marked. The early plants, which omit the rosette stage, were in culture 72.33 taller, lighter green, with smooth leaves and smaller, curled bracts; while the late plants produced a rosette followed by a stem, they were darker green, the stem leaves \pm crinkled, the bracts larger and less curled. The evidence from successive years of culture indicates that the early and late types, which have been observed in several *Oenothera* species and sometimes show striking differences, are not inherited but are simply an epharmonic response, occurring as the result of some reaction to environment early in the development of the

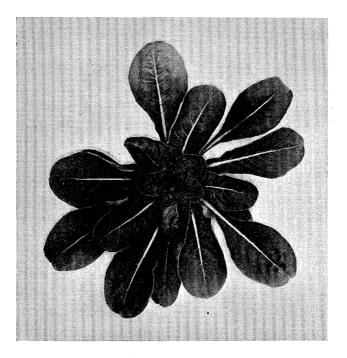


Fig. 69—O. insignis mut. lata, rosette, culture 14.34.

young plant. Culture 75 and its descendants from Barrie, N.D., will be treated as the type culture.

Table XXVI

1933	Fargo 72 (50)	Kindred 73 (50)	Barrie 75 (50)
1934	96 (2) 97 (6)	98 (4)	100 (10)
1935	99 (40)		101 (17)

Description—Rosette leaves reaching 23 cm. × 70 mm., elliptic-oblanceolate, apex acute, or obtuse with acute point, usually strongly crinkled and margin strongly undulate, obscurely and distantly repand-denticulate, glands green, scarcely

visible, markedly repand-dentate towards the base, usually with large reddish patches, very sparsely suberect-pubescent above, pubescence longer below, midrib white (fig. 70).

Stem erect, ca. 90-100 cm., strongly ribbed, green, sparsely \pm appressed or patulous-hirsute with usually only green papillae or none, densely suberect or arcuate-subappressed-pubescent, basal branches many or none, appressed prostrate and arcuate, the apices ascending, often nearly as long as central stem, pinkish

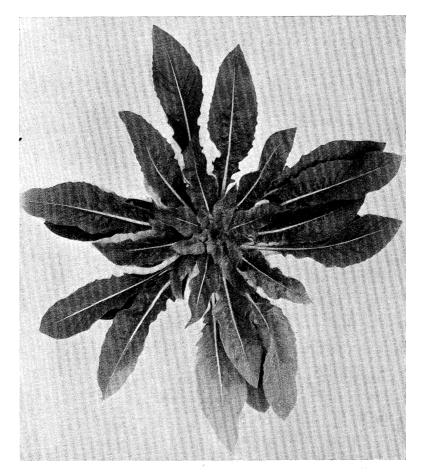


Fig. 70—O. albinervis, rosette, culture 100.34.

towards base, cauline branches usually none. Bark brown at base of stem, excorticating. Stem leaves 11.5-21 cm. \times 35-60 mm., deflexed, upper often very steeply, lanceolate or elliptic-lanceolate, strongly crinkled, lower usually with large reddish patches, margin wavy, repand-dentate in lower two-thirds (lower sub-pinnatifid at base) repand-denticulate above, glands green or reddish, both surfaces densely suberect-pubescent, midrib white, \pm subappressed-crisped-pubescent above, sparsely pilose and densely \pm subappressed pubescent below.

Lower bracts lanceolate, arcuate-deflexed, very concave, wavy, and crinkled, $5-6.5 \times 2-2.5$ cm. Upper bracts arcuate-spreading, curled, up to ca. 1 cm. long and

1 cm. wide. Apex of inflorescence flattish or convex, comose, overtopped by highest developed bud-cones. Spike fairly dense. Ovary $12-15 \times 3.5$ mm., densely hoary and subappressed pubescent (no red papillae), hypanthium $20-37 \times 2.5-3$ mm., stout, patulous-ascending hirsute, arcuate-subappressed-pubescent and spreading glandular-pubescent, remaining stiff when petals wilt. Bud-cone green, \pm cylindric, $11-15 \times 5-7$ mm., hoary and densely subappressed pilose-pubescent,

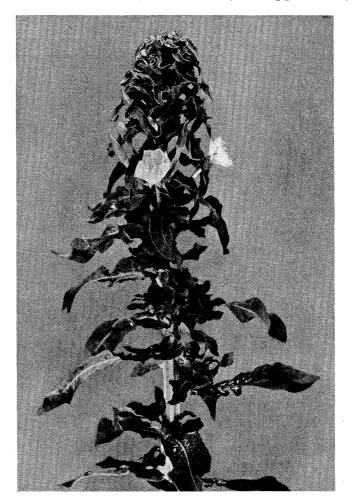


Fig. 71—O. albinervis, in flower, culture 100.34.

sepal tips 3-4 mm., terminal, appressed or divergent, with a touch of red at the extreme tip. Petals $13-18 \times 14-23$ mm., truncate and irregularly toothed, opening to cup-shape, overlapping. Base of stigma 0-2 mm. above hypanthium, stigma lobes 5-9 mm. long, appressed or spreading, filaments 9-11 mm., anthers 6-7 mm., slightly overtopping stigma lobes (fig. 71).

Fruits green, long, 40×7 mm., with variable numbers of long and short hairs.

Diagnosis—Folia radicalia elliptico-lanceolata, plerumque valde bullata, margine admodum undulata, obscure repando-denticulata, glandulis viridibus, vix evidentibus,

repando-dentata ad basim, fere cum magnis maculis rubescentibus, costa alba. Caulis erectus, viridis, papillae fere virides aut non. Folia caulina valde bullata, similia foliis radicalibus. Ovarium 12-15 mm. longum non rubropapillatum, hypanthium robustum, cum pilis patulis ascendentibus. Alabastra subcylindrica, viridis, apices sepalorum 3-4 mm. longi, terminales, rubrotincta in extremo acumine. Petala 13-18 mm. longa, superjacentia, stigmatis basis paulum suprahypanthium.

The foliage, particularly of the cultures from Kindred, was exactly like that of O. mut. rubrinervis DE VRIES, except that the midribs were white. This species differs very markedly, however, having white midribs, small flowers, and differences in stem apex and in habit. It is markedly unlike O. strigosa (RYD.) MACK. and BUSH, which occurs in this region, and even more sharply separated from the new Dakotan species, O. rubricapitata. O. albinervis is evidently widely distributed in North Dakota.

The 1933 cultures of this species showed marked "early" and "late" types, which could be scored without difficulty in cultures 72 and 73, but in culture 75 the differences were not marked enough for scoring. The early type is taller with lighter green foliage, leaves not crinkled, bracts smaller, curled. The late type has darker green foliage, leaves \pm crinkled, bracts larger, less curled. Cultures 96 and 97 of 1934 were derived from selfing late and early plants respectively of culture 72.33. The resulting offspring were all alike, producing good rosettes, some of which did not flower until 1935. Hence the "early" condition is not inherited.

In the 1935 cultures certain interesting differences were observed between 99 and 101, which had no doubt been overlooked in the previous years owing to less minute observation. (1) In 99 the petals turned dirty orange colour in fading, while in 101 they did not change colour in fading, but every petal in every plant had a small pale orange spot at the base on the outside. This was first observed on 3 August, but the flowers opening on 8–14 August showed no trace of this spot. It is therefore an evanescent character, appearing in the Barrie strain, but not in that from Fargo. As cultures 99 and 101 were grown in rows side by side and the difference was constant when it appeared, it cannot be accounted for environmentally. Culture 99 differed from 101 in (2) having stem leaves slightly wider (16 cm. \times 47 mm. as against 16 cm. \times 43 mm.) and with patches of paler green between the lateral veins; (3) having a longer style (this difference persisted for at least 12 days); (4) bud-cone less stout (15 \times 6 mm.); (5) sepal tips not appressed, but spreading towards their apex. All these differences were constant throughout the two cultures.

O. rubricapitata n. sp.

A very distinct species, from seeds collected in a wooded area by a pond at Kindred, N. Dakota, some 30 miles from Fargo, 15 October, 1932.

Description—Rosette leaves dull, somewhat greyish-green, oblanceolate, or elliptic-oblanceolate, reaching 24 cm. × 57 mm. (petiole 3–5.5 cm. long), apex acute, shortly cuspidate or obtuse and apiculate, crinkling conspicuous, undulation usually present towards base, margin repand-dentate to sub-pinnatifid below, repand-denticulate to subentire above, glands not visible, midrib conspicuously pink, densely suberect or erect pubescence on both surfaces (fig. 72).

Stem ca. 60 cm. high, erect, strongly ribbed, green with purple patches, patulous-hirsute and arcuate-subappressed-pubescent. Few papillae, green or red in coloured

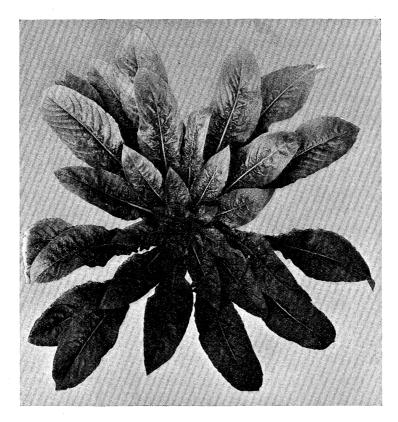


Fig. 72—O. rubricapitata, rosette, culture 99.34.

patches, excorticating at base in early type which omits the rosette. Long basal branches prostrate-decumbent, numerous short cauline branches \pm arcuate-ascending, usually deep red. Stem leaves \pm arcuate-deflexed, lanceolate, elliptic-lanceolate below to ovate-lanceolate above, flattish or convex, smooth or \pm crinkled near (red) midrib, 6·5–19 cm. \times 22–43 mm., lowest dentate to subpinnatifid at base, pubescence suberect, midrib \pm appressed-crispulous above. Bracts arcuate-spreading or strongly deflexed, lanceolate, cordate, sessile, lowest 9 cm. \times 40 mm., flattish; tip wavy, uppermost bracts very small; apex of inflorescence convex, overtopping highest developed buds, spike rather lax. Ovary 12 \times 2·5 mm., patulous-hirsute, arcuate-subappressed-pubescent and very sparsely spreading

glandular-pubescent, papillae green or sometimes reddish. Hypanthia \pm arcuate, $25-28 \times 2$ mm., sparsely spreading or patulous-hirsute and glandular-pubescent, papillae green. Bud-cone greenish-yellow, upper quarter conspicuously deep red, subcylindric, ca. 11×5 mm., sparsely patulous-hirsute and sparsely spreading glandular-pubescent, small red papillae on red portion of bud. Sepal tips 3-5 mm., green in upper, red in lower half, or throughout, stout, terminal, appressed or very

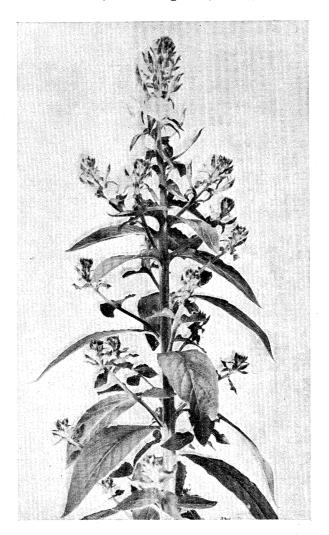


Fig. 73—O. rubricapitata, in flower, culture 99.34.

slightly divergent. Petals 13×13.5 mm., opening at 45° , rather widely overlapping, truncate, and "irregularly toothed". Base of stigma just above mouth of hypanthium, stigma lobes 3-4 mm. long, not separating, filaments ca. 9 mm., anthers 6-7 mm., far overtopping stigma lobes (fig. 73).

Diagnosis—Folia radicalia surda, aliquantum canoviridia oblanceolata aut elliptico-oblanceolata, acuta, breviter cuspidata aut obtusa et apiculata, bullata,

margine repandodentata ad subpinnatifida ad basim, costa rubicunda. Caulis erectus, viridis cum maculis purpureis, paucae papillae virides, aut rubrae in partibus purpureis caulis, exuens corticem ad basim.

Folia caulina inferiora lanceolata, ad basim dentata ad subpinnatifida, superiora ovato-lanceolata; ± bullata prope costam rubicundam. Spica sublaxa, hypanthia arcuata, sepala viridescentia-flava, quadrans superior insigniter atroruber. Apices sepalorum 3–5 mm. longi, robusti, terminales, appressi; petala 13 mm. longa, stigmatis basis paulum supra hypanthium.

This species is very distinct and uniform, the ornamental red shoulders to the buds being a new character in the genus. The plants showed "early" and "late" types under the weather conditions of 1933 only. The foliage is curiously like that of O. deflexa, especially var. bracteata, but there is probably no very close relationship to that species. A plant in culture 74.33 was examined by Mr. Ford and found to have a ring of 14 chromosomes.

O. Lamarckiana Ser.

The origin and history of this species has been much discussed and will only be touched upon here, especially as the matter has lost its prime importance now that similar mutation phenomena have been described in various species taken directly from the wild, and whose wild origin there is no chance to dispute. DE VRIES (1914) and Davis (1927) have discussed at length the origin of O. Lamarckiana, and have published photographs of several herbarium specimens in the Museum d'Histoire Naturelle in Paris which bear on this question. It seems certain that both O. grandiflora Sol. and O. Lamarckiana Ser. are represented in these specimens. I am in agreement with DE VRIES that his plate XVII represents O. Lamarckiana SER., but I incline to the view that his plate XVIII belongs to O. grandiflora Sol. On a recent visit to the Jardin des Plantes in Paris, the specimen represented by Plate XIX of DE VRIES'S paper and by Plate V of DAVIS'S was re-examined with particular interest. It was evidently grown from seeds collected by Michaux somewhere in eastern North America late in the eighteenth century. DE VRIES regarded it as belonging to the type of O. Lamarckiana, while Davis thought it was a very different species. I have compared some of its measurements and other characters with those of recently-made herbarium specimens from the DE VRIES strain of O. Lamarckiana.

This Michaux specimen differs in certain respects from the Lamarckiana of DE VRIES: (1) the stem leaves have petioles, which may be of considerable length, (2) the leaves are somewhat narrower, (3) they may be somewhat less crinkled, although this character is very difficult to assess in dried specimens, (4) the flowers were somewhat larger. The petioles on the middle stem leaves of this specimen were 8-10 mm. in length, a peculiar character not known in any other Onagra. Three leaves from the middle part of the stem measured respectively 12.5 cm. × 27 mm., 12 cm. × 33 mm., and (a lower leaf) 15 cm. × 27 mm. (including petiole 2 cm. long). By

comparison, mid-stem leaves from dried specimens of O. Lamarckiana from my cultures of 1935 measured 10–11 cm. \times 33–34 mm. but were practically sessile. The buds are very similar in form and pubescence in the two types, as DAVIS also admits, the largest bud cones on the MICHAUX specimen being 40×9 mm. with sepal tips ca. 6 mm. long, whereas in my specimens they were somewhat smaller, bud-cone 34×10 –11 mm. with sepal tips 5–7 mm. In pubescence and other characters they were alike.

The only differences between the two types are therefore in the presence or absence of leaf petioles, a small difference in leaf-width and in flower-size, and some possible difference in crinkling. These differences are varietal only, and both types clearly belong to the same species. The contention of Davis that Michaux's plant represents a very distinct species is inadmissible, although it would evidently rank as a variety of O. Lamarckiana, distinguished from the strain of De Vries by certain well-marked differences. It is highly probable that wherever this strain of Michaux grew wild, the strain represented by the O. Lamarckiana of De Vries would not be far distant geographically.

The present genetic survey has brought out the fact that seeds of O. Lamarckiana agreeing with the English garden strain, which differs slightly in colouring and crinkling from that of DE VRIES's cultures, have not infrequently been introduced into private gardens in Eastern Canada, from whence they have sometimes escaped more or less successfully. In company with Professor Marie-Victoria in 1932, we found at Lotbinière, above Quebec on the south side of the St. Lawrence, a small group of plants of this species growing on the edge of a field by the roadside. They were probably a recent escape from a garden in the neighbourhood and they showed no definite signs of spreading. Very different was the case of a colony found in September, 1935, at Barss Corner, Lunenburg Co., Nova Scotia. On a farm I descried, some hundred yards from the road, a colony of O. Lamarckiana which was growing and spreading on a hillside in a pasture or hayfield among grass. About one hundred plants were counted, many in flower and others rosettes. locality is almost in the middle of the peninsula of Nova Scotia, protected from the coastal winds. The climate is exceptionally mild and these plants flourish and spread rapidly. Enquiry from the owners of the farm elicited the information that seeds of this species had been obtained from a seed firm of New York about ten years ago. They have "grown like weeds ever since" and have "gone all over the farm". The success of this species in establishing itself and spreading even through pasture richly stocked with vegetation, indicates either that the home of this large-flowered species was further north than is generally supposed, or that the species is by no means narrowly adapted to a southern climate. It was particularly surprising to see an Oenothera succeeding in competition with grasses in an undisturbed soil.

In Table XXVII is given the known distribution of the various species investigated. No doubt the distribution of many of these species will be extended with further knowledge.

R. RUGGLES GATES

Table XXVII—Distribution of the Various Species

TABLE AAVII—DIS	TRIBUTION OF THE VARIOUS SPECIES
Species	Localities
O. paralamarckiana	Woods Hole, Massachusetts.
O. pycnocarpa ATK. and BARTL	. Ithaca, N.Y.
var. parviflora	Hamilton and Georgetown, N.Y.
var. cleistogama	Clinton, N.Y.
O. novae-scotiae GATES	Middleton, Annapolis Co., N.S., and vicinity.
var. serratifolia	Kentville, King's Co., N.S.
var. distantifolia	Newport, Hants Co., N.S.
O. comosa	Wilmot, Annapolis Co., N.S.
O. intermedia	Bear River, Digby Co., N.S.
O. flecticaulis	Mouth of Lahave River, Lunenburg Co., N.S.
O. Hazelae	Lockeport, Shelburne Co., and Wentworth, Cumberland Co., N.S.
var. parviflora	Port Mouton, Queen's Co., Chester, Lunenburg Co., and
1 3	Middleton, Annapolis Co., N.S.
O. subterminalis	Higgins Brook, Cumberland Co., and North River,
	Colchester Co., N.S.
O. grandifolia	Wentworth and Port Howe, Cumberland Co., and Waugh's
3	River, Colchester Co., N.S., and Point de Bute, West-
	moreland Co., N.B.
O. Royfraseri	Sackville, Westmoreland Co., N.B.
O. sackvillensis	Sackville, N.B.
var. albiviridia	Sackville, N.B.
O. ammophiloides	Guysborough Co., N.S.
var. laurensis	Port Elgin, Westmoreland Co., N.B.
O. parva	Near the St. Lawrence, from Bic, Rimouski Co., to L'Islet,
· · · · · · · · · · · · · · · · · · ·	L'Islet Co., Quebec.
O. leucophylla	St. Valier, Bellechasse Co., and Berthier-en-bas, Mont-
O. toutophyttu	magny Co., Quebec.
O. biformiflora	St. Valier, Bellechasse Co., Charny, Levis Co., and St.
O. ogomigiora	Antoine les Fonds, Lotbinière Co., Quebec.
O. laevigata BARTL	White Sulphur Springs, W. Virginia.
var. similis	St. Valier, Quebec.
var. rubripunctata	St. Valier, Quebec.
O. Victorini Gates and Catch.	·
var. parviflora	
van parogiora	binière Co., and St. Hubert, Montreal, Quebec.
var. intermedia	St. Valier, Ste. Anne de Bellevue, Jacques Cartier Co.
	and Cap Tourmente, Montmorency Co., Quebec.
var. undulata	Near Toronto, Ontario.
O. angustissima GATES	Ithaca, N.Y.
var. quebecensis	Cap Tourmente, Montmorency Co., Quebec.
O. niagarensis	Niagara Gorge, N.Y.
O. repandodentata	Colchester, Essex Co., Ont.
O. deflexa	Windsor, Ont., and vicinity (Essex Co.).
var. bracteata	Sandwich, Ont. (Essex Co.).
O. insignis BARTL.	Duluth, Minn., and Saskatoon, Sask.
O. albinervis	Fargo, Kindred and Barrie, N. Dakota.
O. rubricapitata	Kindred, N.D.

CATENATION

Material was collected by Mr. C. E. Ford from many of the 1933 cultures to determine their catenation. His results are given in Table XXVIII, each determination being made from a single plant. A ring of 14 chromosomes was present in the pollen mother cells in every case except O. rhombipetala, which has seven free pairs. This extensive sampling makes it highly probable that all the Oenotheras in eastern North America have a ring of 14.

Table XXVIII—Chromosome Catenation in Various New Species and Varieties

Cu	lture
O. paralamarckiana	1.33
O. novae-scotiae with large flowers	3.33
	5.33
O. Hazelae var. parviflora	7.33
	1.33
O. subterminalis	3.33
O. ammophiloides var. laurensis	0.33
O.parva	5.33
O. laevigata var. similis	8.33
	9.33
,, ,, ,,	1.33
	9.33
	0.33
O. leucophylla	3.33
	3.33
,,	2.33
O. Victorini var. intermedia	3.33
Undescribed species from St. Jerome, near Montreal 53	3.33
	3.33
O. rubricapitata	4.33
Species from Lockeport, N.S., resembling O. biennis 81	1.33
	9.34

MUTATIONS

Various general points regarding these cultures have been referred to in the introduction. Here it will be necessary to discuss first the mutations which have occurred in these wild species. For convenience of reference they are compiled in Table XXIX.

It was formerly often suggested that the mutations of O. Lamarckiana were in some sense a result of its cultivation or hybridity. In so far as a ring of chromosomes is a sign of the heterozygous condition, the latter suggestion is true, but it is shown in the present paper that a number of wild species produce similar mutations, even directly from wild seeds. Table XXIX is a summary of the mutations—all probably

trisomic except the periclinal chimaera and one which is triploid—produced in quite small cultures of seven different species. It is already known that wild species such as O. novae-scotiae and O. eriensis have a high percentage of non-disjunctions (Sheffield, 1927), and it is now clear that other wild species have a high

TABLE XXIX—MUTATIONS FROM WILD SPECIES OF Oenoth	TABLE	XXIX-	-MUTATIONS	FROM WILD	SPECIES	OF Oenother
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Species	Generation	Name	Nature of mutation
O. paralamarckiana*	P_1	dwarf	trisomic?
	$\mathbf{P_2}$	several	trisomics
O. flecticaulis	P_1	linearis	trisomic?
O. sackvillensis	P_2 and P_3	dwarf	trisomic
O. ammophiloides var. laurensis	P_1, P_2, P_3	linearis	trisomic
O. parva	P_2	yellow leaf-margin	periclinal chimaera
O. parva	P_1, P_2	hebetifolia	trisomic?
O. biformiflora	P_1	triploid	21 chromosomes
O. insignis	$\mathbf{P_{1}}$	lata	trisomic

^{*} For later mutations from this species see GATES and NANDI (1935).

frequency of trisomic mutations. In O. paralamarckiana at least it is much higher than in O. Lamarckiana, and it appears probable that it is higher also in certain other species here described.

The lata from O. insignis is in leaf-form an exact counterpart of the lata from O. Lamarckiana or O. biennis, which indicates that one pair of chromosomes is probably common to the three species. If a specialized species from the Canadian prairies has at least one pair of chromosomes in common with two species which probably originated near the Atlantic seaboard, this is a striking testimony to the stability of the germplasm in the genus. It is possible, however, that a less simple explanation of these parallel trisomics may ultimately be required. The question can only be answered by further breeding experiments.

The blunt-leaved mutant hebetifolia from O. parva, on the other hand, has no known parallel, although it resembles O. Lamarckiana mut. oblonga in some respects. That O. flecticaulis and O. ammonphiloides var. laurensis both produce linear-leaved trisomics is not surprising, since both are coastal forms related to O. ammophiloides. It is of interest that O. paralamarckiana and O. sackvillensis, which show no obvious relationship, should both produce trisomic dwarfs. These dwarfs differ in their foliage, however, and it is not necessary to conclude that they have the same chromosome in common. Perhaps they have in common only a dwarf gene, which becomes dominant when triplicated.

THE ST. VALIER COLONY

As will be seen from Table XXVII, two species of *Oenothera* frequently occur in the same locality, but St. Valier on the south shore of the St. Lawrence is remarkable as the meeting place of at least four very distinct species with four varieties. This

large colony extends for some distance along the freshwater estuarine shore of the St. Lawrence at the mouth of the River Boyer in gravel and shale, not sand. The forms found here have been classified as O. leucophylla, O. laevigata var. similis and var. rubripunctata, O. biformiflora and its variety cruciata, with O. Victorini var. intermedia. Of these forms, O. leucophylla has some resemblances to O. eriensis further west, but nearer relations with O. ammophiloides in the Gulf of St. Lawrence. O. laevigata originates from Virginia, O. biformiflora shows some connexions with Massachusetts and Vermont, while O. Victorini spreads westwards to Montreal, and beyond. In the small area at St. Valier all these forms are growing freely together, and there is definite evidence that the two varieties of O. laevigata at least occasionally intercross.

In 1933, 17 cultures were grown from St. Valier, each from seeds of a different wild plant, and in 1934 the same number of P_2 cultures was grown from selfed plants of the previous generation. The following year six further (P_3) cultures were studied, to confirm various characters observed. Of the 17 original cultures, many proved to be identical through two or three generations; but as it is impossible to be certain about the significance of differences observed in the field until they have been carefully studied in the experimental garden, it is quite possible that the wealth of forms in this colony is by no means exhausted by the present studies.

THE RATE OF EVOLUTION

Finally, it remains to discuss briefly the nature of the species and the principles of specific differentiation in the genus Oenothera. The principles of phylogeny in the genus were considered elsewhere (GATES, 1933) and are generally confirmed and extended by the present results, which indicate that lines of relationship can be traced north and south for O. laevigata BARTL. from West Virginia, and its varieties similis and rubripunctata from St. Valier, Quebec; O. angustissima GATES from Ithaca, New York, and its variety quebecensis from the north shore of the St. Lawrence; O. biformiflora from the St. Lawrence, whose nearest relatives appear to be in Vermont and Massachusetts. In Eastern Canada there appears to be a coastal series consisting of O. flecticaulis, O. ammophiloides and its var. laurensis, O. parva and leucophylla, all having strongly bent stems and many red, light-sensitive papillae on the sepals and ovaries. In September, 1935, about 60 more collections of seeds were made in Eastern Canada, which will fill in many lacunae. Further discussion of this aspect is postponed until they have been investigated.

The present study has been sufficiently intensive in certain areas to give a fuller picture than has hitherto been attained of the rich multiformity in the genus and particularly in certain local populations. In some localities there appears to be a single form showing only the most minute type of genetic variations, with in some cases one or two other genes for such conditions as red or white midribs. In other areas the population is much more multiform, reaching a maximum with several species and their variations represented. The cause of this multiformity must be

sought in gene mutations, but it must be remembered that an *Oenothera* population is very different from an ordinary open-pollinated Mendelian population. Among the small-flowered forms here described, crossing must be a relatively rare occurrence, and there is little or no segregation, each individual, although heterozygous for a large number of factors, breeding true owing to the chromosome catenation. Crossing therefore produces a new type generally more or less intermediate between the parents, or rather between the two uniting complexes. Further genetic analysis of all these species must therefore be undertaken to determine their complexes, and many crosses for this purpose have already been made.

The wealth of multiformity in these cultures and the number of characters new to the genus have been somewhat surprising. The diversity is much greater than in some other genera occupying the same area. This leads to the question of relative rates of evolution. It seems necessary to conclude that evolution or differentiation of types has taken place much more rapidly in *Oenothera* than in many other genera. Fernald (1925), in his extensive studies of the flora of Eastern Canada, has shown that a series of areas around the Gulf of St. Lawrence, including the Long Range of Western Newfoundland, the Torngat Mountains of north-eastern Labrador, considerable parts (Shickshock Mountains) of the Gaspé Peninsula, the Magdalen Islands, much of Prince Edward Island, and the north-eastern end of Cape Breton Island, which escaped glaciation more or less completely, are the home of many endemic plant species which are only found elsewhere in such distant regions as the Rocky Mountains or Greenland. Fernald concludes that these plants persisted through the Ice Age on local areas and nunataks in Eastern Canada. He finds that these lands around the Gulf of St. Lawrence have 81 such endemic species, in strong contrast with the White Mountains further south which have only 3 endemic species, and Nova Scotia which was thoroughly glaciated and has but one endemic, Agalinis neoscotica (Greene) Fernald, whose specific status is somewhat doubtful. It is generally recognized that the Atlantic slope of Nova Scotia derived its flora via the submerged Atlantic continental shelf from the southern Coastal Plain. Fernald states that its species are "nearly all typical of the Coastal Plain region from New Jersey to Florida and Mississippi in a much warmer climate". Besides the above-mentioned species, which may be only a variety of A. purpercula, the greatest departures from the southern types are "divergencies in pubescence, size, texture or habit, but not in fundamental reproductive characters". Eleven such geographic varieties have been recognized as endemic derivatives from the southern Coastal Plain. He concludes that "the best that nature has been able to do in 25,000 years with species of Alabama, Florida, and the Carolinas in the bleak climate of Atlantic Nova Scotia is to lengthen the trichomes or slightly to modify the foliage".

Regarding these views, it may be remarked that 25,000 years appears to be rather an excessive time allowance, and that other botanists are not agreed that "fundamental reproductive characters" are alone worthy of recognition as specific characters. Nevertheless, Fernald's views appear fairly moderate and representative

of taxonomic opinion regarding specific differences among Angiosperms in general. Now I have described eight species and three varieties from the parts of Nova Scotia already explored. Clearly these species are either founded on smaller differences in general than those which systematists customarily recognize, or else evolution has proceeded at a more rapid pace in *Oenothera* than in most other genera. As regards the first alternative, while I have by no means taken the attitude of the extreme "splitter", yet some of the species here described are probably based upon smaller differences than the herbarium taxonomist would recognize. On the other hand, it is impossible to believe that any taxonomist would refuse specific rank to forms as distinct as O. novae-scotiae, O. grandifolia, O. Hazelae, and O. ammophiloides, all from Nova Scotia. It therefore seems necessary to conclude that evolution or differentiation of species has proceeded in the genus Oenothera at an exceptionally rapid pace. Before a final opinion can be formed on this matter, however, a corresponding genetic survey should be made of some relatively stable genus, collecting forms from many localities and studying their geographic variation in cultures.

SUMMARY

The present work is the beginning of a genetic survey of the genus *Oenothera* mainly in Eastern Canada and adjacent territory. It combines genetical with taxonomic methods, describing 17 new species, 15 new varieties, and many smaller variations, as well as recognizing 7 already described species in new localities, as a result of three years of pedigree cultures from about 100 collections of wild seeds from different localities.

Much light is thrown upon the geographic distribution and relationships of the various forms, indicating south to north movements in several different lines, and also a coastal series of forms. Six species have produced known or probable trisomic mutations, one species a triploid mutation and one a periclinal chimera (Table XXIX), most of these mutations being directly from wild seeds.

Plants of "early" and "late" development occur in cultures of several species, but the condition is not inherited and appears to be an epharmonic response to the environmental conditions occurring at an early stage of the young plant's development. The prairie species, O. insignis and albinervis, show marked alterations when grown in the English climate, the former losing its sub-acaulescent habit and developing long internodes, while the latter loses its silky pubescence and its leaves become crinkled.

In several species a new category of evanescent characters appears, such as the development of a pale red spot at the base of all the petals during a part only of the flowering season in one strain of O. albinervis; a touch of red at the base of the stem leaves in O. niagarensis during part of the season; and orange coloured filaments in the flowers at the end of the season only, in an undescribed species from near Montreal.

From numerous samples (Table XXVIII), the catenation of all these forms is found by Mr. C. E. FORD to be, without exception, a ring of 14 chromosomes.

Several large colonies of *Oenothera* have been studied by these methods, especially one at St. Valier on the St. Lawrence, where at least four species with four varieties were found. The relationships of these species were with the east, the west, and the south.

The polymorphic character of the genus, even in areas such as Nova Scotia, which were heavily glaciated and are believed to contain no other endemic species but only varieties, leads to the conclusion that evolution has proceeded more rapidly in this genus than in most others. Gene mutations have been active in supplying the raw materials for specific differentiation. Crossing has also probably played a part in increasing the number of specific types, since the hybrids breed true owing to catenation. Such new constant types are indistinguishable from the older species. Parallel mutations have also occurred many times in the different species. Their great importance in evolution has not yet been fully recognized.

REFERENCES

```
ATKINSON, G. F. (1918). 'Proc. Amer. Phil. Soc.,' vol. 57, pp. 130-143.
BARTLETT, H. H. (1913). 'Rhodora,' vol. 15, pp. 81-85.
—— (1914a). 'Amer. J. Bot.,' vol. 1, pp. 226–243.
—— (1914b). 'Twelve Elementary Species of Onagra,' "Cybele Columbiana,"
        vol. 1, pp. 37-56.
—— (1915). 'Rhodora,' vol 17, pp. 41–44.
Boedijn, K. (1924). 'Z. indukt. Abstamm.-u VererbLehre,' vol. 32, pp. 354-362.
CATCHESIDE, D. G. (1935). 'Genetica,' vol. 17, pp. 313-341.
CLELAND, RALPH E. (1935). 'Proc. Amer. Phil. Soc.,' vol. 75, pp. 339-429.
DAVIS, B. M. (1927). 'Proc. Amer. Phil. Soc.', vol. 66, pp. 319-355.
DE VRIES, HUGO (1902). "Die Mutationstheorie," vol. II.
— (1913). "Gruppenweise Artbildung, unter spezieller Berücksichtigung der
         Gattung Oenothera." 'Gebrüder Borntraeger,' Berlin.
—— (1914). 'Bot. Gaz.,' vol. 17, pp. 345-361.
Fernald, M. L. (1925). 'Mem. Amer. Acad. Arts Sci.,' vol. 15, pp. 239-342.
GATES, R. RUGGLES (1915). "The Mutation Factor in Evolution, with Particular
         Reference to Oenothera." London, Macmillan.
   — (1916).
              'Trans. N.S. Inst. Sci.,' vol. 14, pp. 141–145.
—— (1917).
              'J. Genet.,' vol. 6, pp. 237–253.
—— (1923). 'J. Genet.,' vol. 13, pp. 13–45.
              'Canad. Field Nat.,' vol. 41, pp. 23-27.
  — (1927).
—— (1928). 'J. Bot.,' pp. 133–136.
              'Bull. Lab. Genet. Leningrad,' vol. 9, pp. 13-28.
—— (1932).
   — (1933). 'J. Linn. Soc., Bot.,' vol 49, pp. 173–197.
```

GATES, R. R., and CATCHESIDE, D. G. (1932). 'J. Genet.,' vol. 26, pp. 143-178.

Gates, R. R., and Nandi, H. K. (1936). 'Phil. Trans.,' B, vol. 225, pp. 227–254.

HEDAYETULLAH, S. (1933). 'Proc. Roy. Soc.,' B., vol. 113, pp. 57–70.

Klebahn, H. (1914). 'Jb. hamburg. wiss. Anstalt.,' vol. 31, pp. 1-64.

MacDougal, D. T., Vail, A. M., Shull, G. H., and Small, J. K. (1905). 'Publ. Carnegie Inst.,' No. 24.

Marie-Victorin, Frere (1935). "Flore Laurentienne," Montreal.

Michaelis, P. (1930). 'Z. Bot.,' vol. 23, pp. 288-308.

Oehlkers, F. (1930a). 'Z. Bot.,' vol 22, pp. 473-537.

—— (1930b). 'Z. Bot.,' vol. 23, pp. 967–1003.

—— (1935). 'Z. Bot.,' vol. 28, pp. 161–222.

RUDLOFF, C. F., and STUBBE, H. (1935). 'Flora,' vol. 129, pp. 347-362.

Sheffield, F. M. L. (1927). 'Ann. Bot.,' vol. 41, pp. 779-816.

Stomps, Theo J. (1913). 'Ber. deuts. bot. Ges.,' vol. 31, pp. 166-172.

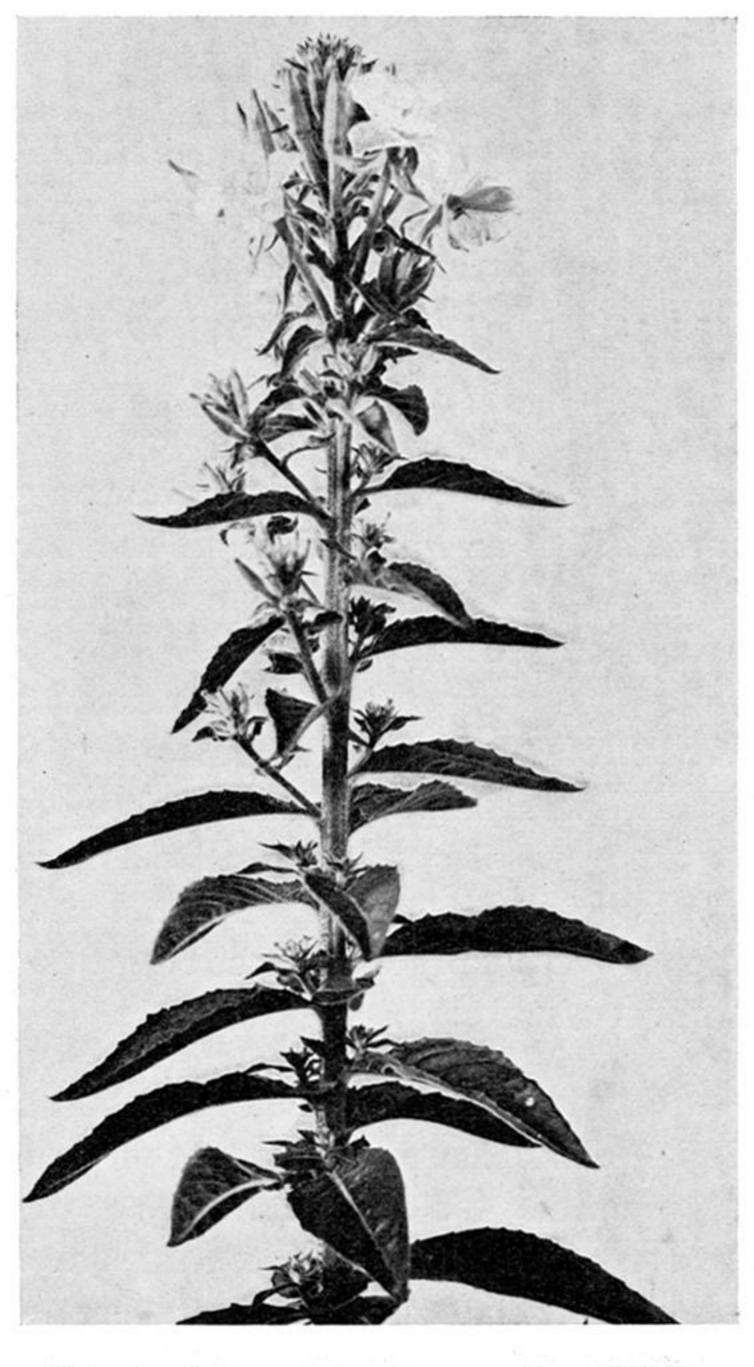


Fig. 1—O. paralamarckiana, culture 19.35.

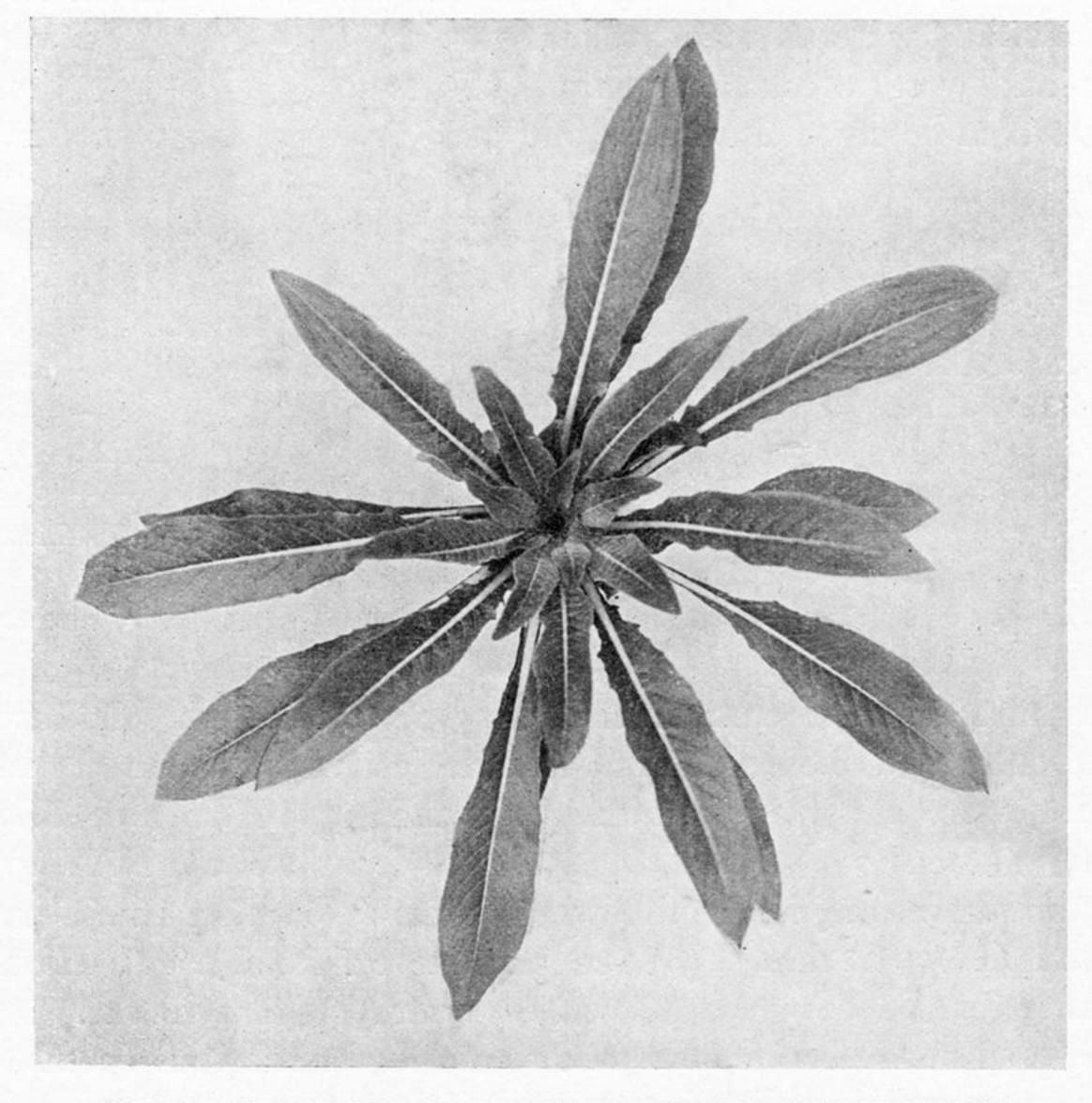


Fig. 2—O. pycnocarpa var. parviflora. Rosette, culture 115.34.



Fig. 3—O. pycnocarpa var. cleistogama, in flower, culture 118.34.

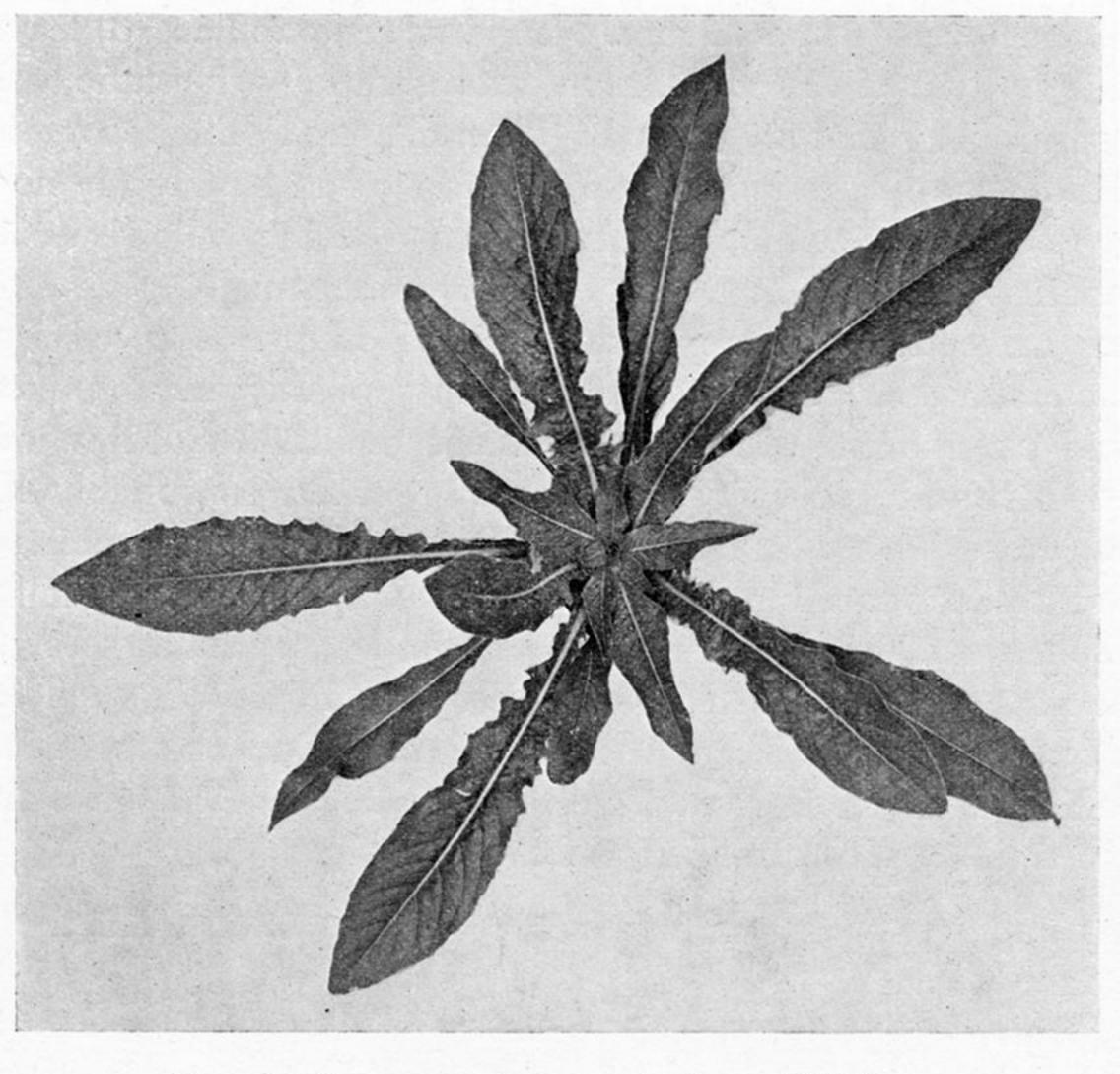


Fig. 4—O. pyncocarpa, rosette, culture 116.35.

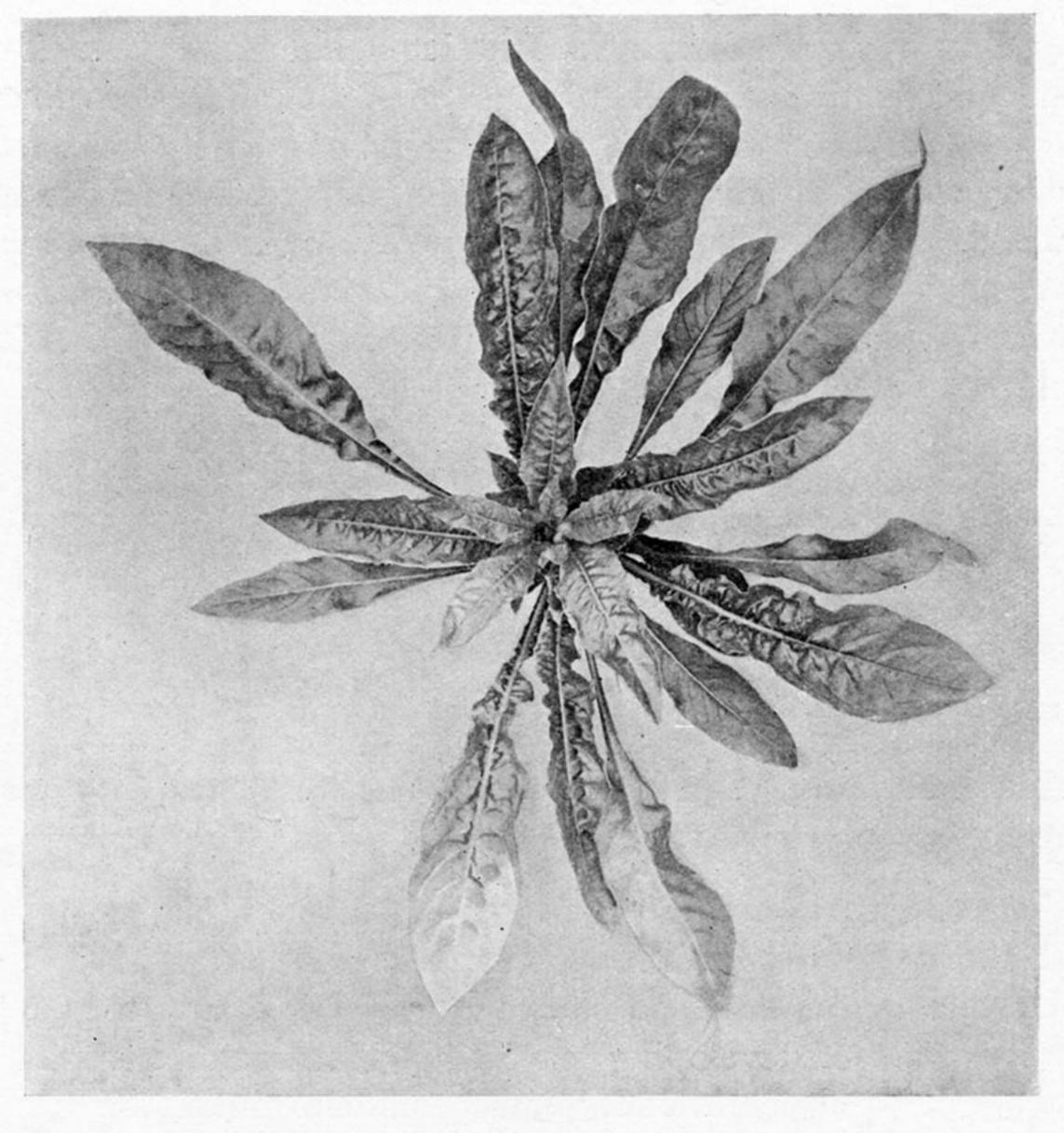


Fig. 5—O. novae-scotiae, rosette, culture 51.35.

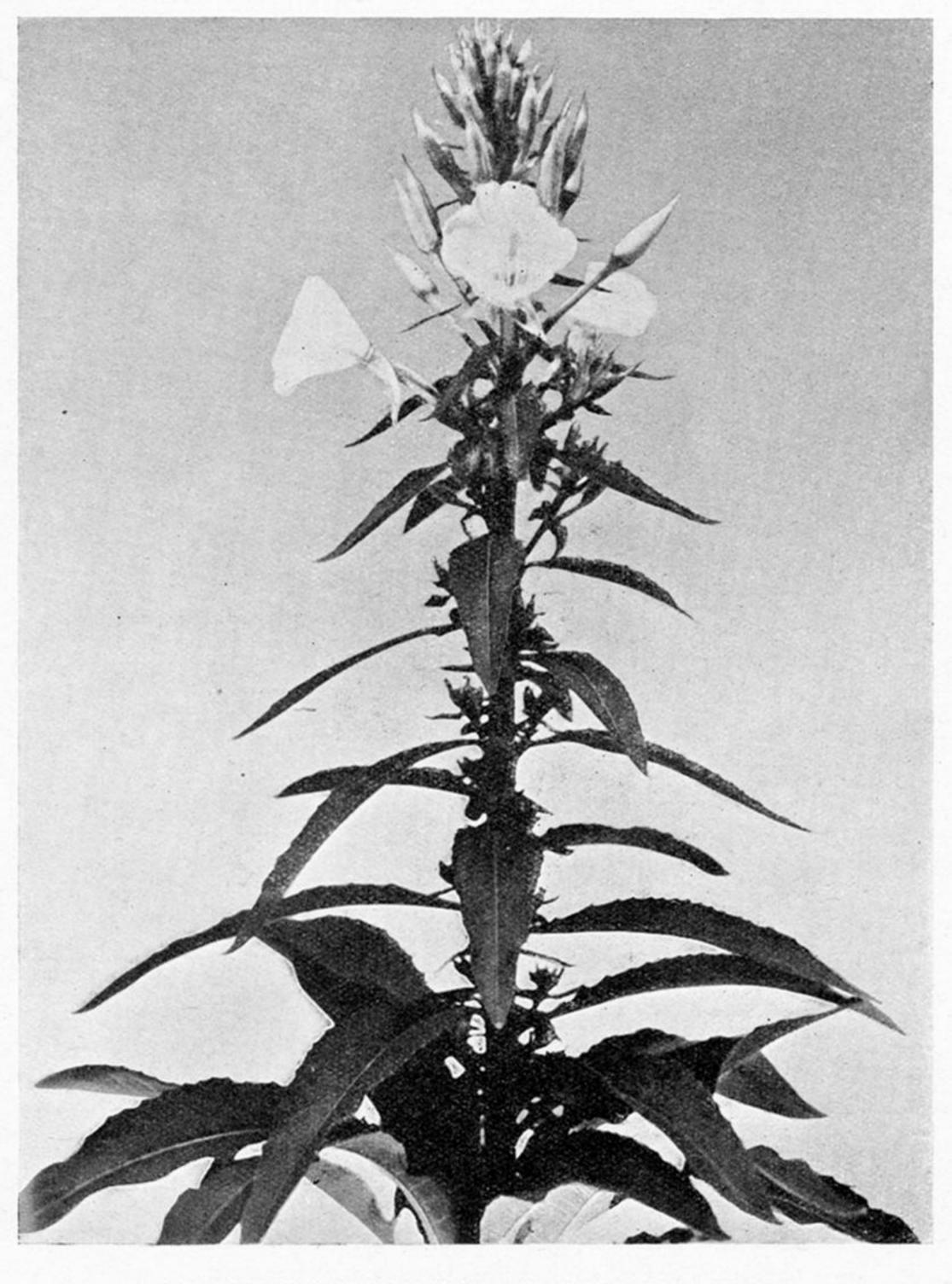


Fig. 6—O. novae-scotiae, in flower, culture 22.34.

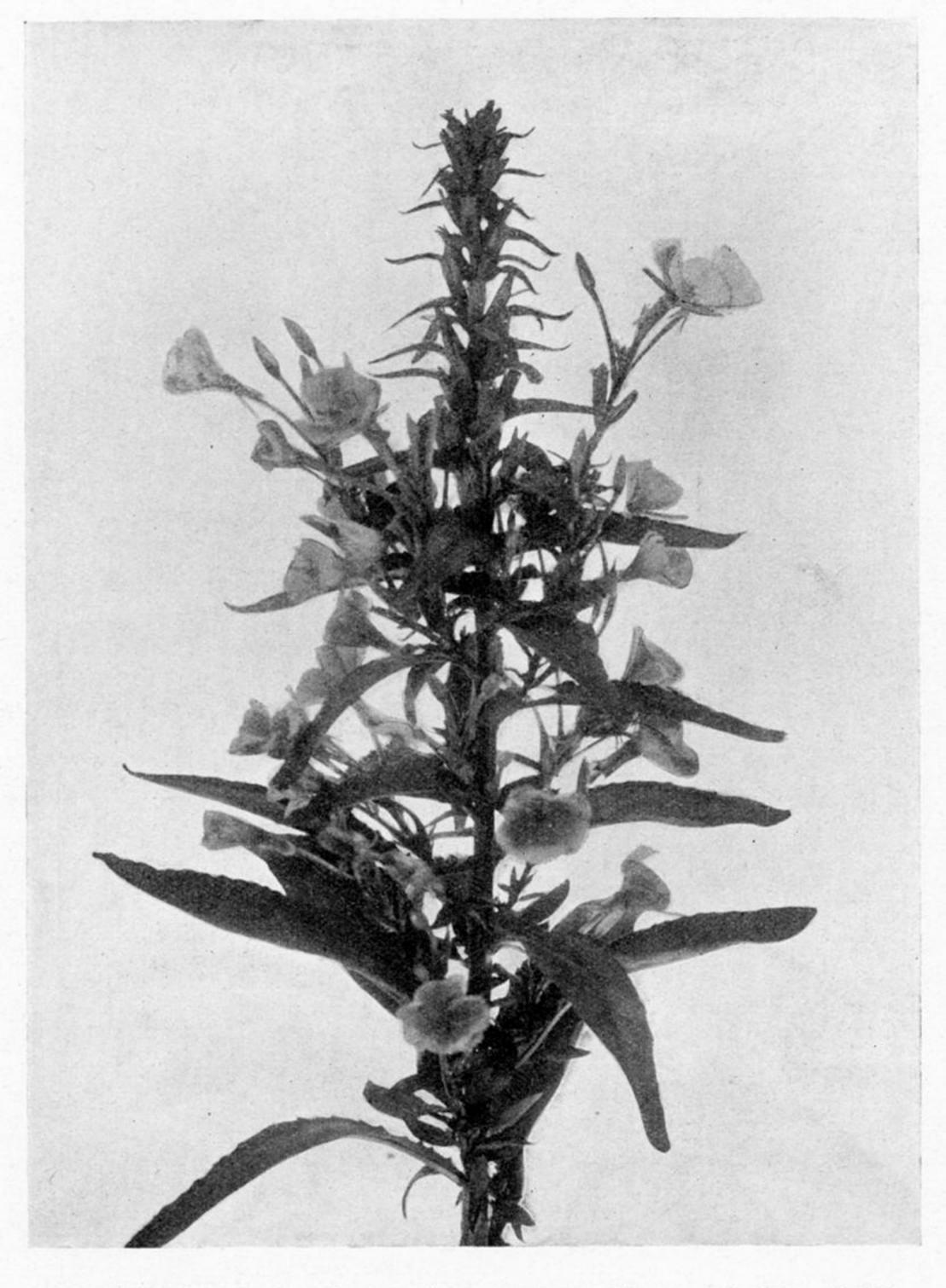


Fig. 7—O. novae-scotiae, strain with large flowers, culture 8.33.

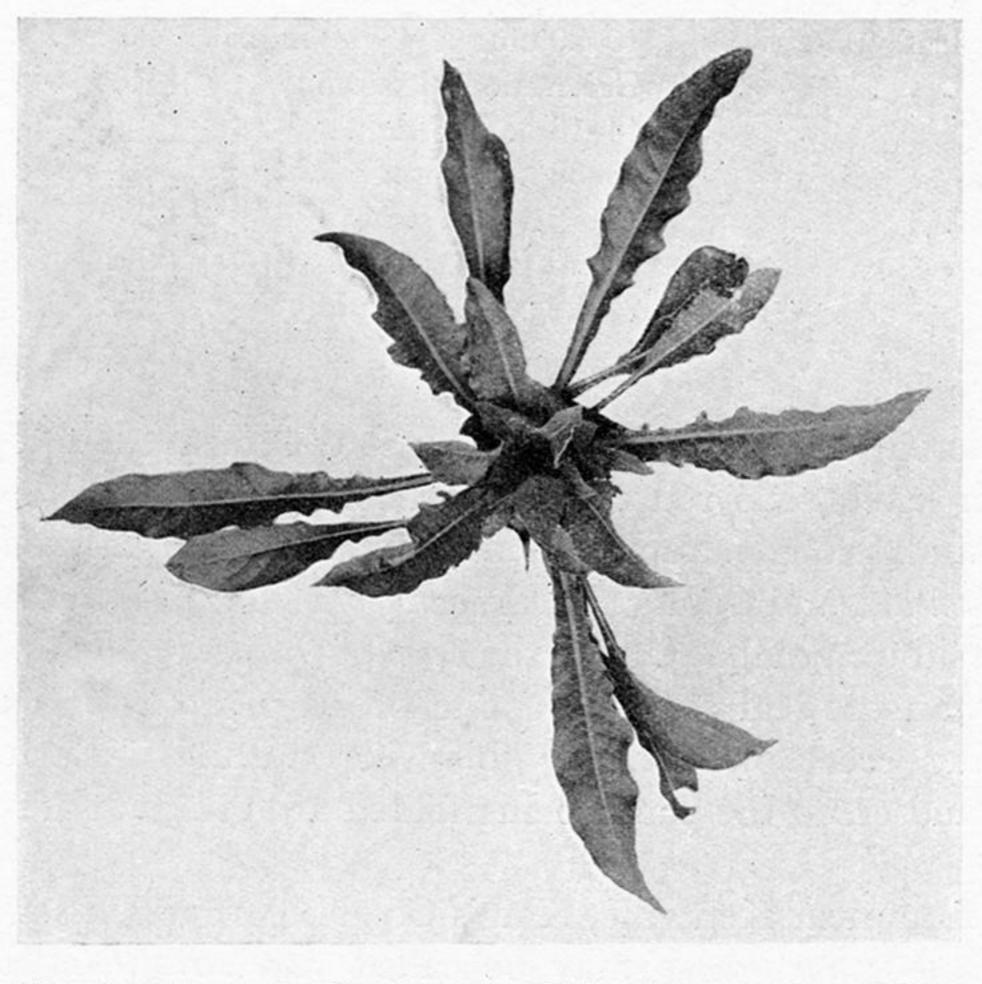


Fig. 8—O. novae-scotiae var. serratifolia, rosette, culture 9.33.

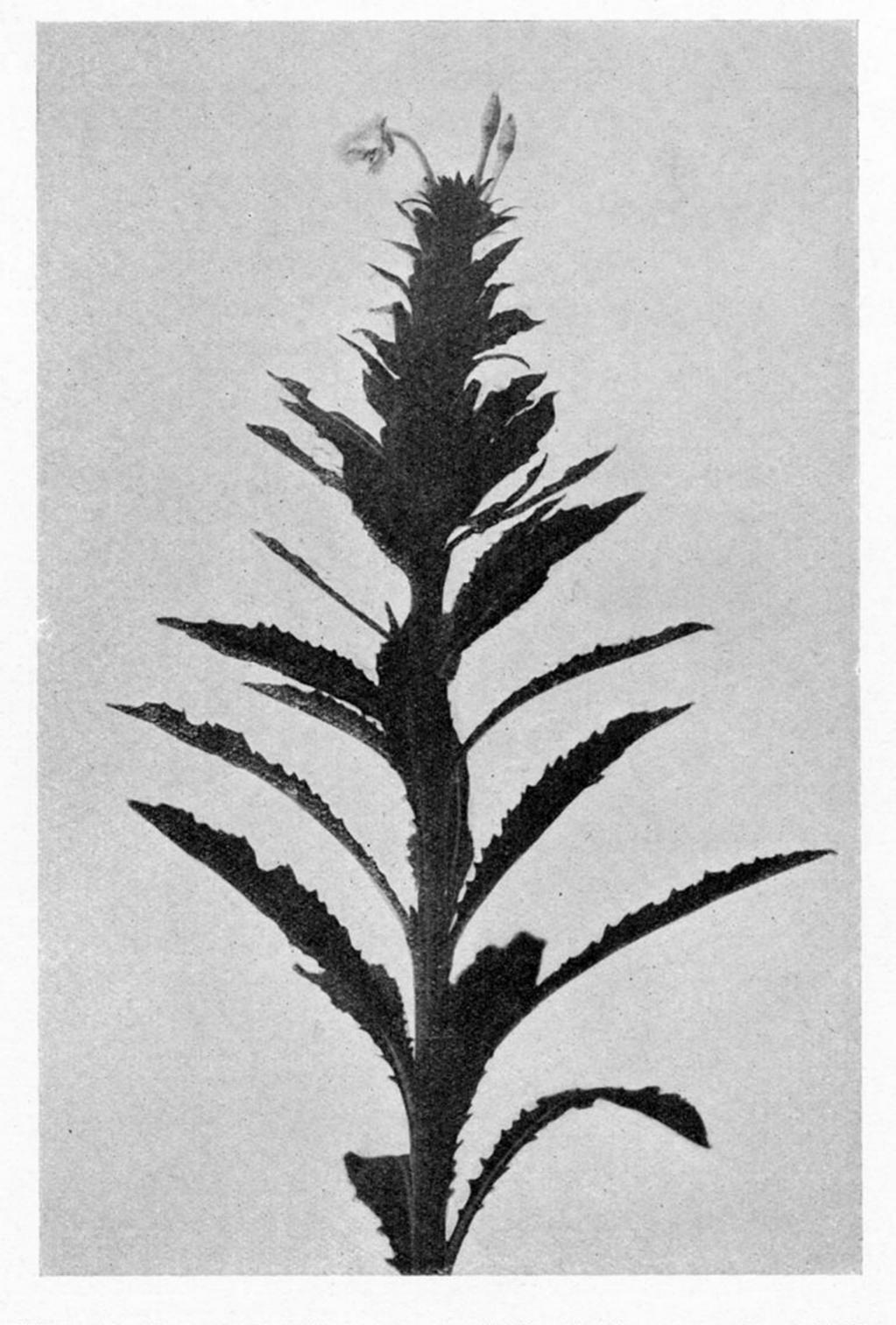


Fig. 9—O. novae-scotiae var. serratifolia, in flower, culture 9.33.

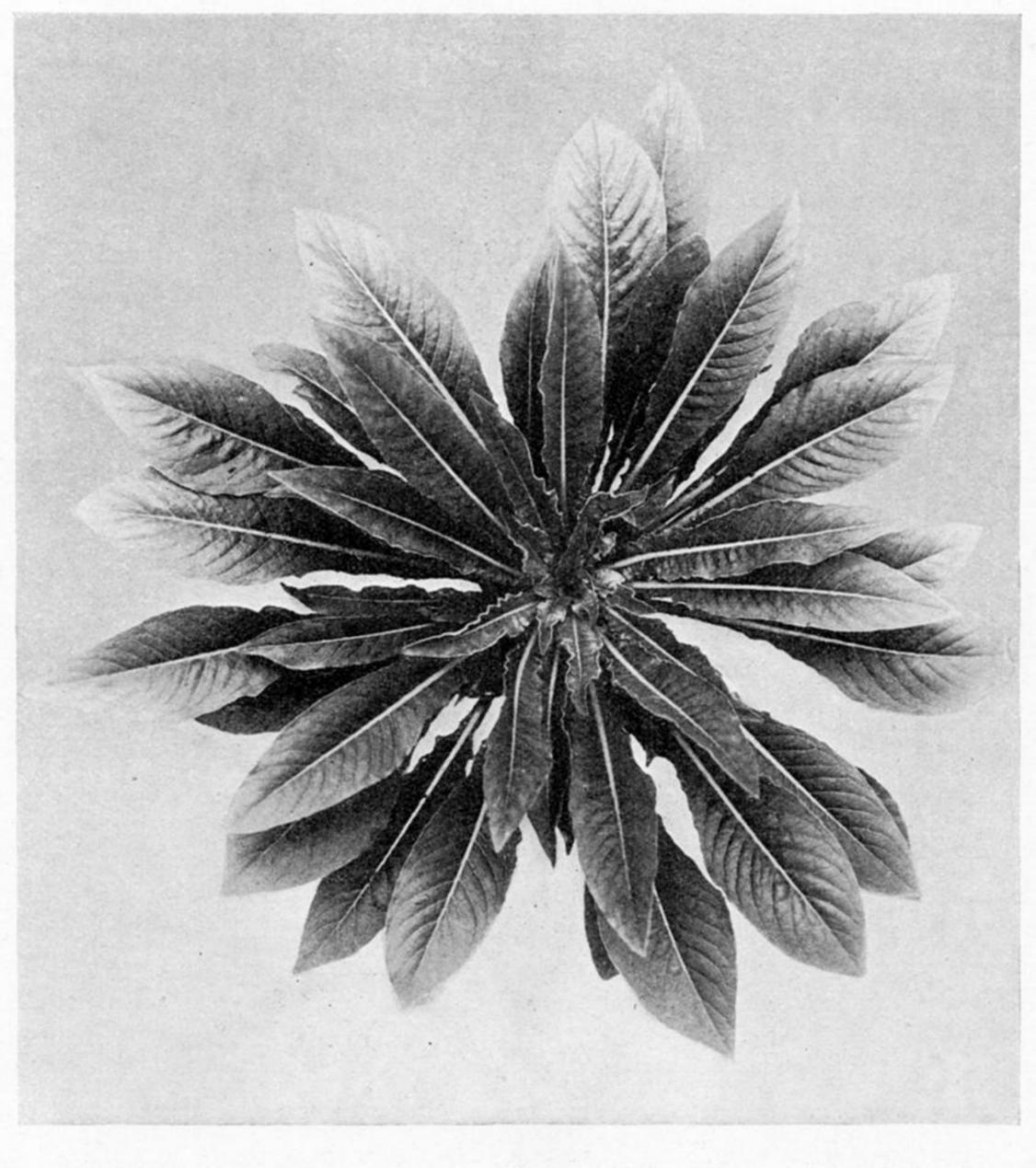


Fig. 10—O. novae-scotiae var. distantifolia, rosette, culture 29.34.



Fig. 11—O. novae-scotiae var. distantifolia, in flower, culture 29.34.

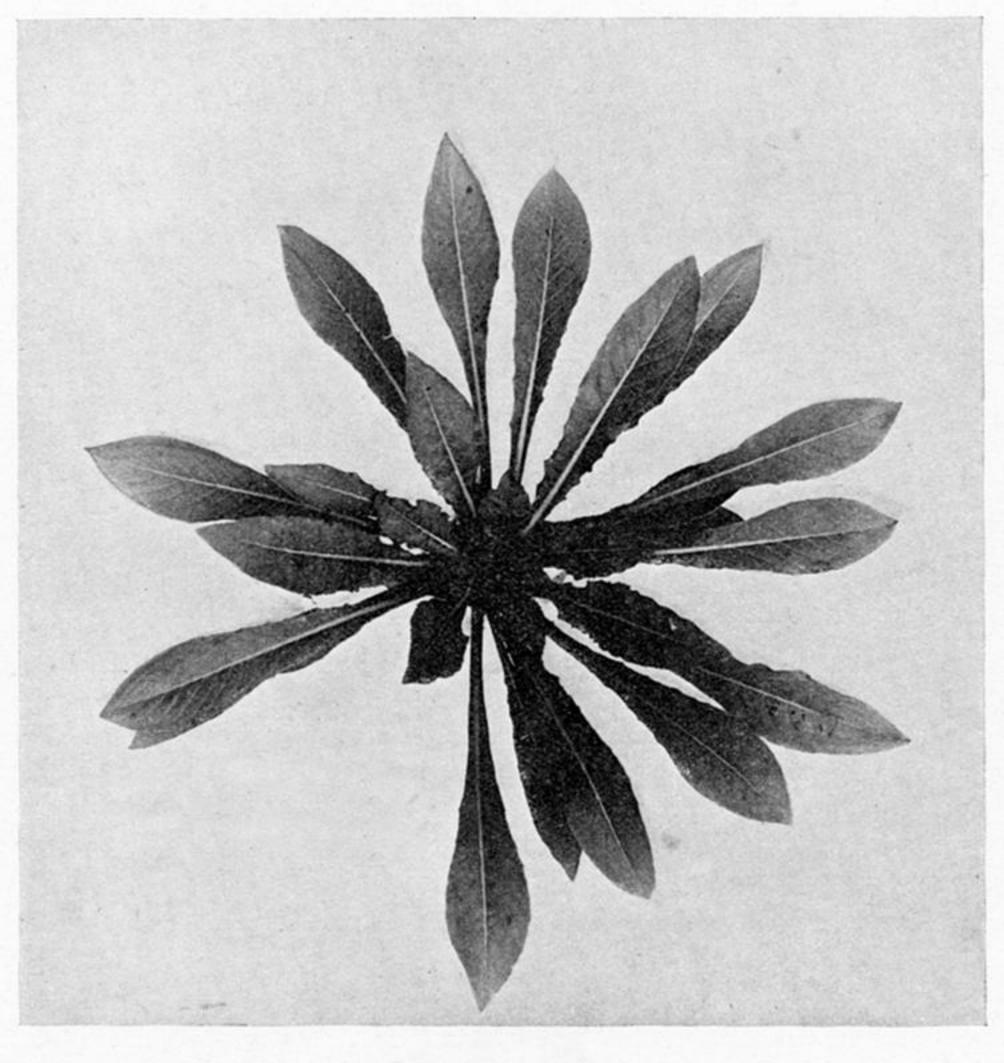


Fig. 12—O. comosa, rosette, culture 23.34.

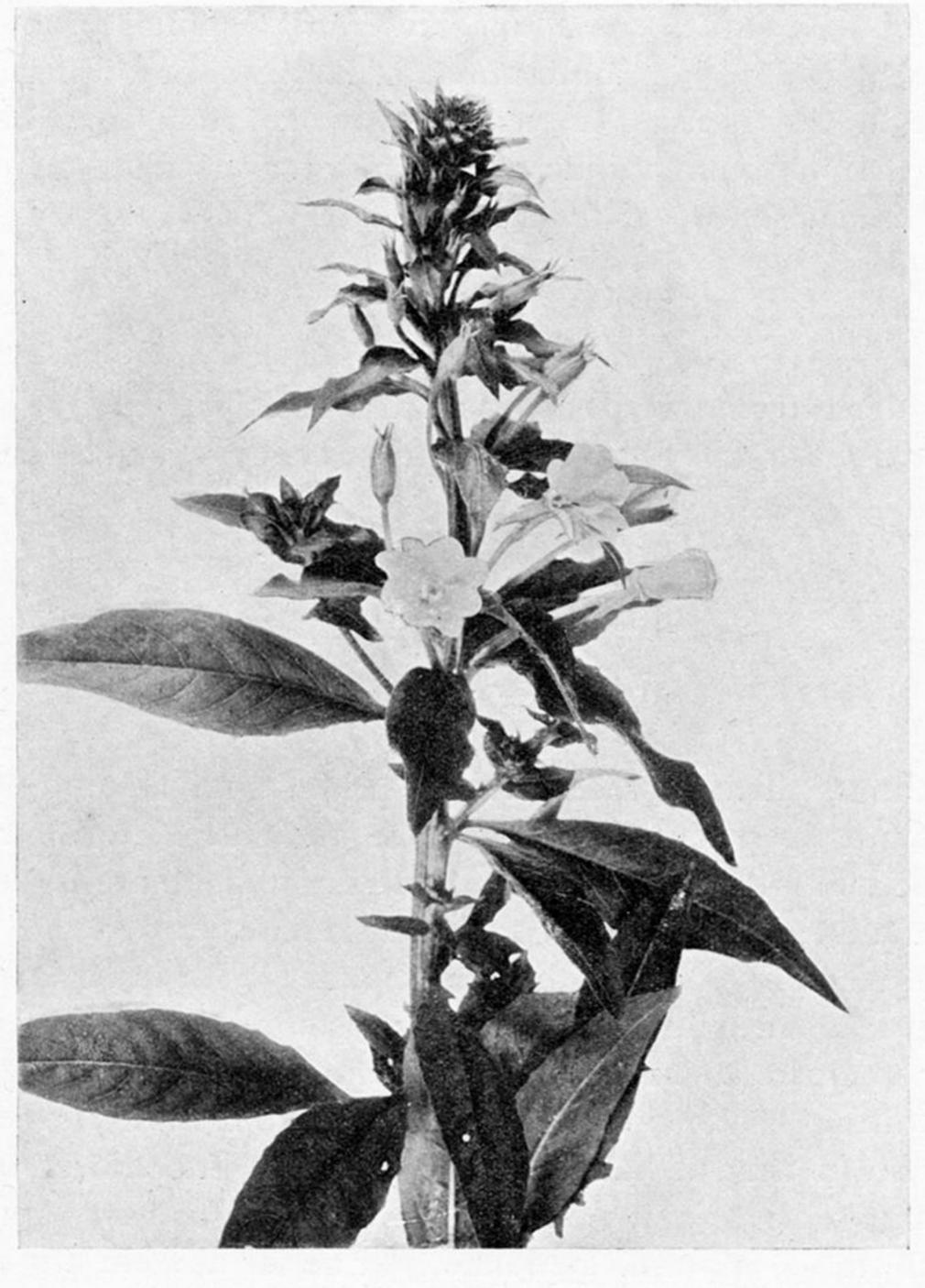


Fig. 13—O. comosa, in flower, culture 23.34.

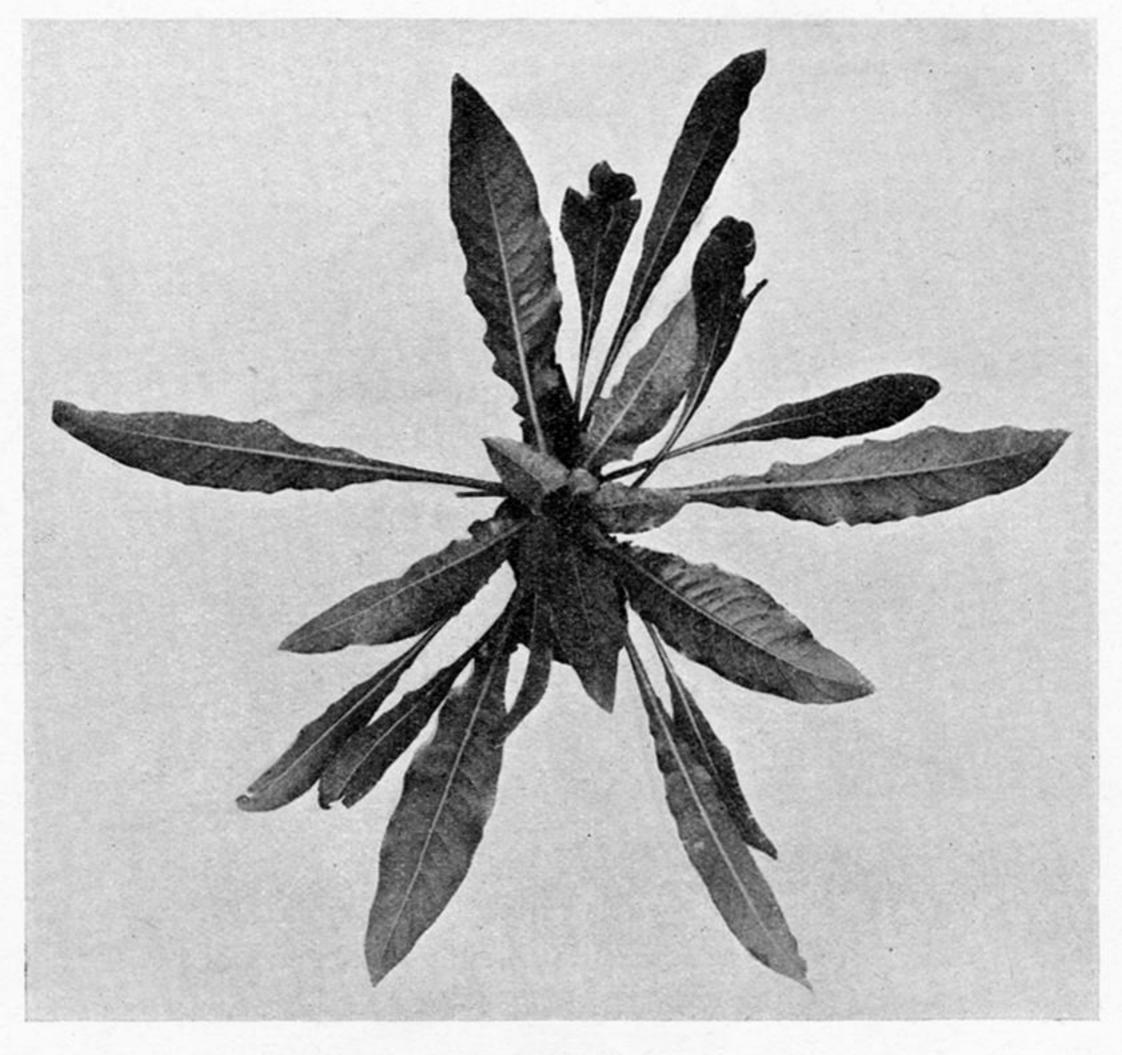


Fig. 14-O. intermedia, rosette, culture 3.33.



Fig. 15—O. intermedia, in flower, culture 50.35.

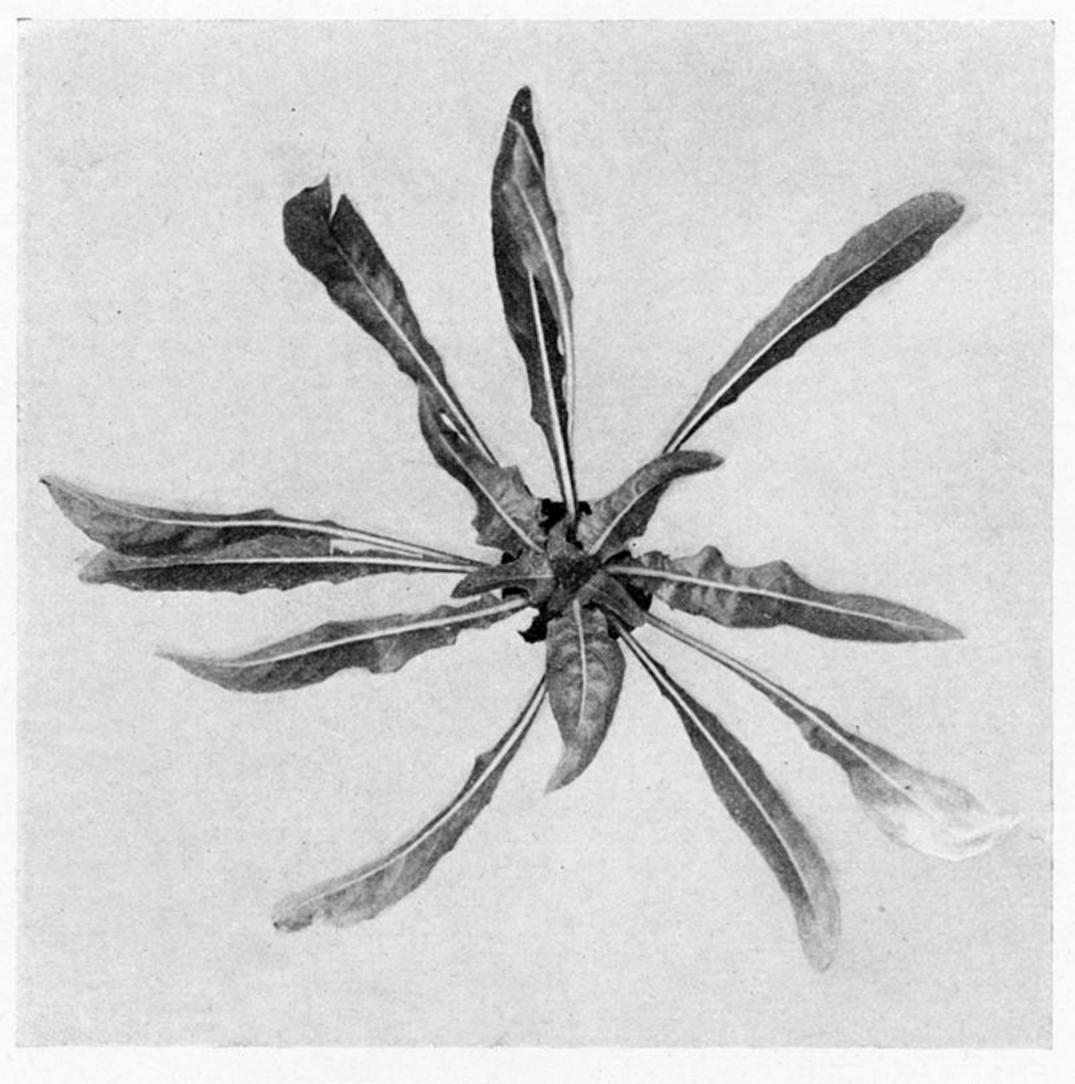


Fig. 16—O. flecticaulis, rosette, culture 78.33.



Fig. 17—0. flecticaulis, in flower, culture 103.34.

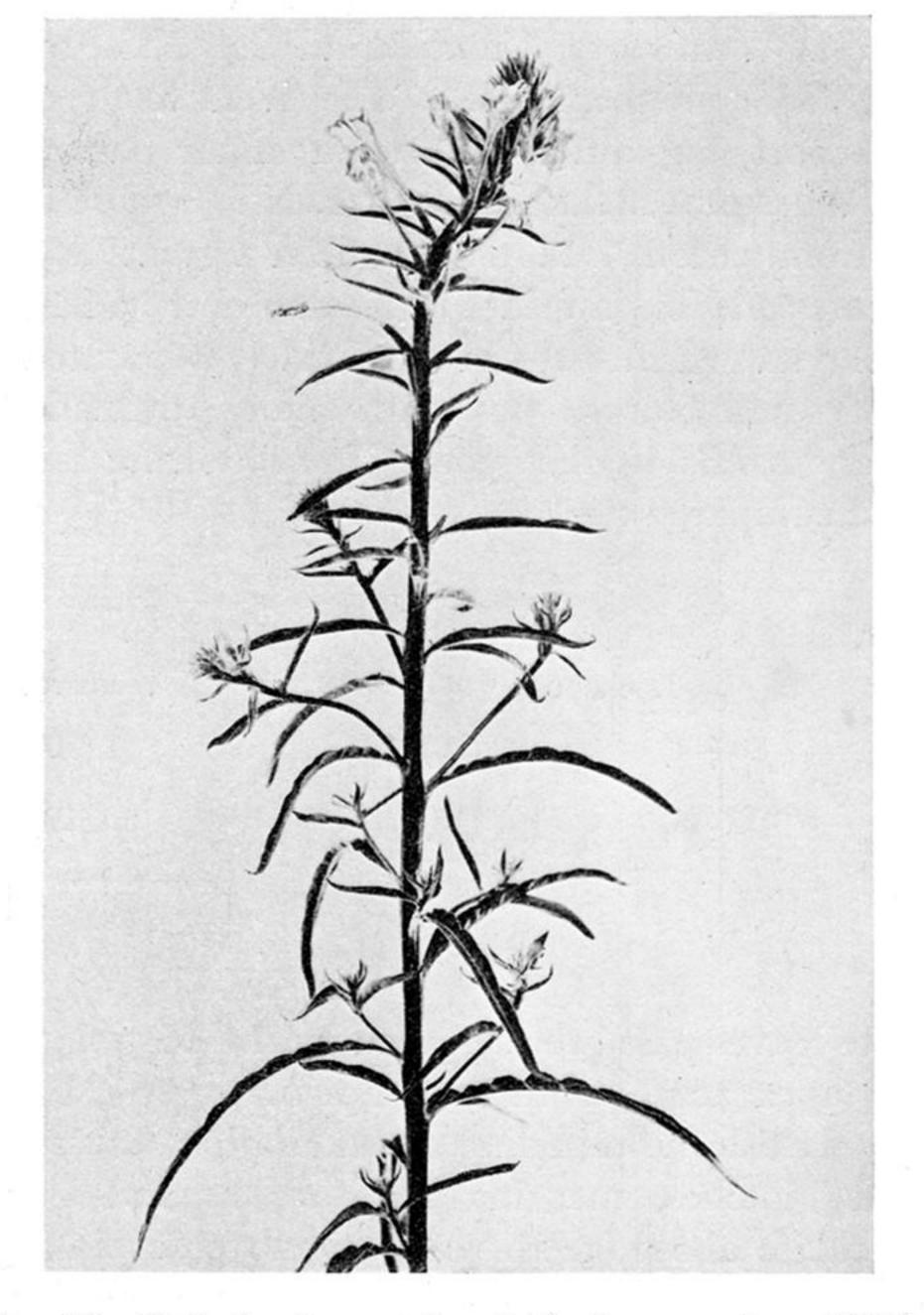


Fig. 18—O. flecticaulis mut. linearis, in flower, culture 79.33.

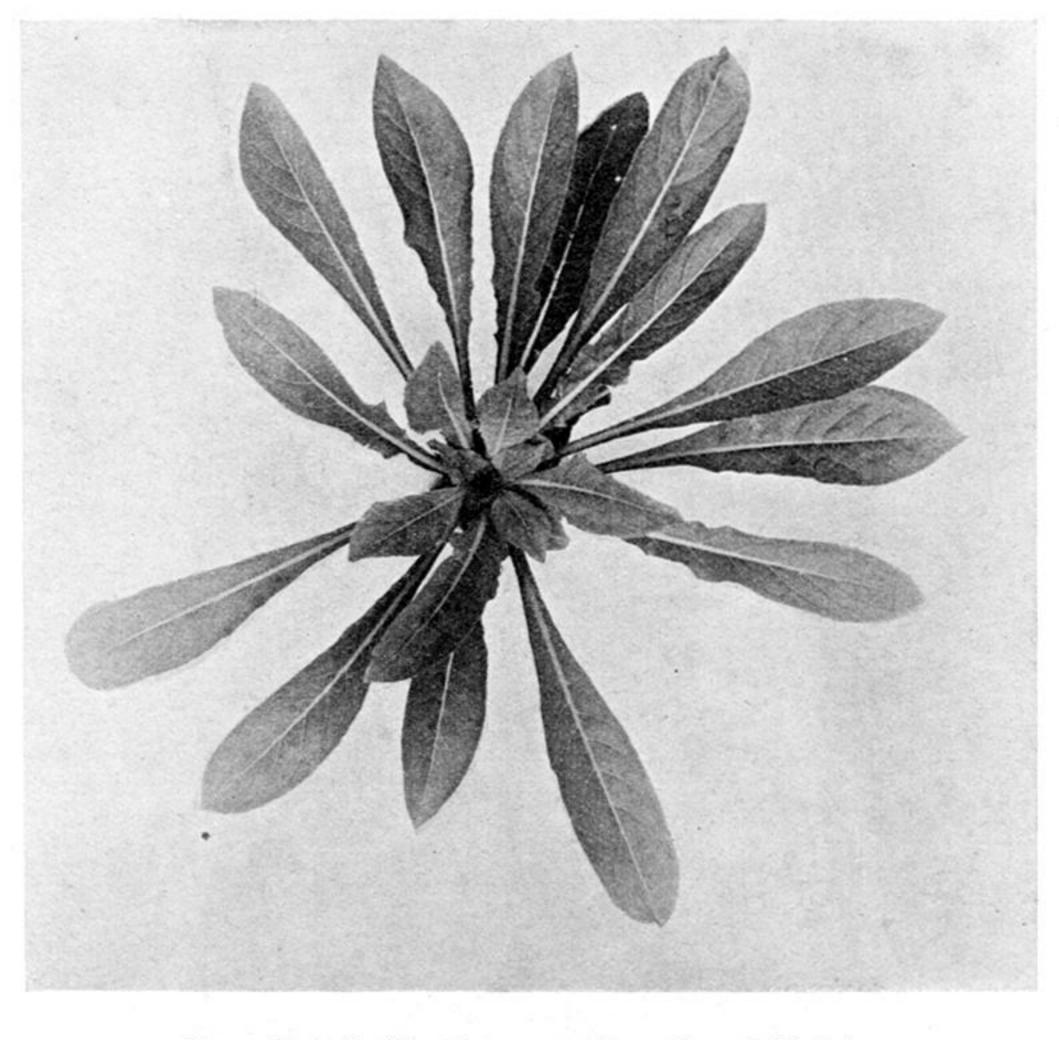


Fig. 19—0. Hazelae, rosette, culture 30.34.



Fig. 20—O. Hazelae, in flower, culture 105.34.



Fig. 21—O. Hazelae, in flower, culture 30.34.

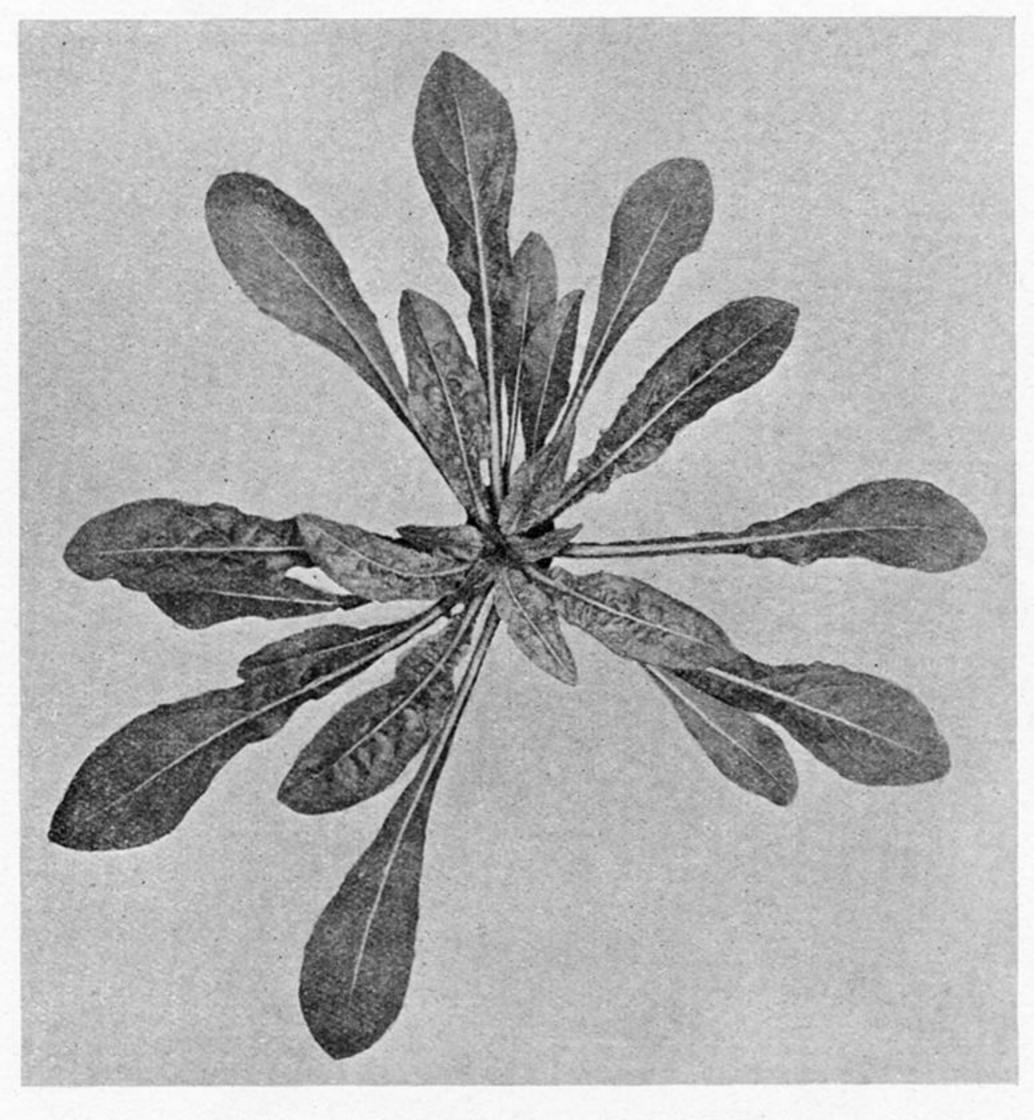


Fig. 22—O. Hazelae var. parviflora, rosette, culture 107.35.

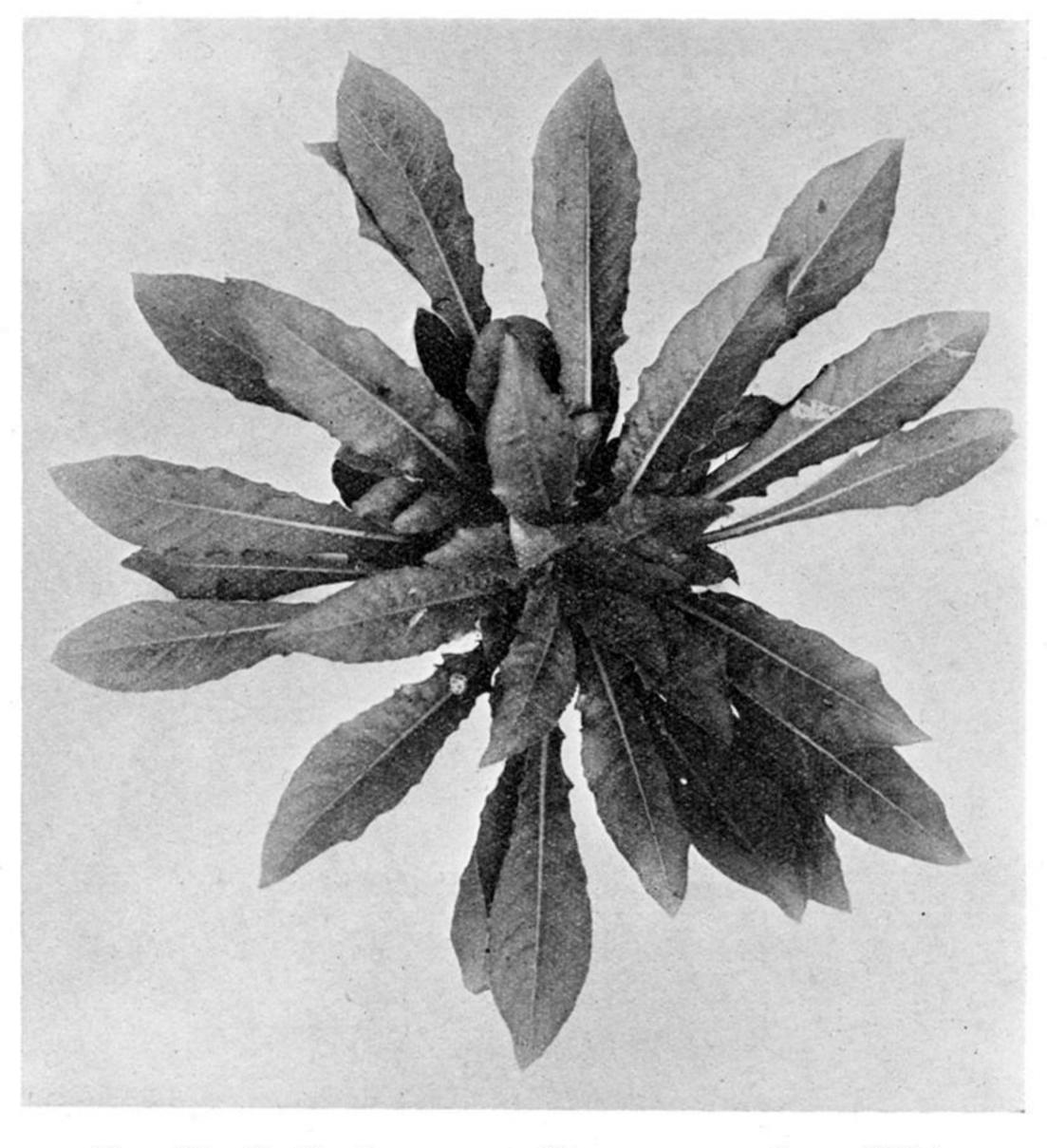


Fig. 23—O. Hazelae var. parviflora, rosette, culture 26.34.



Fig. 24—O. Hazelae var. parviflora, habit, culture 54.35.

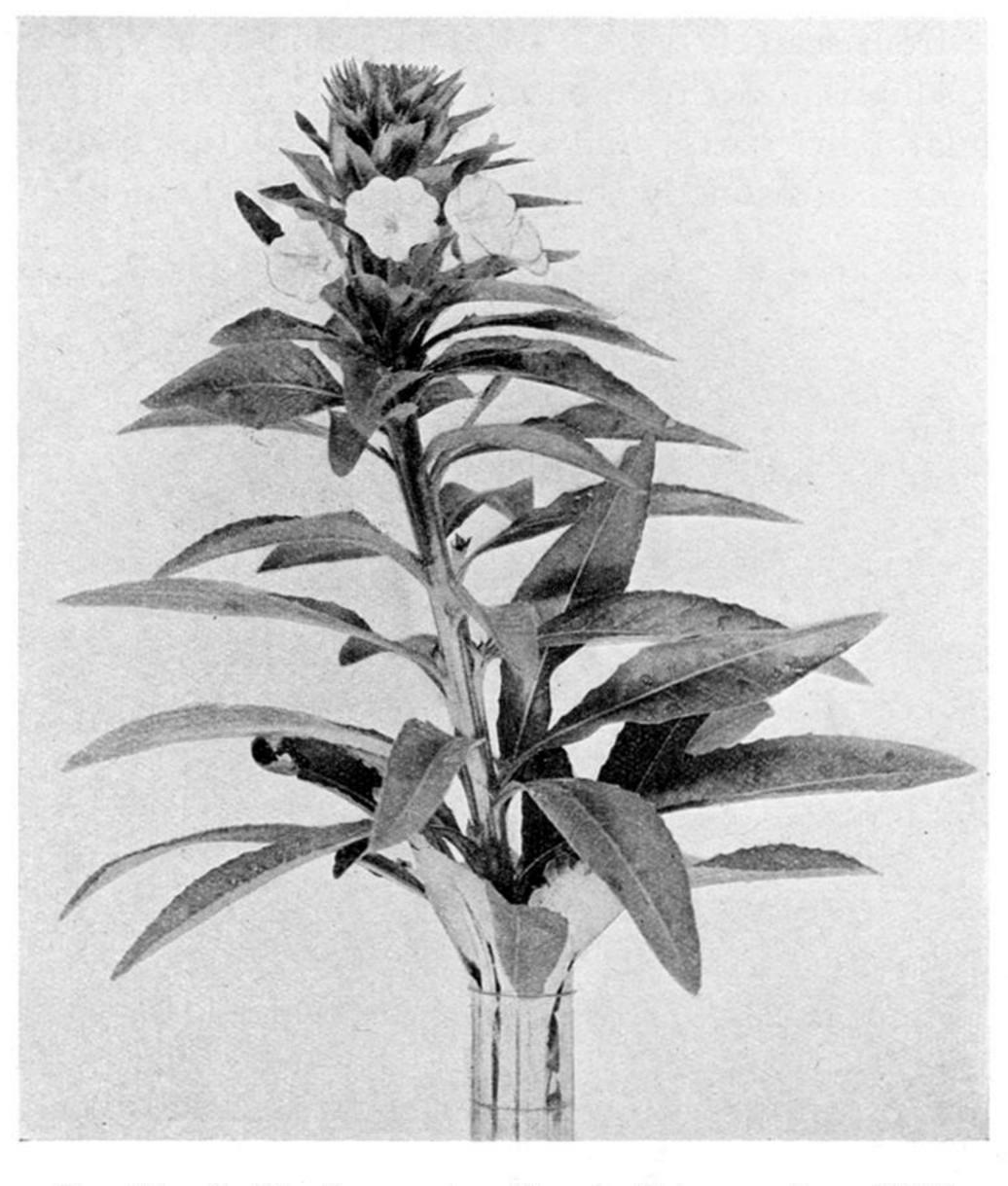


Fig. 25—O. Hazelae var. parviflora, in flower, culture 26.34.

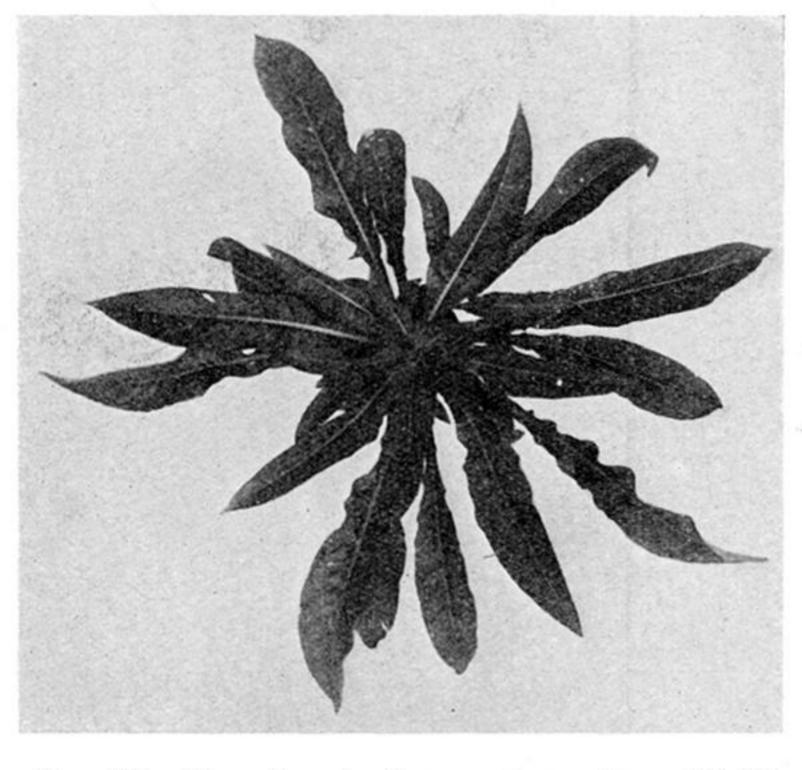


Fig. 26—O. subterminalis, rosette, culture 13.33.

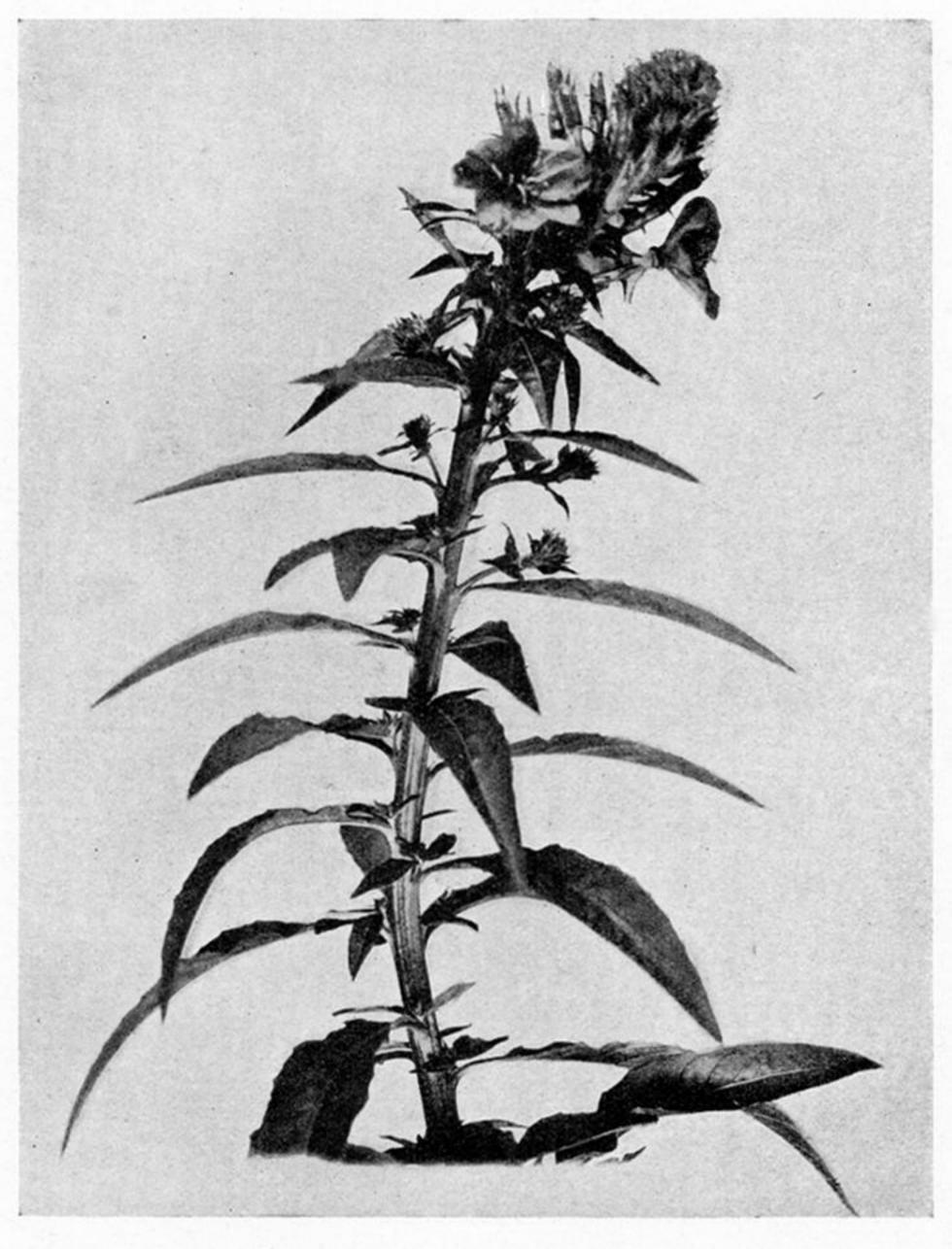


Fig. 27—O. subterminalis, in flower, culture 34.34.

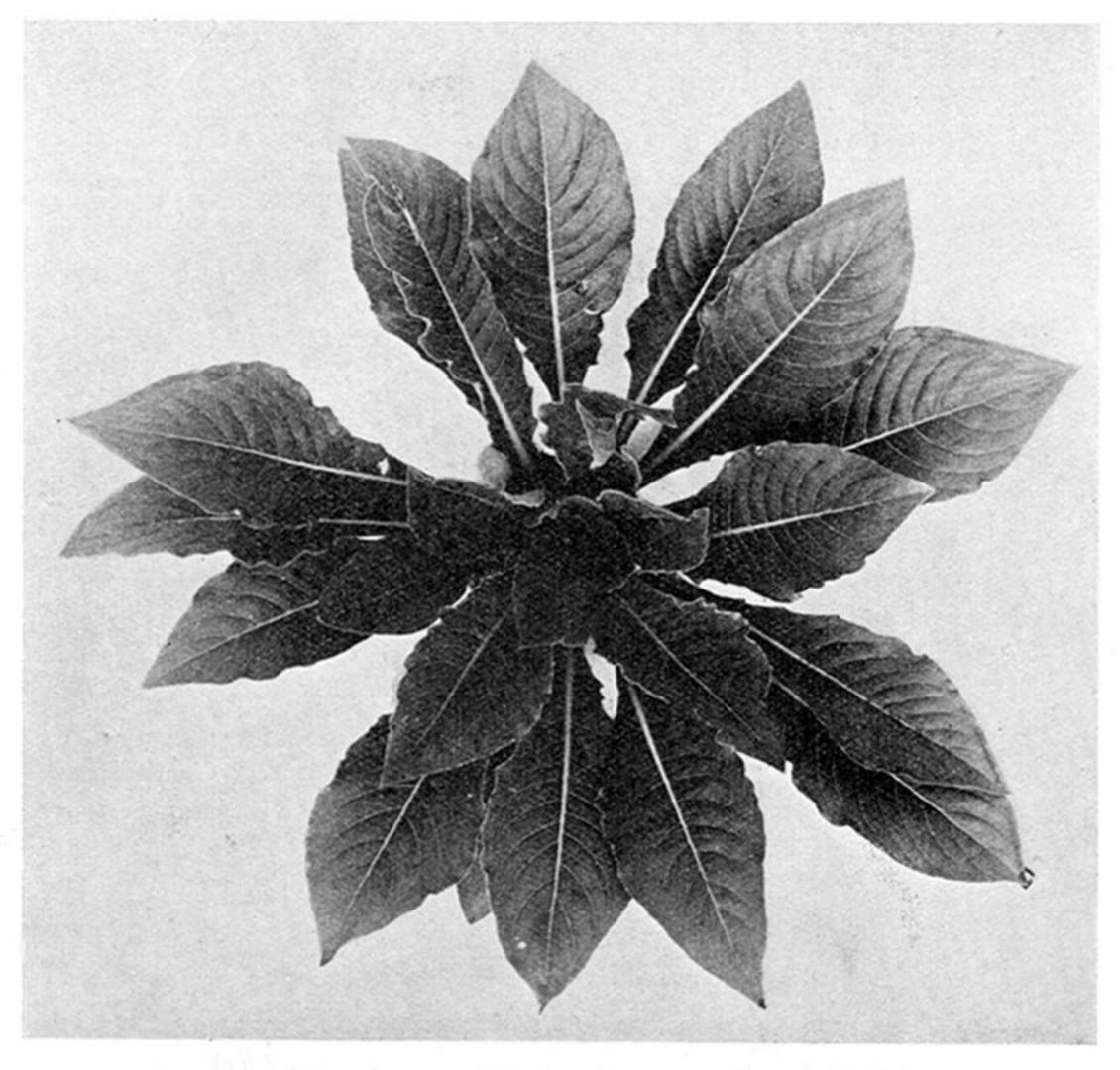


Fig. 28—O. grandiflora, rosette, culture 31.34.



Fig. 29—O. grandiflora, in flower, culture 15.33.

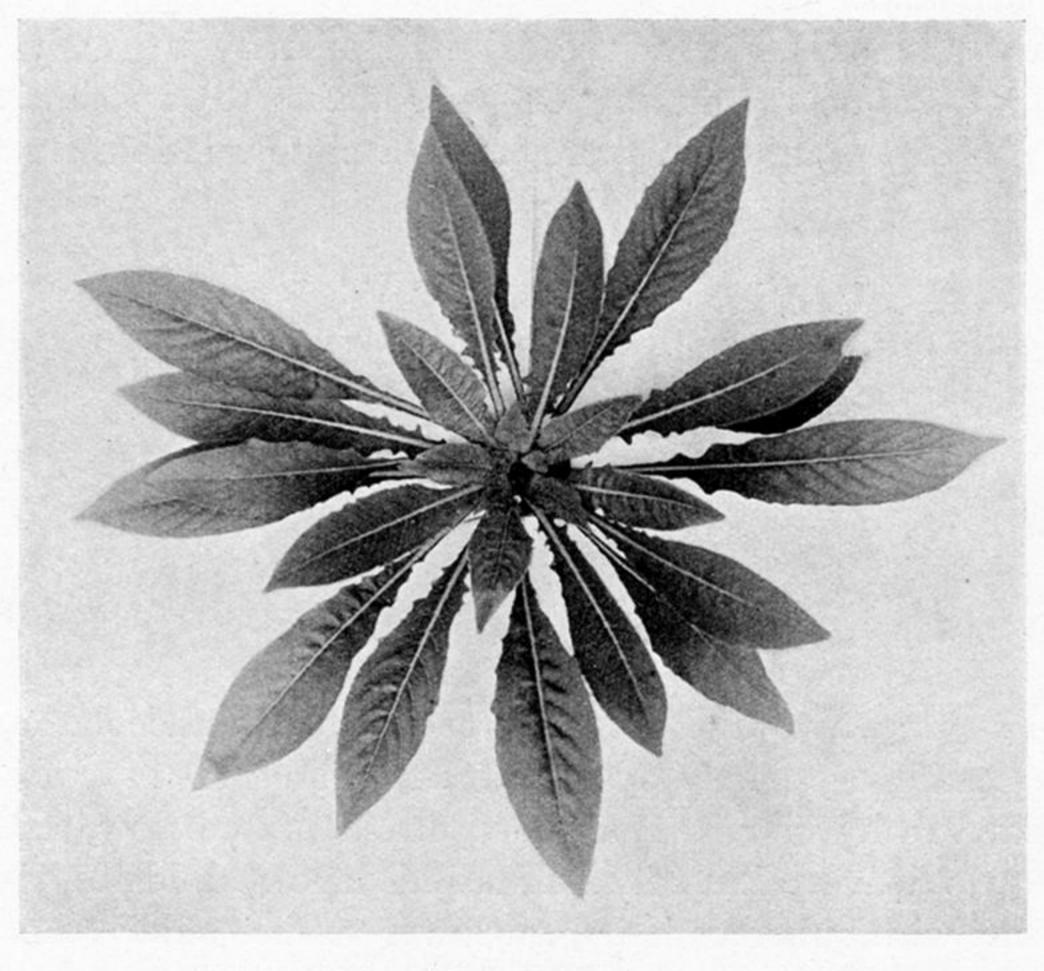


Fig. 30—O. Royfraseri, rosette, culture 1.34.



Fig. 31—O. Royfraseri, in flower, culture 1.34.

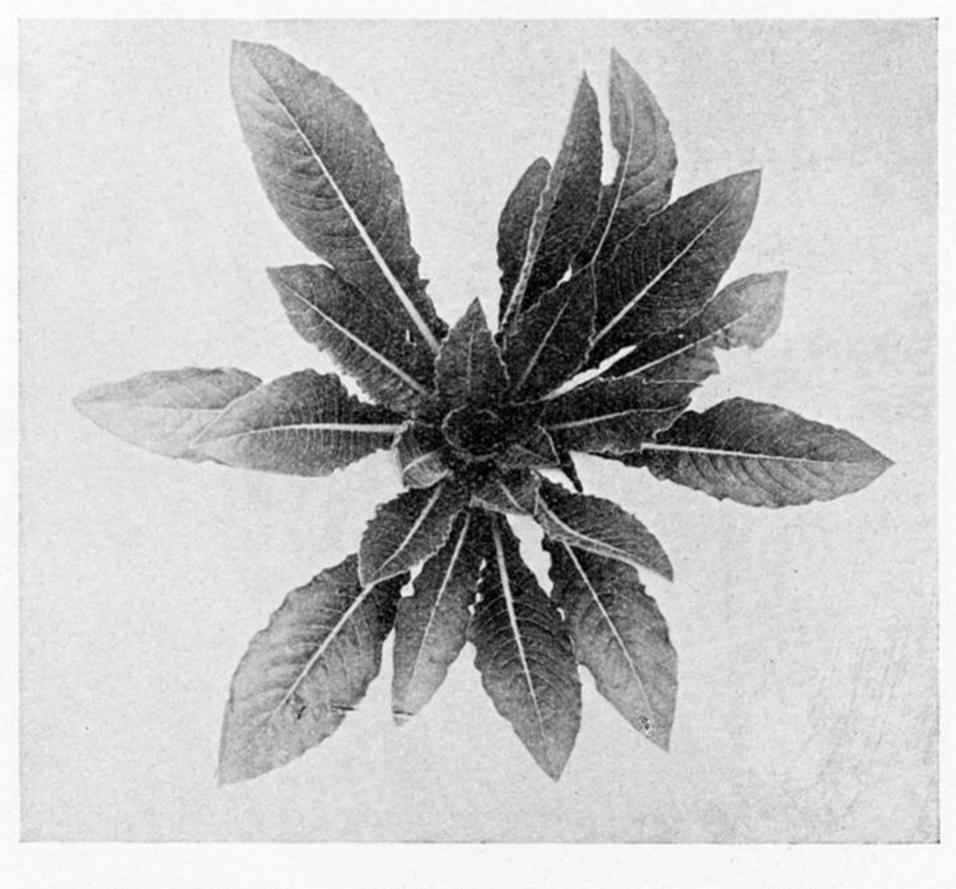


Fig. 32—O. sackvillensis, rosette, culture 38.34.

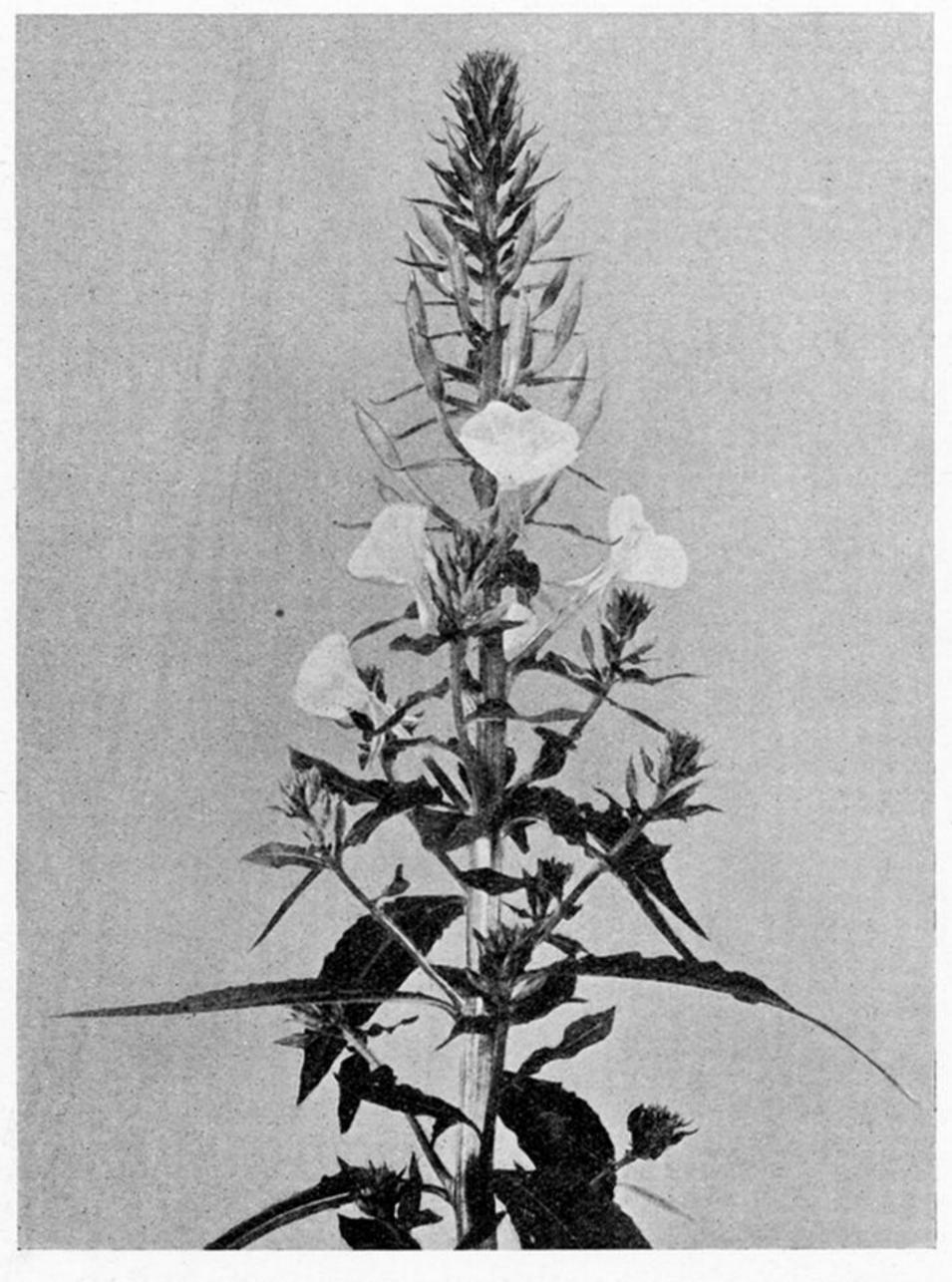


Fig. 33—O. sackvillensis, in flowers, culture 40.34.

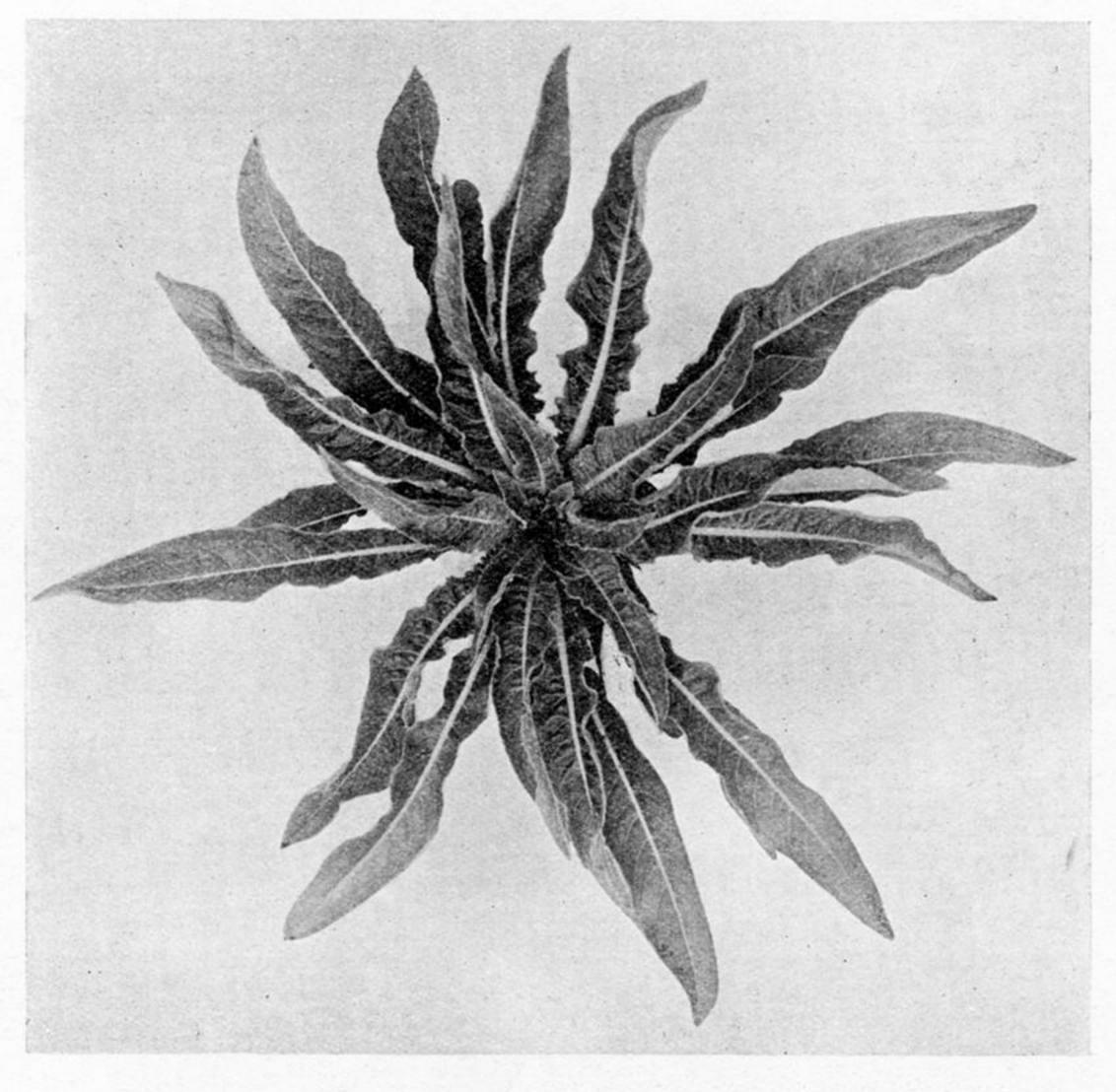


Fig. 34—O. sackvillensis, seg. albiviridia, rosette, culture 40.34.



Fig. 35—O. sackvillensis var. albiviridia, in flower, culture 40.34.

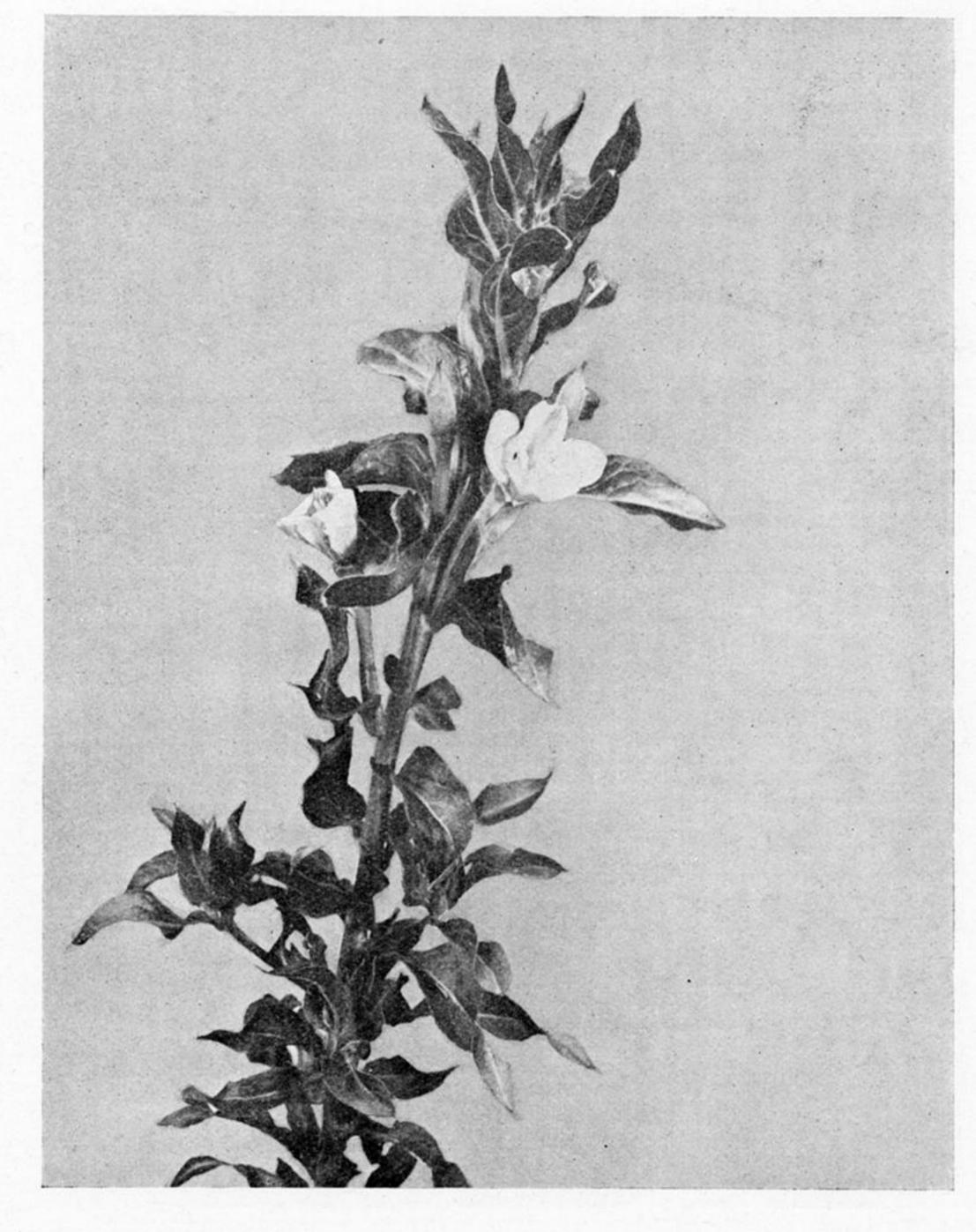


Fig. 36—O. sackvillensis, trisomic dwarf mutation, in culture 65.35.

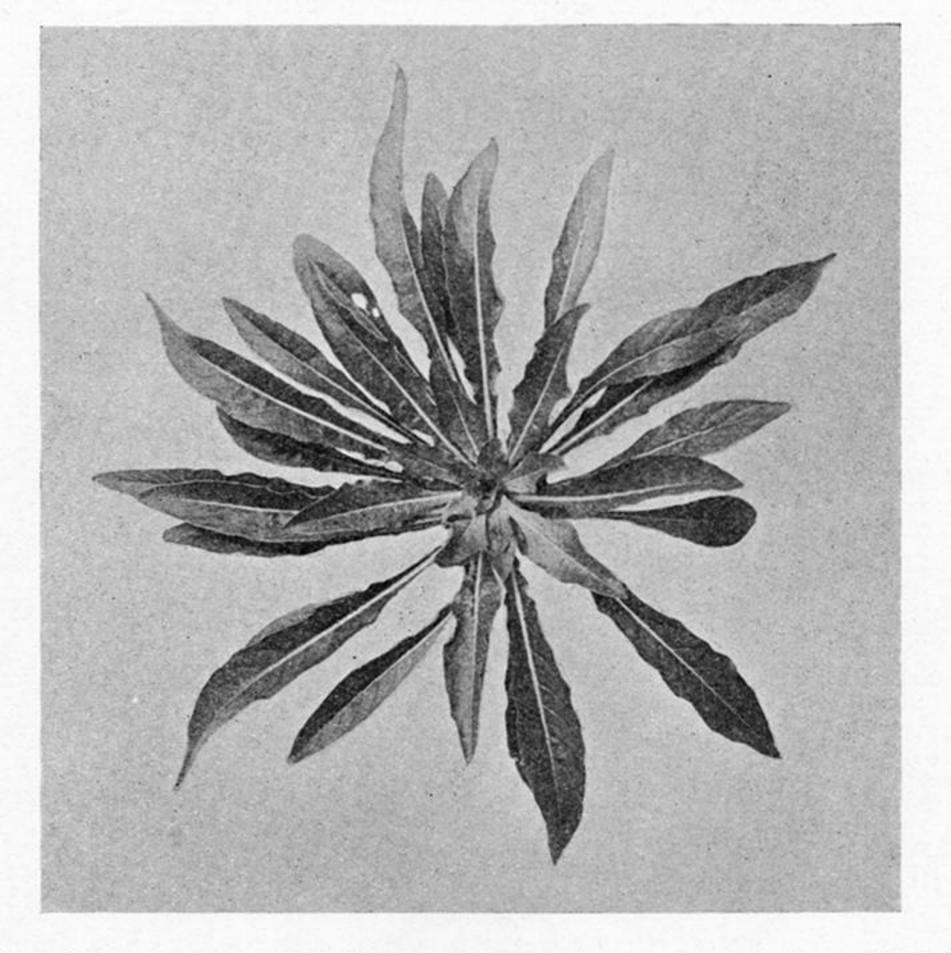


Fig. 37—O. ammophiloides var. laurensis, rosette, culture 22.33.

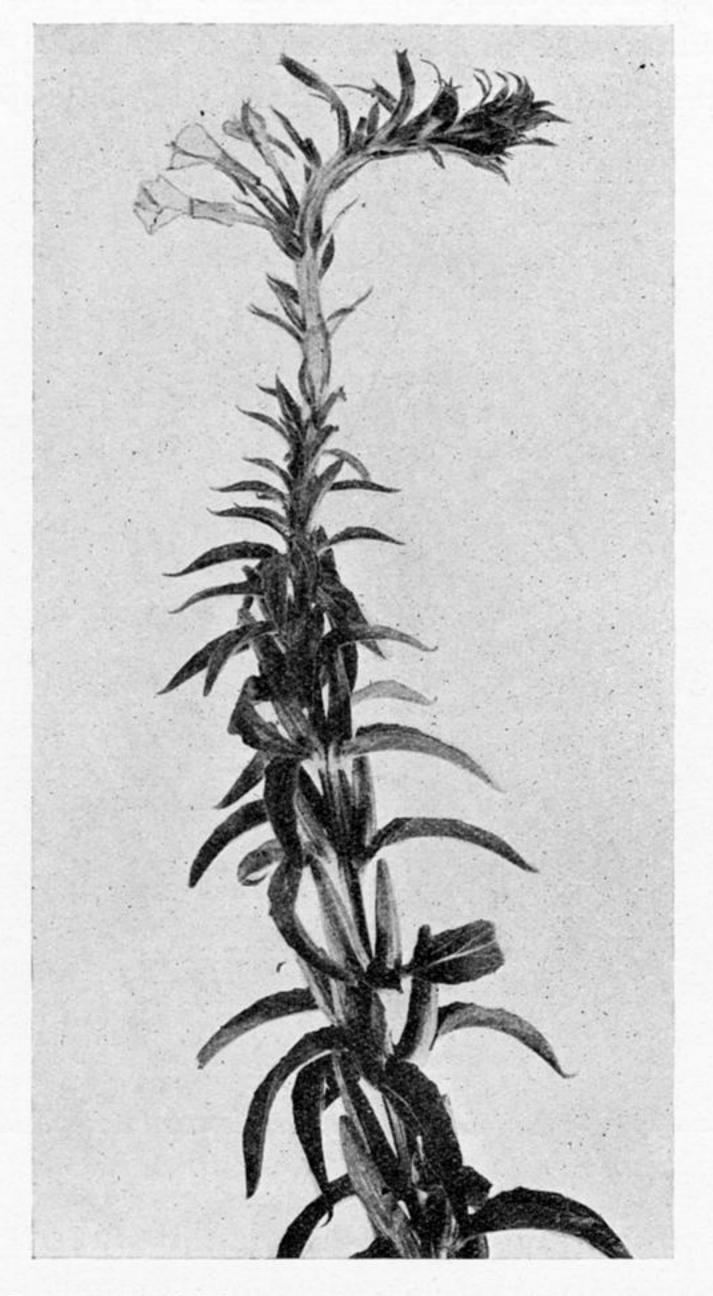


Fig. 38—O. ammophiloides var. laurensis, in flower, culture 19.33.



Fig. 39—O. ammophiloides var. laurensis mut. linearis, culture 43.34.

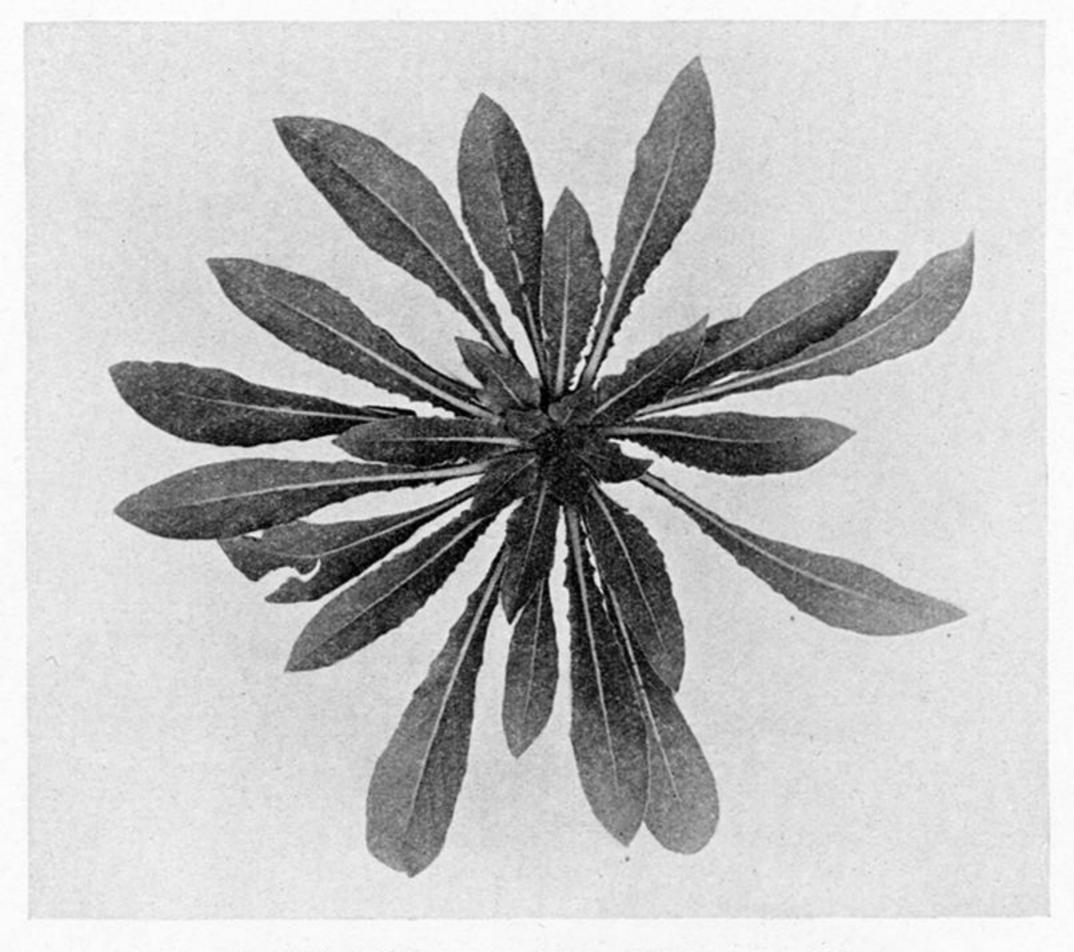


Fig. 40—O. parva, rosette, culture 47.34.



Fig. 41—O. parva, in flower, culture 70.35.

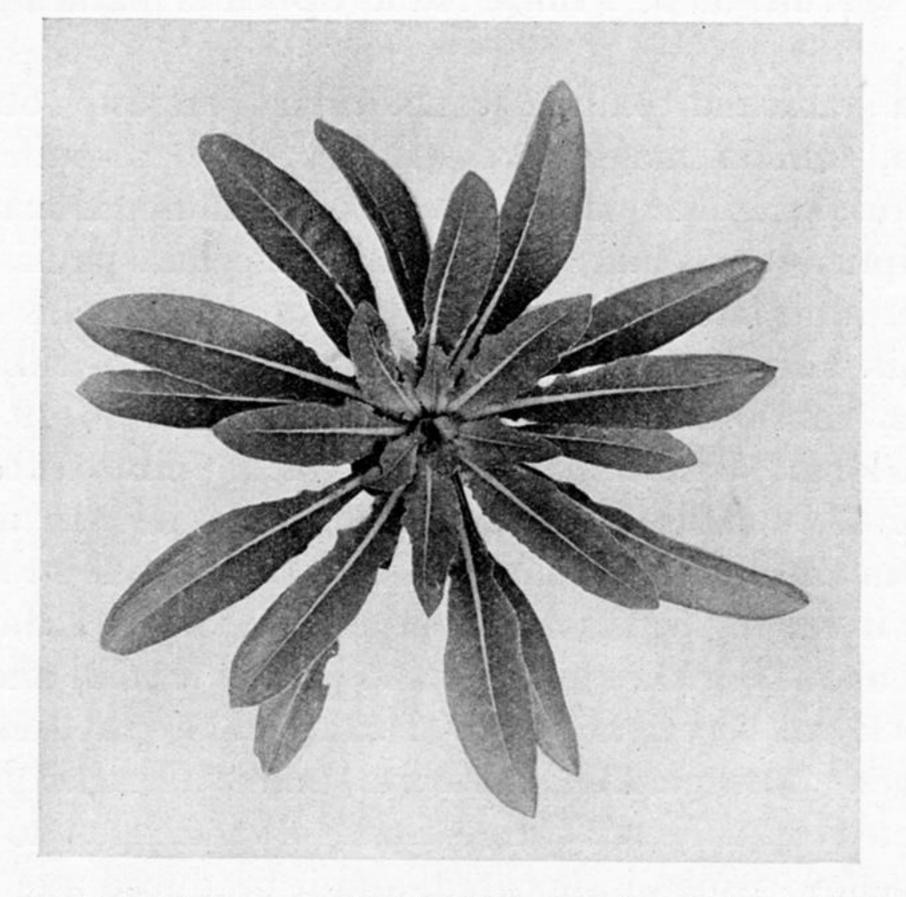


Fig. 42—O. parva mut. hebetifolia, rosette, culture 50.34.

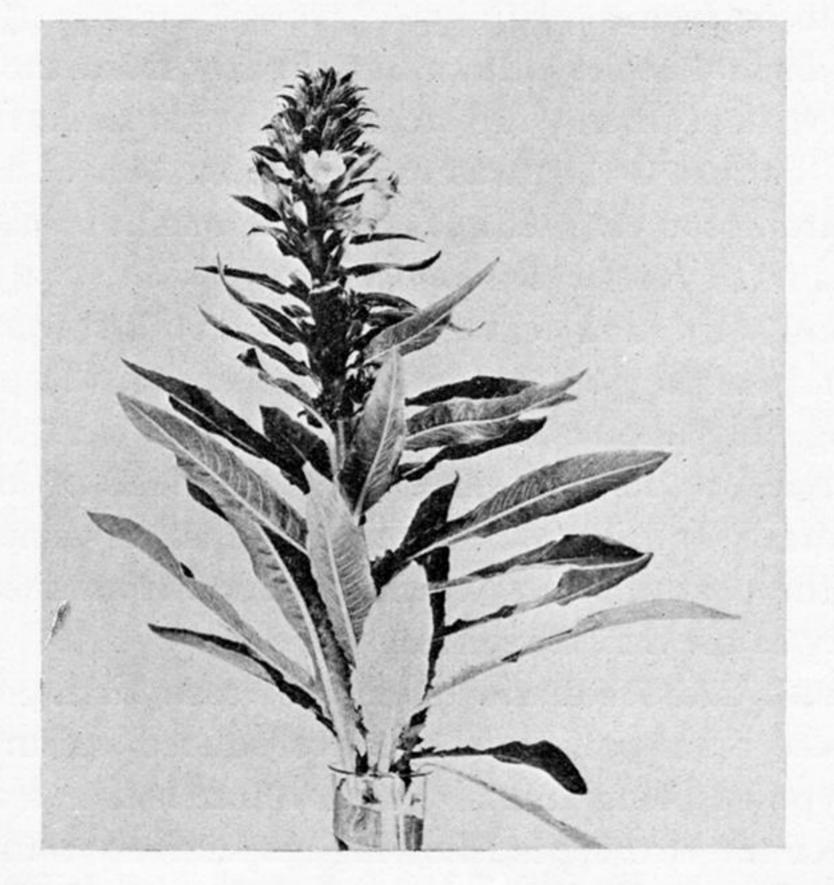


Fig. 43—O. parva mut. hebetifolia, in flower, culture 50.34.

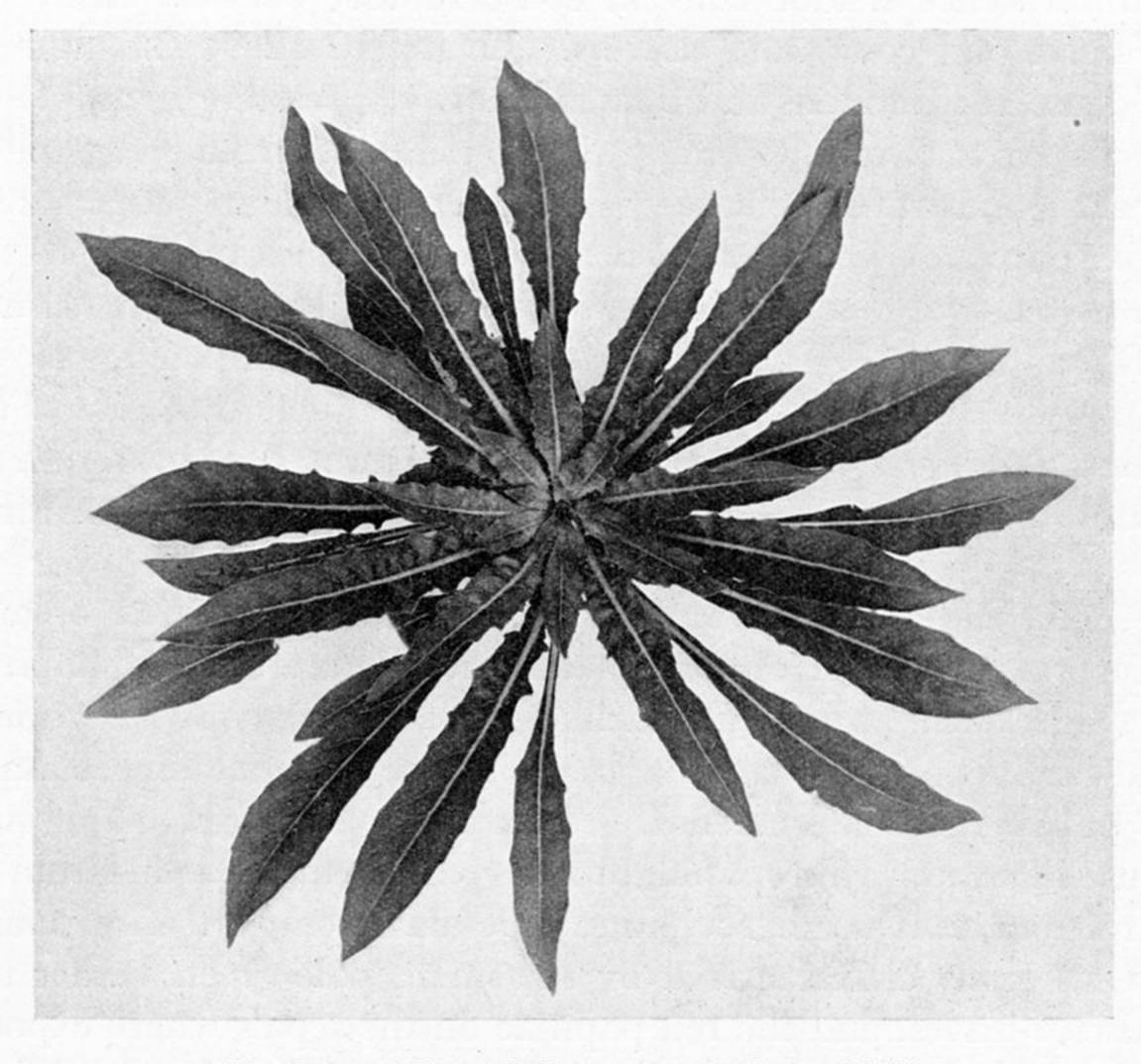


Fig. 44—O. leucophylla, rosette, culture 59.34.

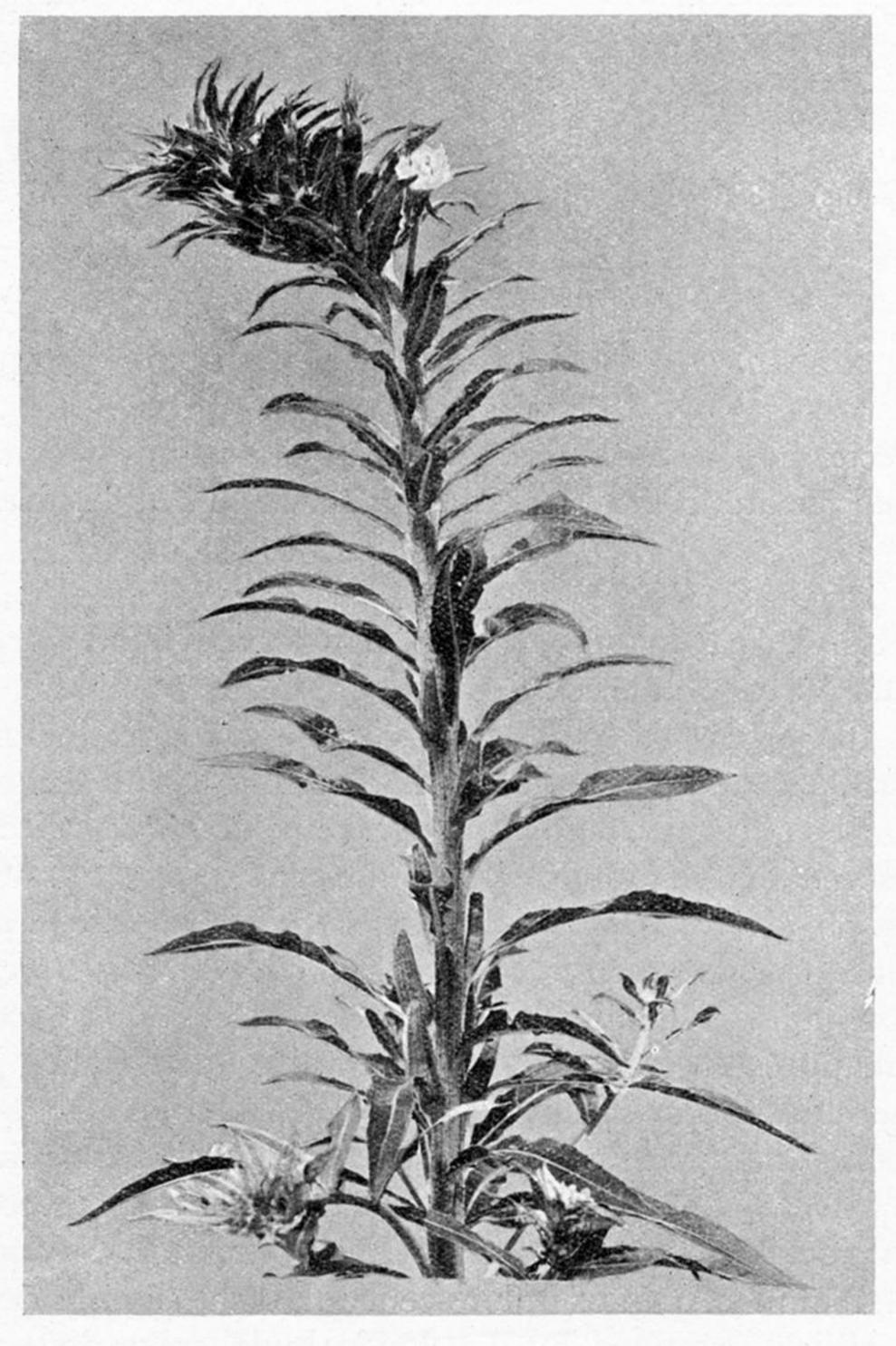


Fig. 45—O. leucophylla, in flower, culture 36.33.

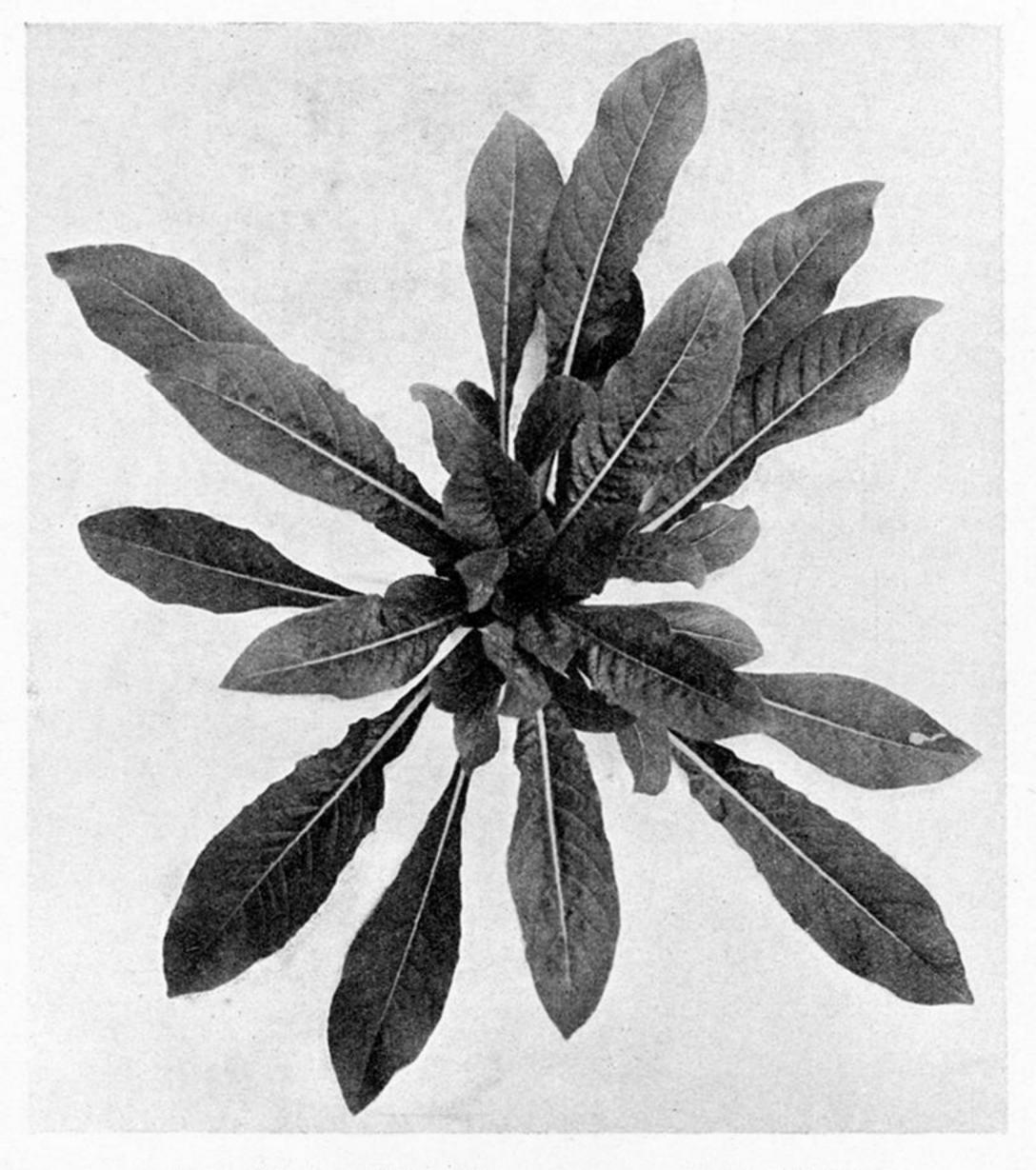


Fig. 46—O. biformiflora, rosette, culture 71.34.

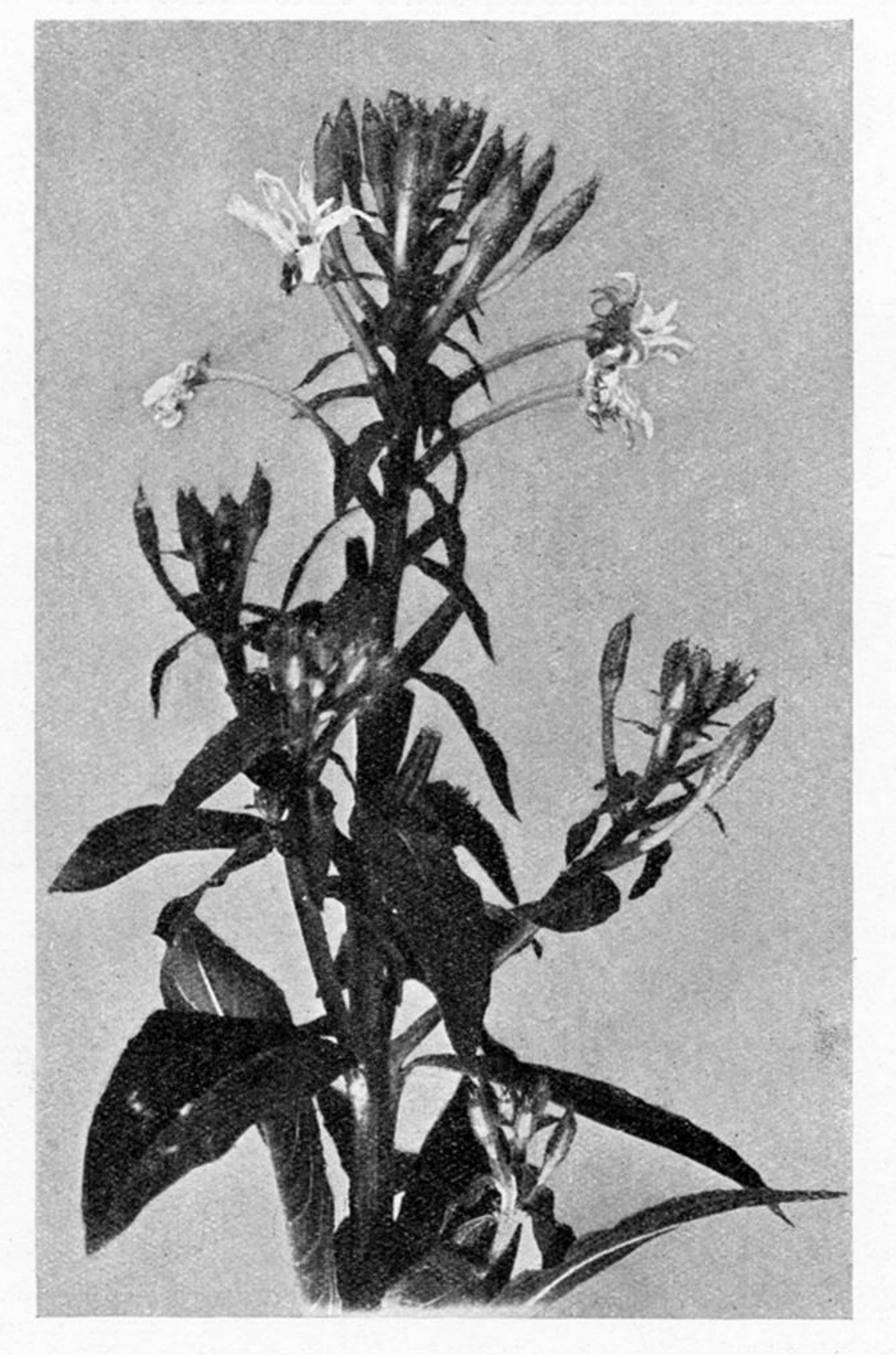


Fig. 47—O. biformiflora var. cruciata, in flower, culture 71.34



Fig. 48—O. biformiflora var. cruciata, near view of flowers showing the cruciate character.

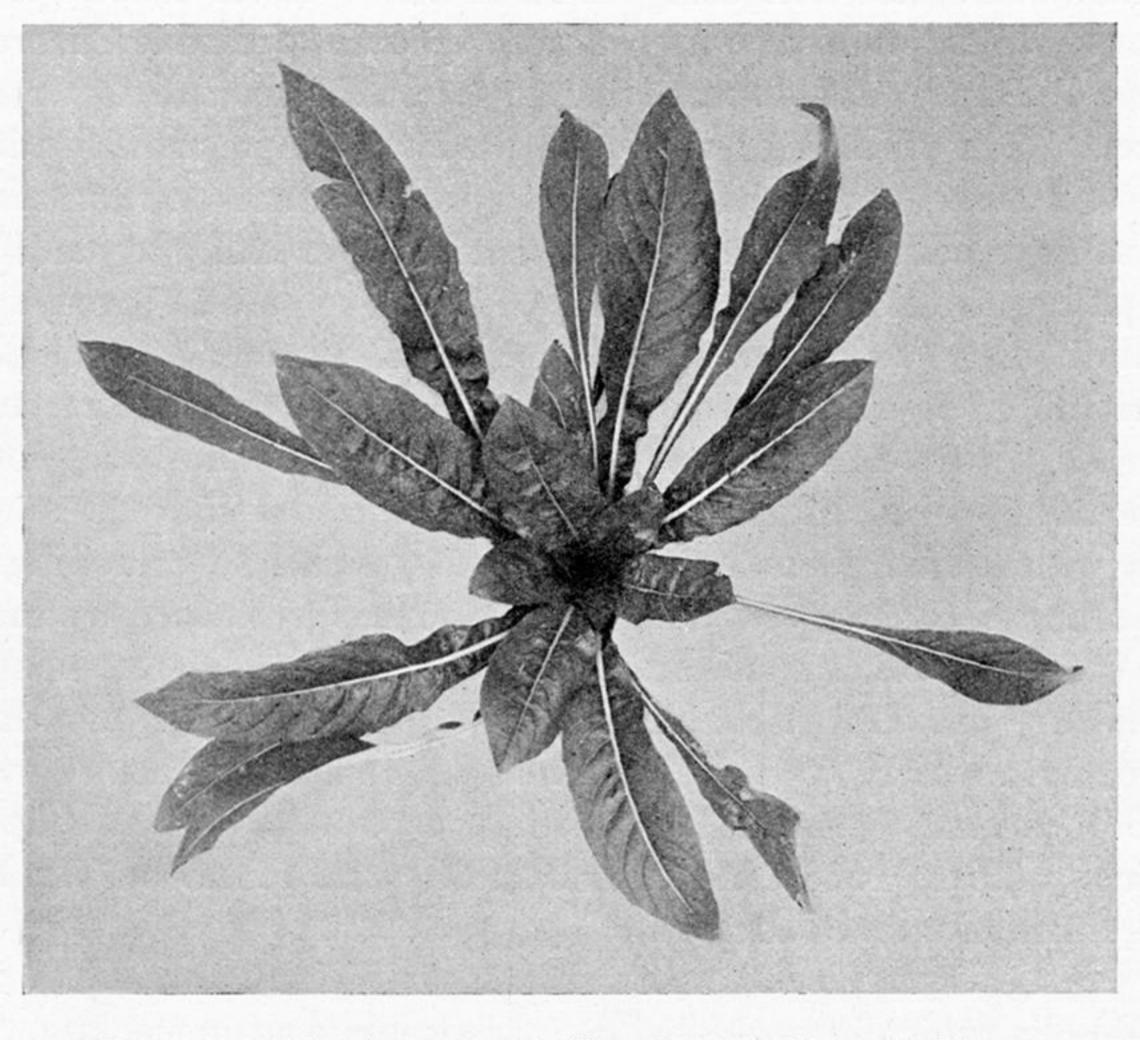


Fig. 49—O. laevigata var. similis, rosette, culture 28.33.



Fig. 50—O. laevigata var. similis, in flower, culture 28.33.

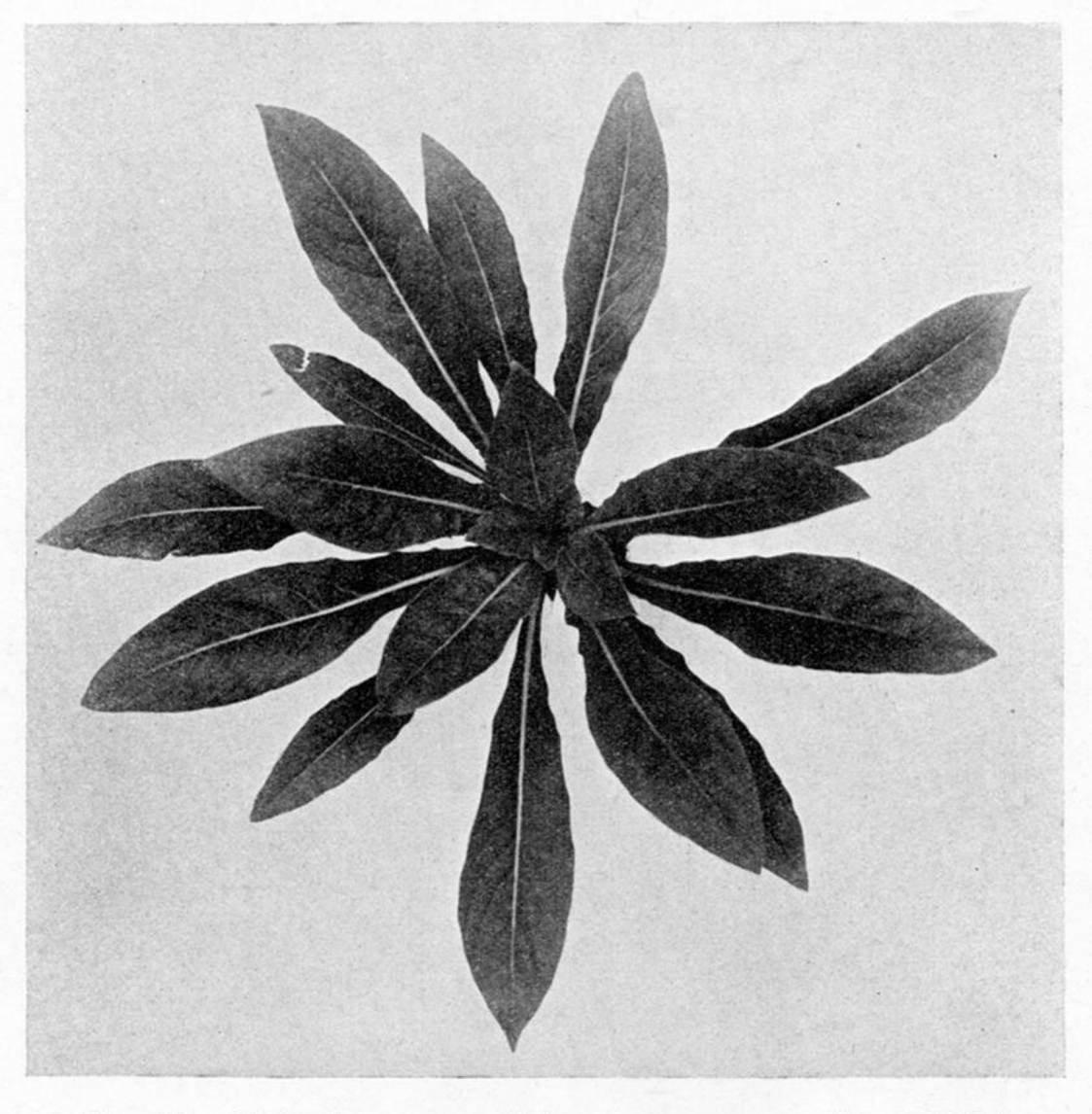


Fig. 51—O. laevigata var. rubripunctata, rosette, culture 53.34.



Fig. 52—O. laevigata var. rubripunctata, in flower, culture 30.33.

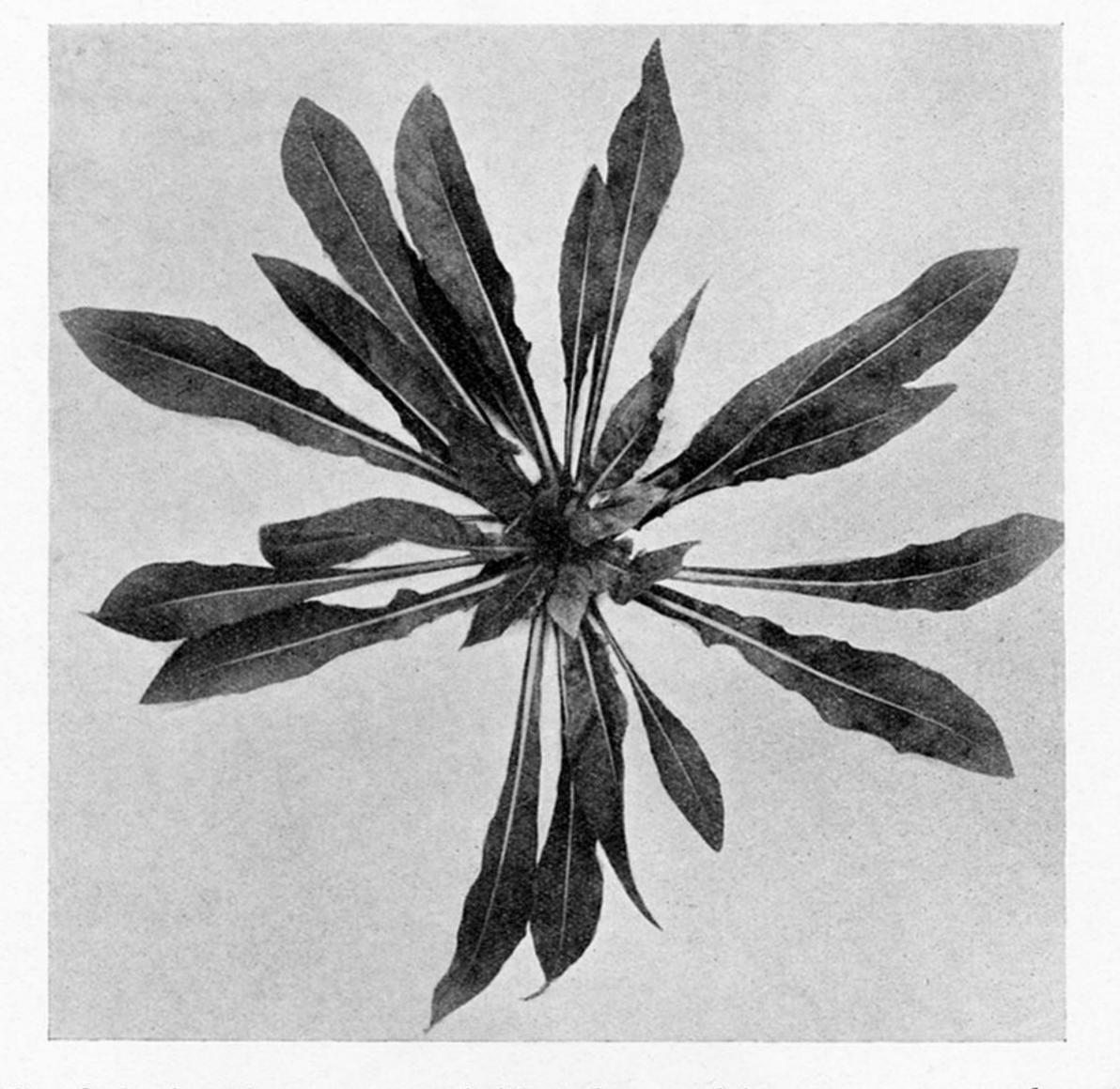


Fig. 53—O. laevigata between var. similis and var. rubripunctata, rosette, culture 62.34.

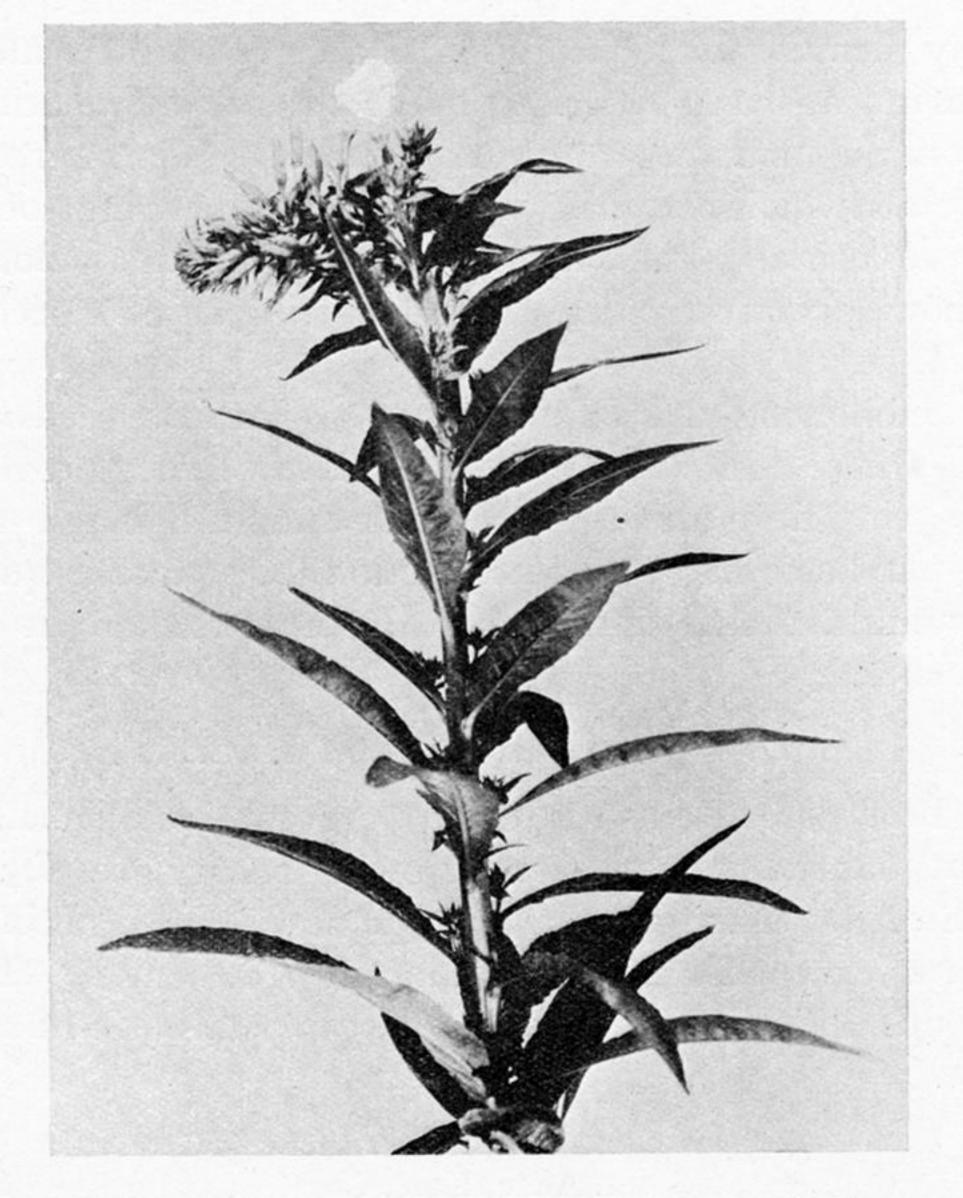


Fig. 54—O. laevigata between var. similis and var. rubripunctata, in flower, culture 62.34.



Fig. 55—O. Victorini var. intermedia, in flower, culture 5.34.

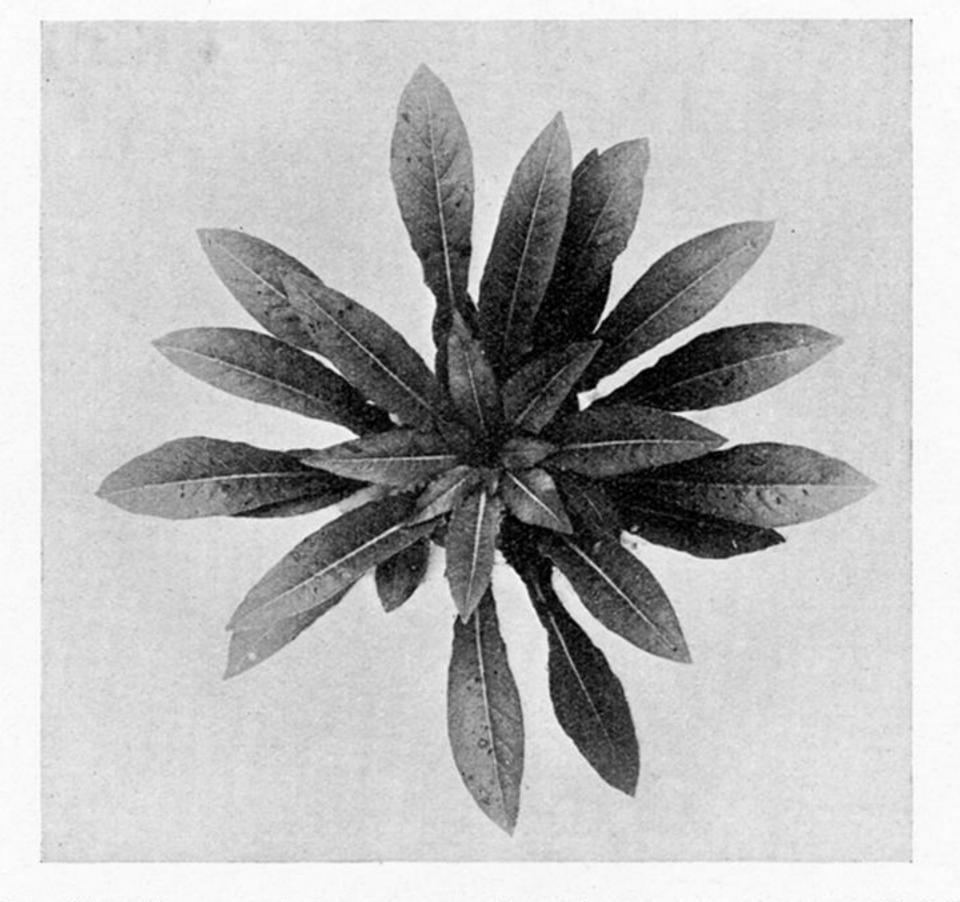


Fig. 56—O. angustissima var. quebecensis, rosette, culture 11.34.



Fig. 57—O. angustissima var. quebecensis, in flower, culture 8.34.

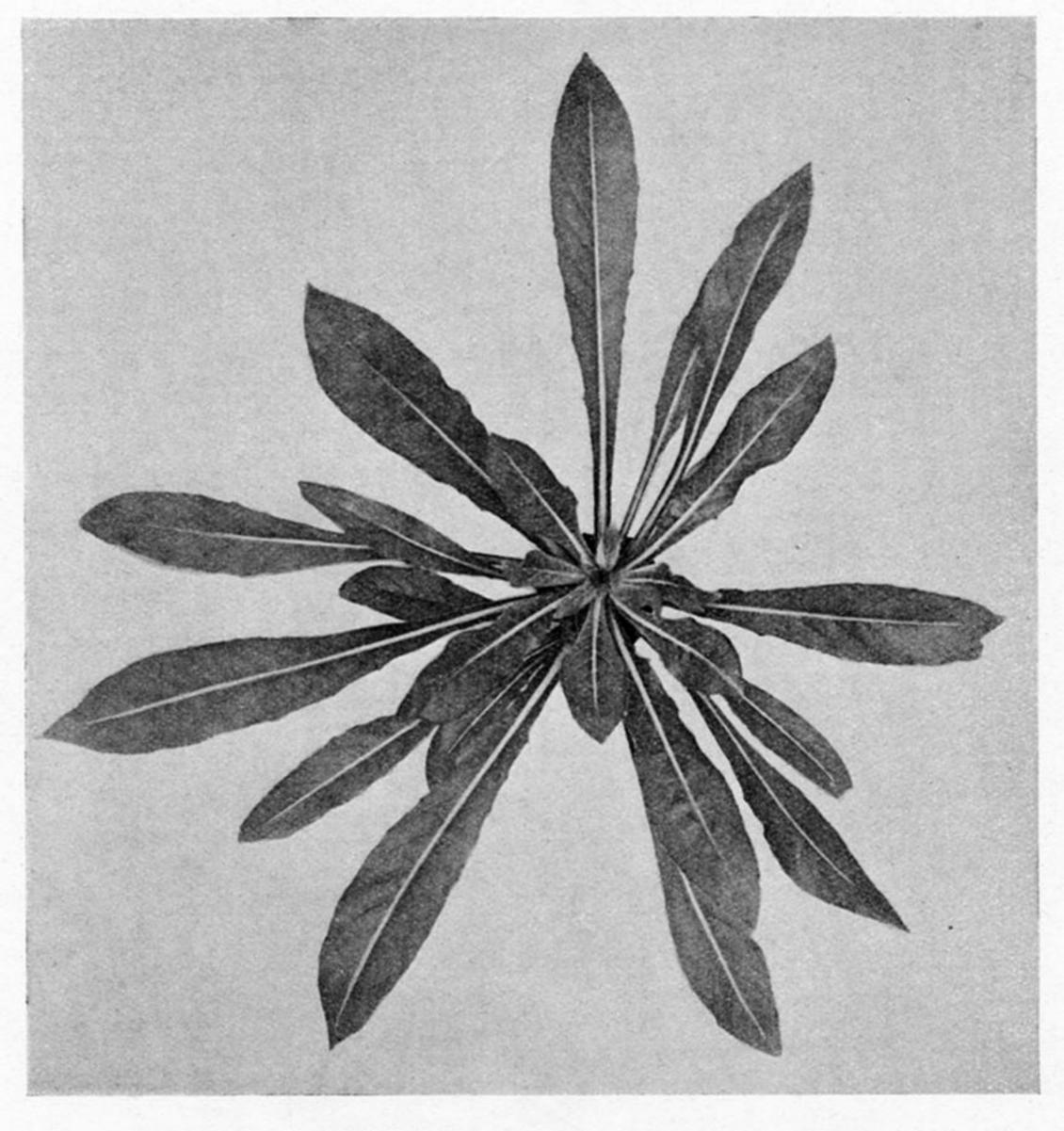


Fig. 58—O. niagarensis, rosette, culture 47.35.



Fig. 59—O. niagarensis, in flower, culture 47.35.

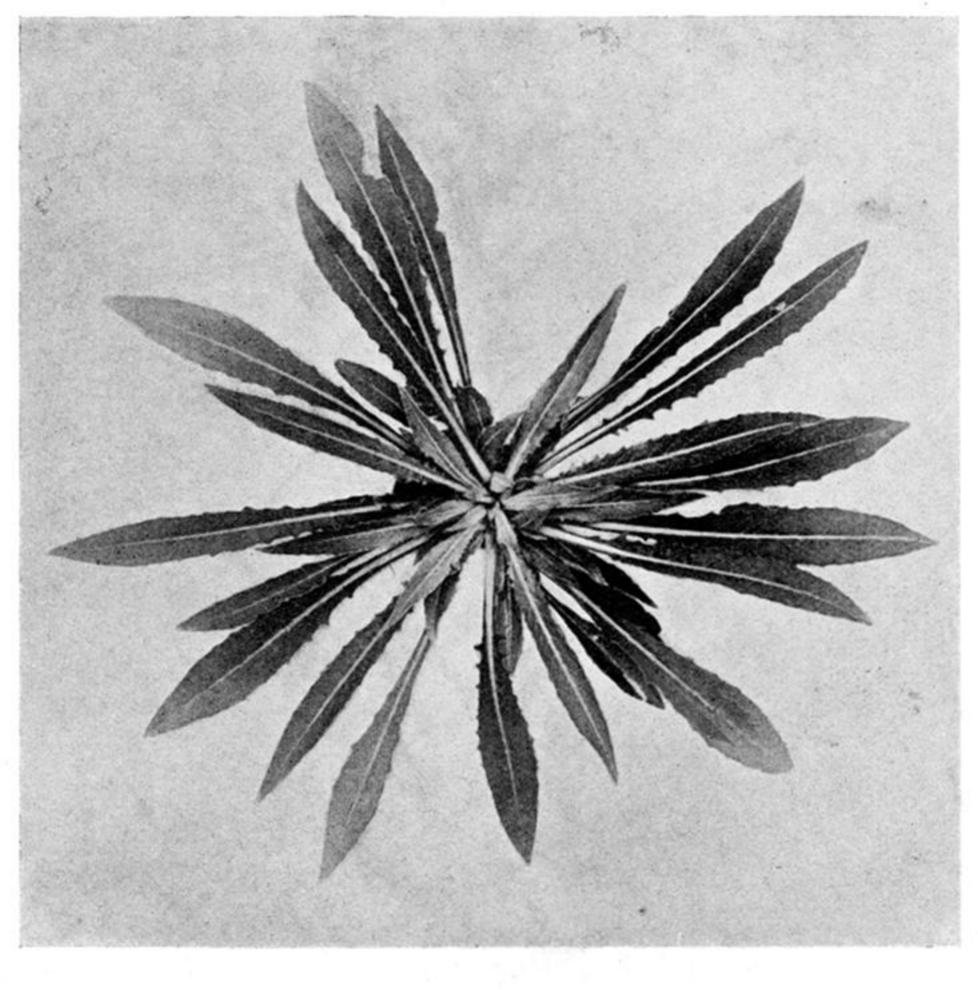


Fig. 60—O. repandodentata, rosette, culture 94.34.



Fig. 61—O. repandodentata, habit, culture 70.33.



Fig. 62—O. repandodentata, in flower, culture 94.34.

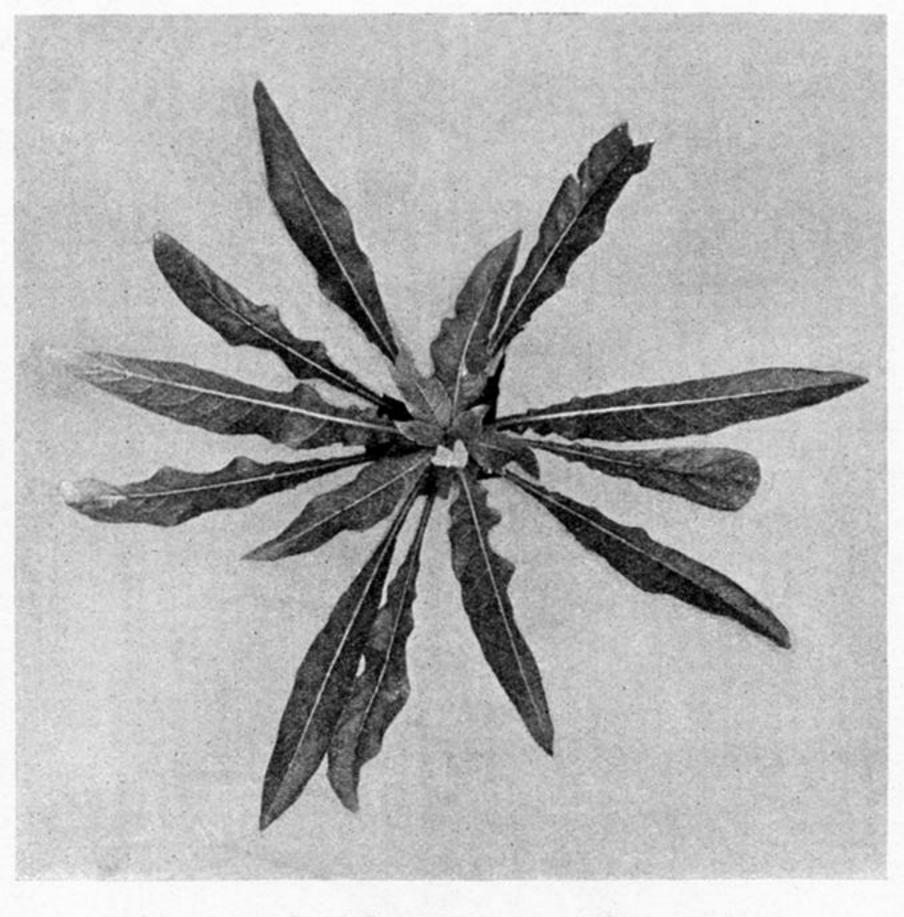


Fig. 63—0. deflexa, rosette, culture 65.33.



Fig. 64—O. deflexa, in flower, culture, 65.33.

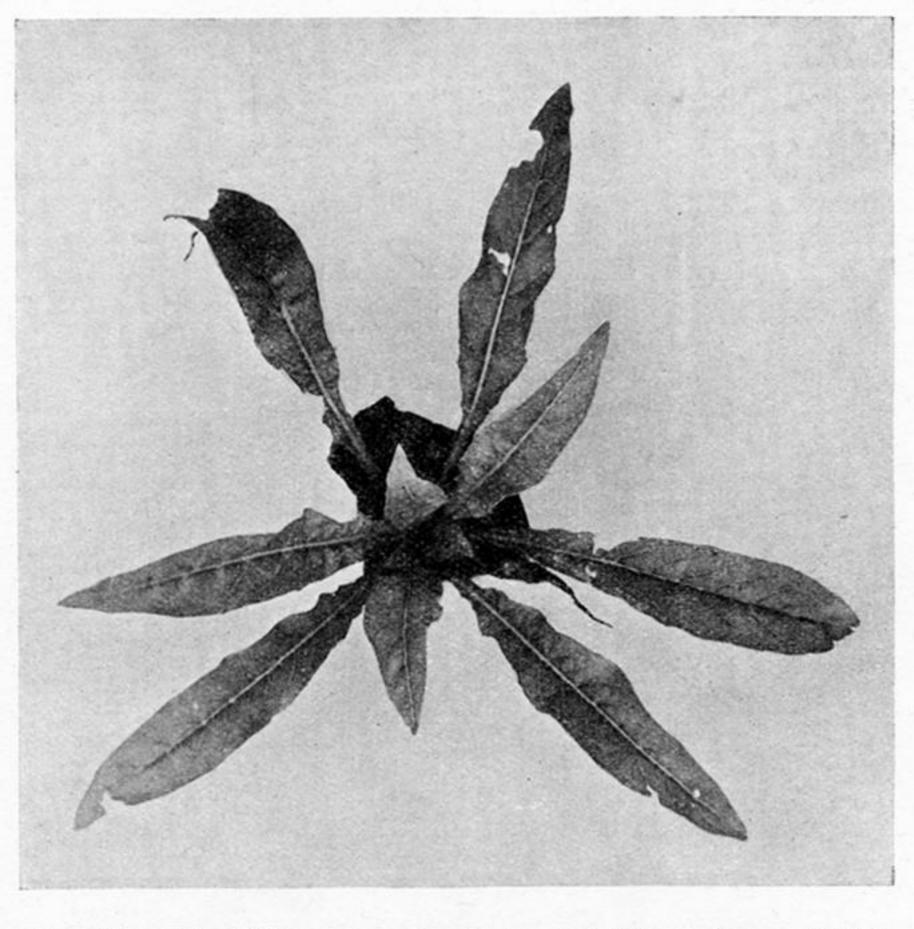


Fig. 65—O. deflexa var. bracteata, rosette, culture 68.33.



Fig. 66—O. deflexa var. bracteata, in flower, late type, culture 67.33.

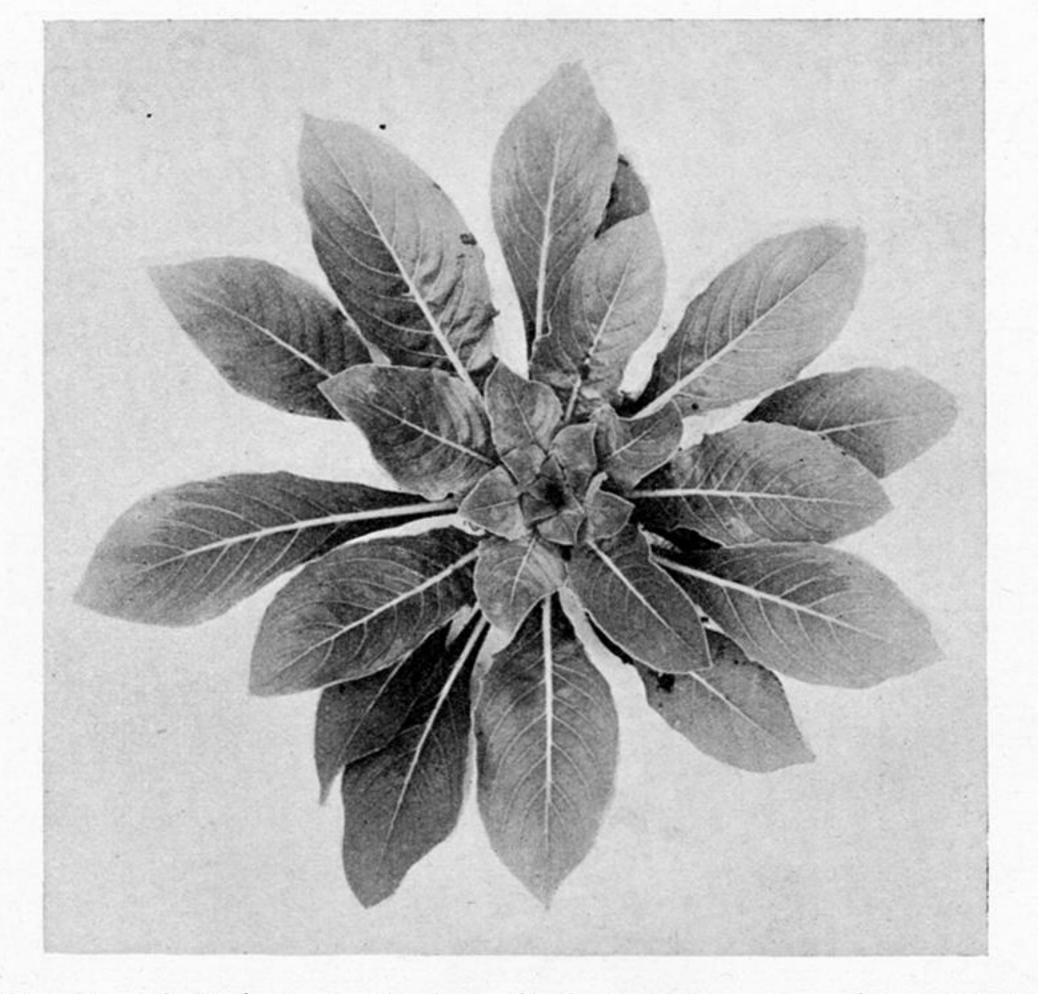


Fig. 67—O. insignis Bartl., from Saskatoon, rosette, culture 14.34.

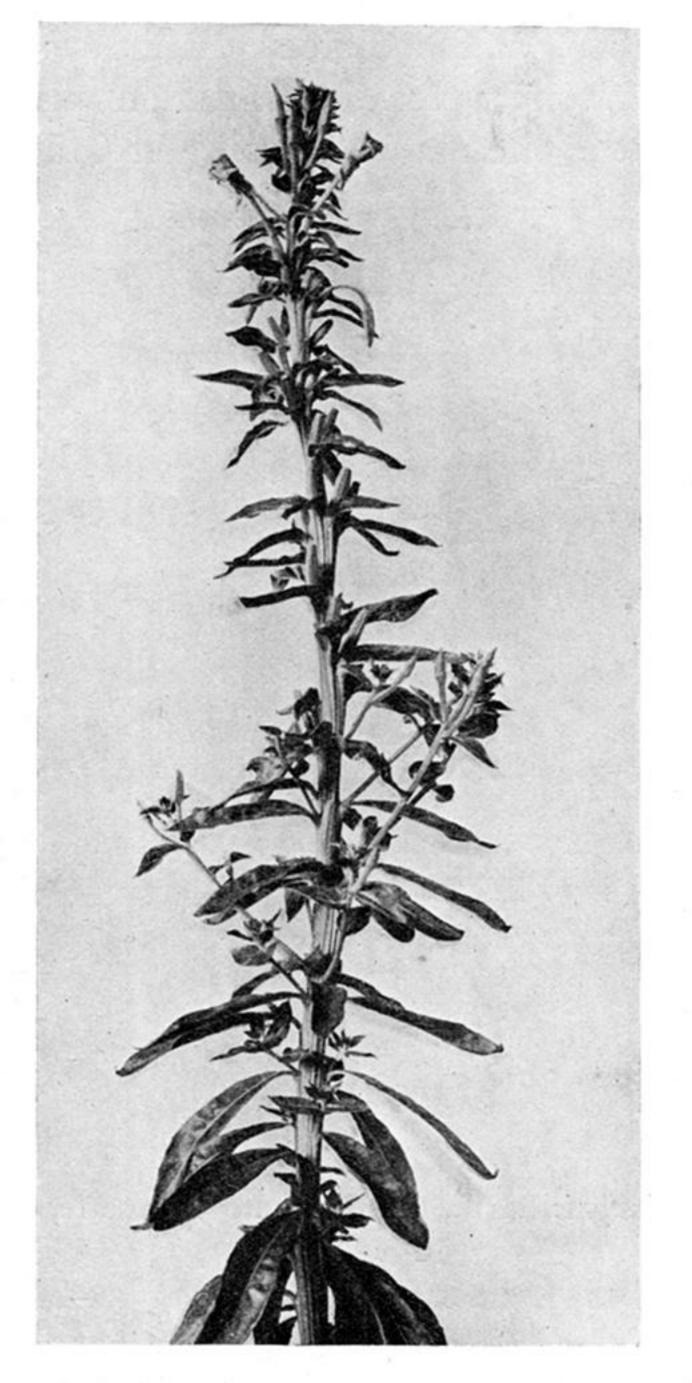


Fig. 68—O. insignis Bartl., from Saskatoon, in flower as biennial, culture, 14.34.

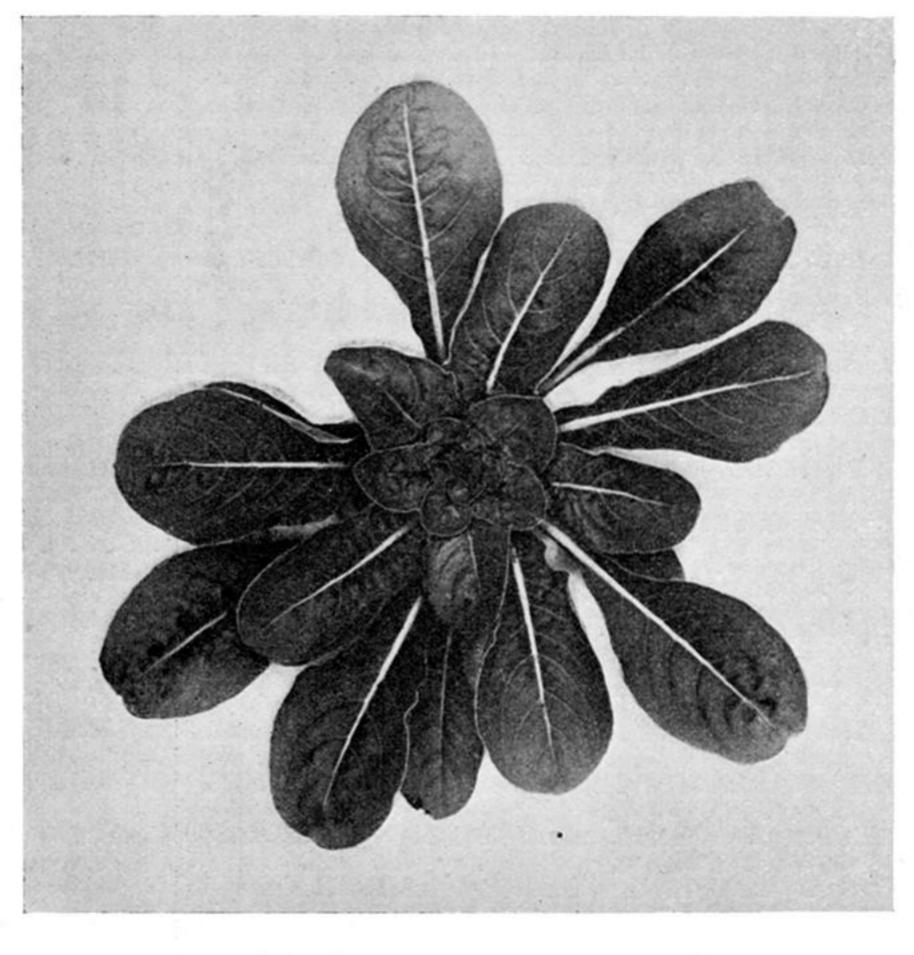


Fig. 69—O. insignis mut. lata, rosette, culture 14.34.

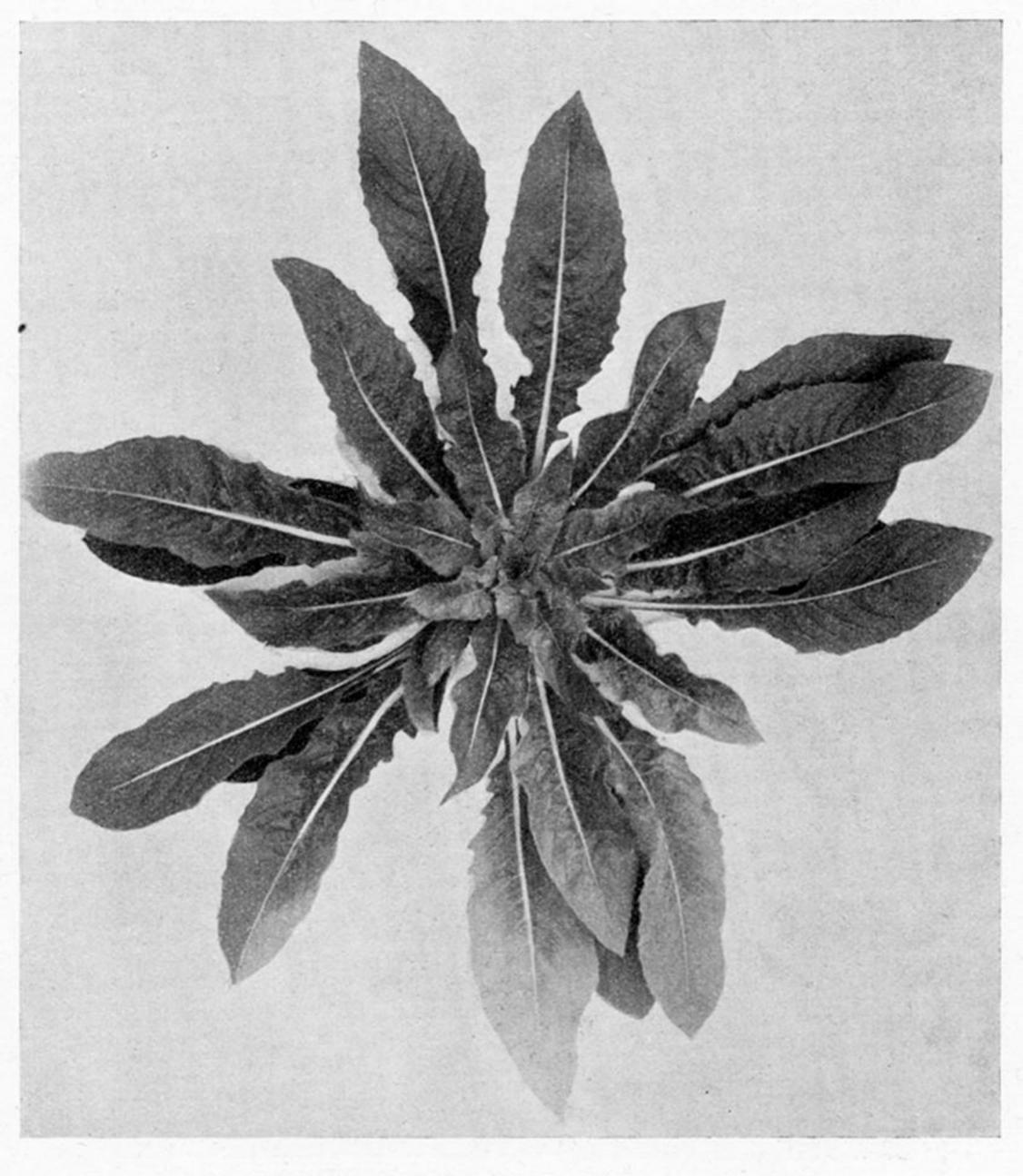


Fig. 70—O. albinervis, rosette, culture 100.34.



Fig. 71—O. albinervis, in flower, culture 100.34.

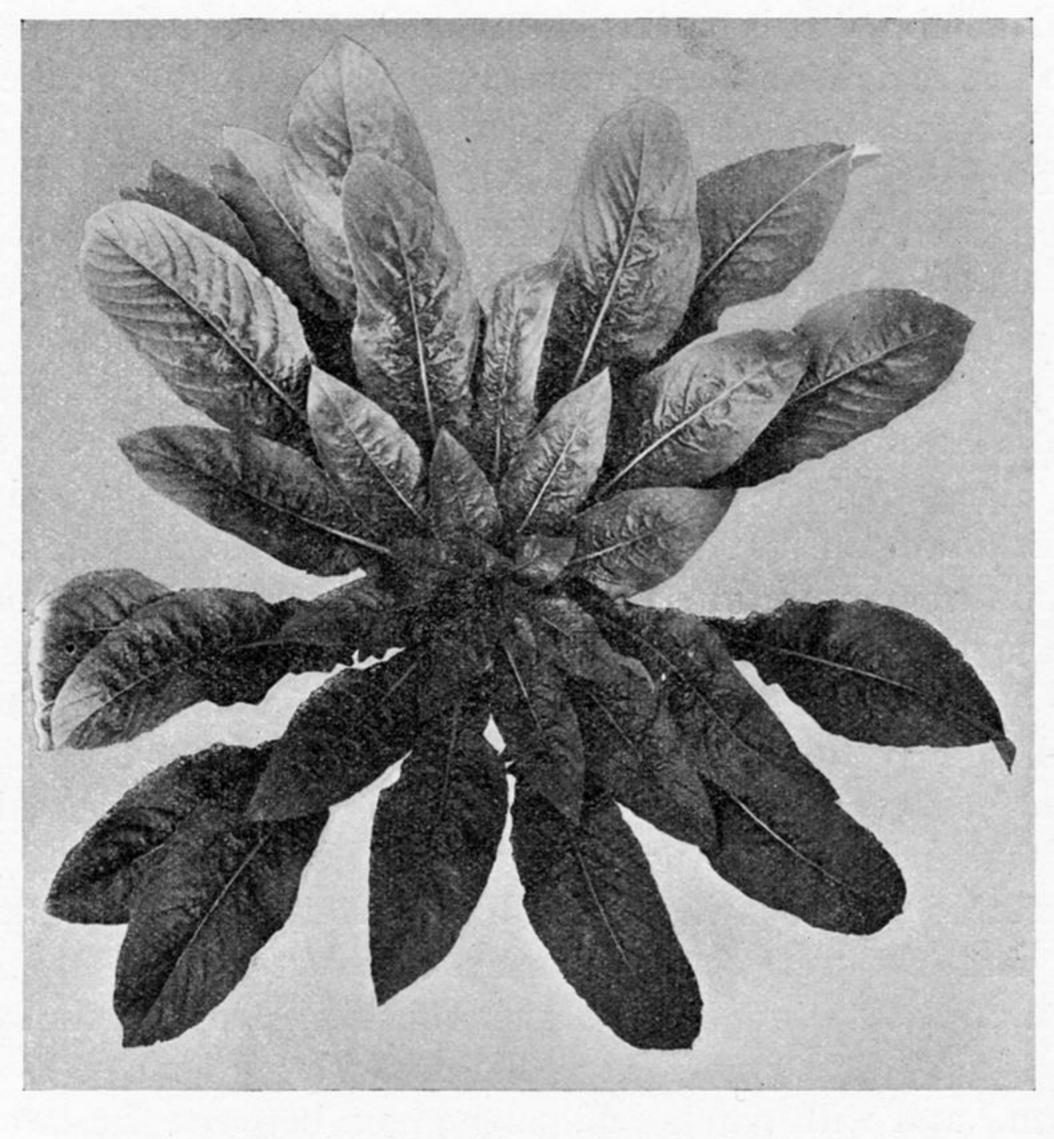


Fig. 72—O. rubricapitata, rosette, culture 99.34.

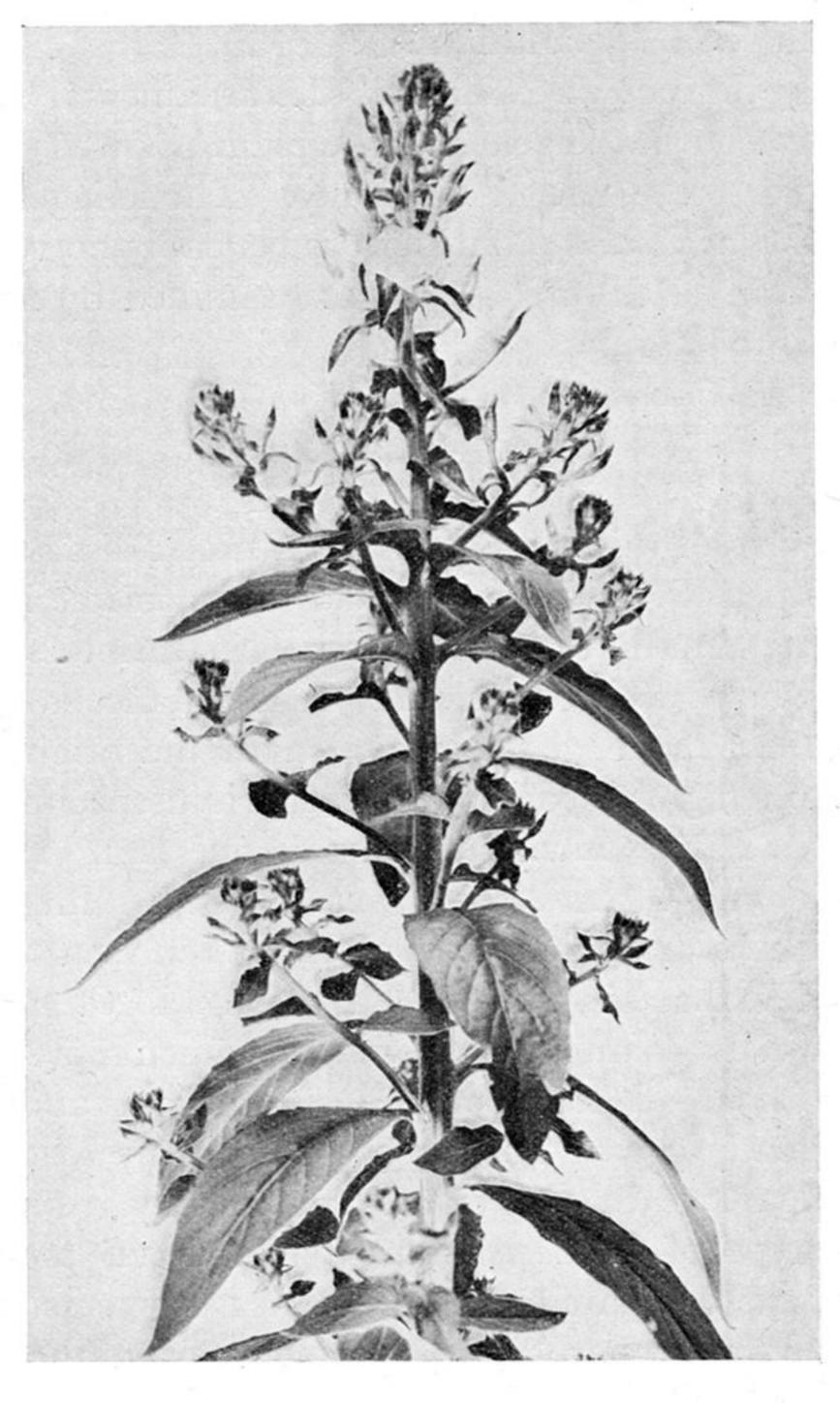


Fig. 73—O. rubricapitata, in flower, culture 99.34.