

THE ORIGIN OF NEW VARIETIES OF NEPHROLEPIS BY ORTHO- GENETIC SALTATION

II. REGRESSIVE VARIATION OR REVERSION FROM THE PRIMARY AND SECONDARY SPORTS OF *BOSTONIENSIS*¹

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INTRODUCTION: A REVIEW OF THE CHARACTERS OF THE PROGRESSIVE SPORTS

A description of the regressive variations of *Nephrolepis exaltata* var. *bostoniensis* requires some review of the characters of the progressive sports of this form.² The nature of these may most simply be indicated by tabulating the outstanding facts relating to them.

1. The progressive varieties so far described all have had their origin by *vegetative* sporting from *N. exaltata* var. *bostoniensis*, or its derivatives. Reproduction is by bud plants on slender stolons.

2. Over *one hundred* new varieties have appeared spontaneously at various florists' establishments in the last twenty years.

3. All these varieties have been *discontinuous*, *i.e.*, separated from the parent form by a definite break in characters—in other words, saltations or mutations. These new varieties have not intergraded by slight differences into their parent forms.

4. The evolution of these forms has been *orthogenetic*, that is, they have developed in series in which each character is successively intensified in succeeding forms. There are three such orthogenetic series:

(a) Division series: *bostoniensis*, once pinnate—*Piersoni*, twice pinnate—*Barrowsi*, more completely twice pinnate—*Whitmani*, three times pinnate—*Smithi*, four times pinnate—*Craigi*, five times pinnate.

(b) Ruffling series: *bostoniensis*, with nearly plane pinnae—*Roosevelti*, pinnae ruffled—sport of *Roosevelti*, pinnae more ruffled and lobed.

(c) Dwarfing series: *bostoniensis*—*Scotti*—*Wagneri*, and *bostoniensis*—*Giatrasi*—sport of *Giatrasi*; the second and third forms in each case are successively smaller than *bostoniensis*.

As further evidence of orthogenesis may be cited the fact that combinations of these three types of variations may occur. Thus, dwarfing may

¹ Brooklyn Botanic Garden Contributions, No. 27.

² For a full account, see Bull. Torrey Bot. Club 43: 207-234. Pl. 10-15. 1916.

appear in the division series and in the ruffling series, and division may appear in the dwarfing series (*cf.* chart, page 144).

5. The varieties, even in a single series, are almost invariably characterized by several *associated differences*. Thus *Giatrasi*, which is half the size of *bostoniensis*, differs also in the possession of red, wiry, somewhat sinuous petioles and rachides, and by differently shaped pinnae. In only a few cases is there but one distinguishing character obvious.

6. The new varieties are *stable*, *i.e.*, they reproduce themselves true to type in a high percentage of cases. Occasionally in the division-series forms, reverting leaves may appear; that is, leaves with less division than is typical; and furthermore, new runner plants may develop which show a return in characters toward the parent form. The latter are uncommon, however, and, as will be indicated later, are actually new saltations or mutations. Some varieties have not as yet been known to show any variations from type.

7. The progressive varieties have been *infrequent*. If reversions are uncommon, as noted in the preceding paragraph, new progressive forms have been much more so. Of the millions of plants of the original *bostoniensis* variety grown for sale, only six or eight sports have been reported. The large number of one hundred progressive sports in twenty years has been due to two factors: to the fact that millions of these plants are grown each year and that florists are on the watch for new forms, and to the fact, also, that the coefficient of mutation has been higher in some of the derived varieties than in *bostoniensis* itself.

As a basis for the description and comparison of the reversionary forms, reference is here made to the revised chart of the relationships of the progressive varieties considered in the earlier paper. The revision consists mainly in the omission of a few forms of some uncertainty of origin and of no particular interest in connection with the present paper. *Schilleri* and *Schultheisi*, before attributed to *bostoniensis* as primary sports, are not in circulation in the trade or likely to be. *Wittboldi*, included doubtfully in the *bostoniensis* chart of the earlier paper, may almost certainly be eliminated from any such relationship. Although no plants have been obtainable from the original producer, specimens have been received from a number of sources, French, English, and American, which by reason of their exact agreement in characteristics may be considered authentic. Judged from this material, *Wittboldi* is a variety of some species other than *exaltata*, to which it was originally attributed. It probably belongs with *biserrata*. At any rate, it is of no interest in the present paper.

The position of the three- to four-pinnate *Amerpohli*, originally placed as a primary sport of *bostoniensis*, has been changed to bring it opposite varieties of a similar amount of division. No more evidence of its exact origin is available, but since this is in doubt in any event, it seems best to place it with similar forms. *Smithi* and *Craigi*, originally attributed in

doubt to *Amerpohli*, have also had their position changed, and on the basis of close resemblance have been placed with the sports of *Whitmani* to which they are probably related.³

THE NATURE OF REGRESSIVE VARIATION

It is common knowledge that some of the Boston-fern varieties as they are obtained from the florist fail to remain entirely true to type. The most familiar manifestation of this aberration occurs in some of the division forms: thus, in a plant of some twice or thrice pinnate variety there may appear one or more once pinnate leaves, and similar leaves may continue to be developed together with the typical leaves of the given variety. The resultant plant often shows a distressingly mixed or mongrel appearance. This sort of reversion is, however, only one of several types, the others being relatively frequent in florists' establishments. The purpose of the present paper is to describe these various types of reversion, both the products and, as far as possible, the processes. The term "reversion," which will be used interchangeably with "regressive variation," is here applied to any modified form which shows a change from some progressive variety back toward *bostoniensis*. Thus, the production by a variety with leaves twice or more pinnate of leaves less divided than the typical form is called a reversion. The production by a dwarf form of a plant with larger leaves is also considered as reversion, and likewise the reduction of ruffling. Broadly, we may recognize three manifestations of such reversion.

1. The simplest possible type is seen in the appearance of single aberrant, *i.e.*, reverting leaves among others which are typical. This is a common occurrence in varieties in the division series.

2. Again, we may find all the new leaves of a single crown or stem axis appearing reverted in form; *e.g.*, in a plant of a thrice-divided variety the typical leaves may be succeeded by once pinnate leaves developed one at a time until the former appearance of the crown is entirely altered.

3. The third type of reversion occurs when the change in character takes place in one of the branch reproductive shoots or stolons, and appears only when from this stolon new bud plants develop which manifest the new character (Pl. IX, fig. 1).

The first two types may be designated as "crown" reversion, partial and complete, and the second may be called "runner" reversion. Only the crown type may be actually watched in the external manifestations of the process. Runner reversion is known only in its products, *i.e.*, the new forms developed as bud plants on lateral stolons. The cytological changes

³ It may be of interest to some to know that a considerable set of varieties of these *Nephrolepis* sports may be obtained from John Lewis Childs, Floral Park, New York. At present the Childs catalogue lists 30 different forms representing all types of variation listed in the chart, both progressive and regressive. The stock plants are grown separately, and the identification of the varieties offered may be generally relied upon.

are scarcely even a matter for conjecture, the evidence dealt with here being entirely macroscopic.

The study of regressive variation offers one distinct advantage over that of progressive variation in the fact that the former is sufficiently common to be frequently observed, and may thus be studied experimentally. This suggests the possibility of determining an external cause for reversion. So far no definite experiments have been carried on, but there are some suggestive facts connected with the possible relations between cultural conditions and the occurrence of some of the reversions.

As with the first paper, the data for the present article have been obtained in two ways: first, by the further extension and study of the collection of *Nephrolepis* at the Brooklyn Botanic Garden. Some of the reversions here described have been developed at the Garden under observation. Second, visits to florists have been continued for the opportunity of seeing hundreds of thousands of plants. During 1916 these visits were made with the aid of a grant from the American Association for the Advancement of Science. A second similar grant was made in 1917 and has served in the preparation of this paper. Acknowledgment is also made to the Bureau of Plant Industry, specifically to Messrs. Peter Bisset, Wilson Popenoe, and David Fairchild, for assistance in the collection of wild forms of *Nephrolepis* from various parts of the tropics.

Special acknowledgment is again tendered the Brooklyn Botanic Garden for the very satisfactory facilities for this study which have been enjoyed.

DESCRIPTION OF THE REGRESSIVE VARIETIES

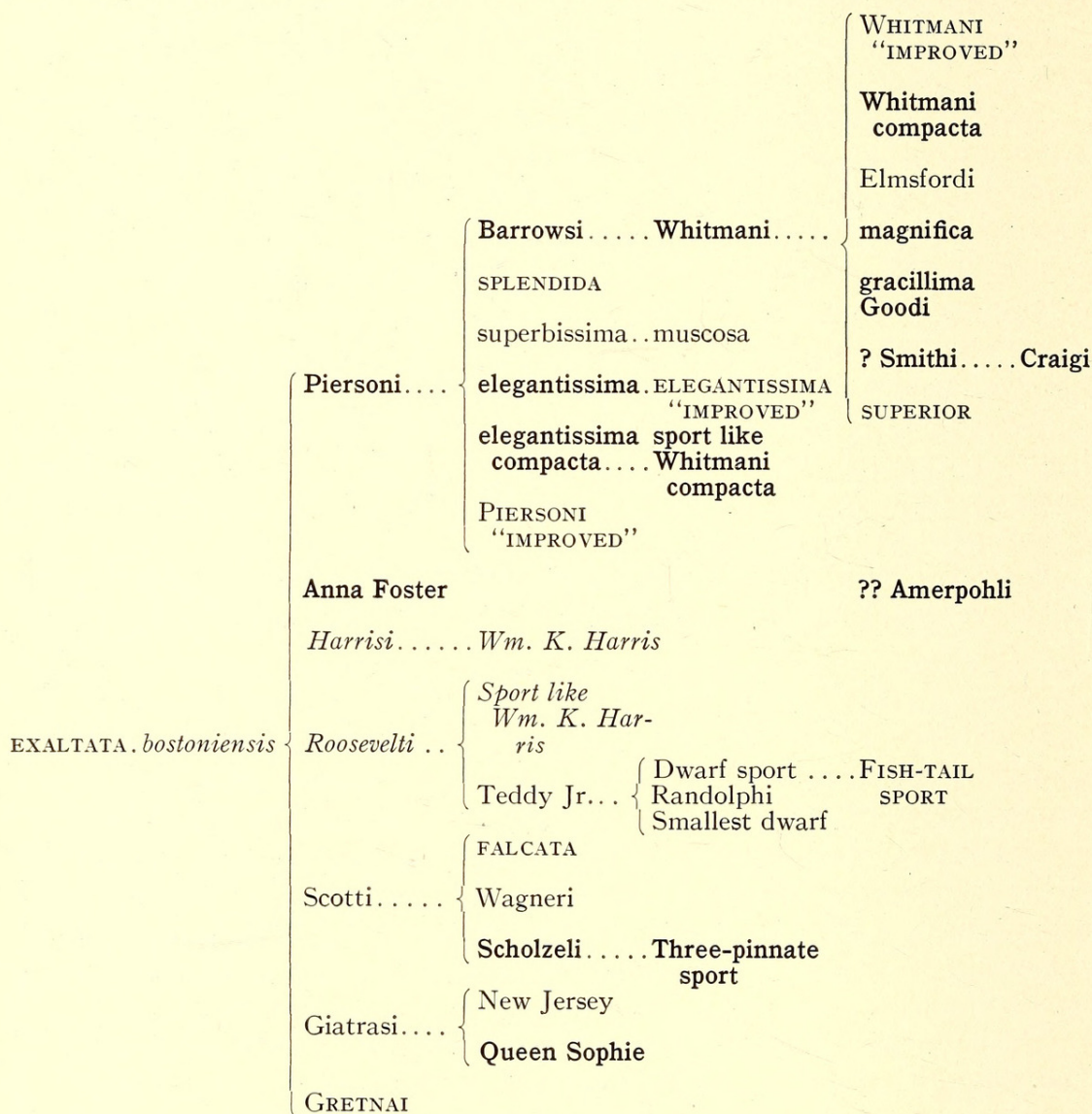
It will forward the description of the regressive variations to state here one of the conclusions based on the detailed observation of all the forms: namely, regressive variations may be expected to occur in any of the progressively developed varieties. This statement has not been checked for all the one hundred varieties known to exist, nor even for the forty listed in the genealogical chart attached herewith, but it has been found true for so many of them that it is a reasonable assumption that it may be characteristic of all.

This multiple origin of reversionary forms makes it impossible to arrange their descriptions in as simple a system as was used for the progressive varieties. With the latter it was merely a case of arranging them in a genealogical table, and describing for each the changes or advances in form it manifested. Each new kind in a series was produced by the intensification of some character of the parent type, or by the appearance of some other of a few well marked characters. Each reversion represents similarly some definite divergence from its parent form, but instead of one common ancestral type there are forty to one hundred possible ancestors. The reversion of any given variety is thus a distinct problem for study and description, and is related to other reversions only as it may produce analogous or

comparable forms. Because of this extremely complex material, the present paper will deal mainly with what are believed to be representative types of regressive reversions.

GENEALOGICAL CHART OF PROGRESSIVE SPORTS OF BOSTONIENSIS

Black face type indicates division sports. Italics indicate sports showing ruffling. Plain Roman type indicates dwarfing. Small capitals indicate other types of variation.



Since the progressive varieties all originated from one form, *bostoniensis*, it will be interesting to consider first the primary sports of that fern. To what extent has the original process been reversed? After that, the reversion of the different grades of the division series will be considered. What are the products of the reversion of twice pinnate forms, of thrice pinnate forms, etc., etc.? Are the progressive steps each retraced in reversion? Can a four-times-pinnate variety produce thrice, twice, and once pinnate reversions, or only one of these? Similar questions suggest themselves in

connection with the dwarfing and ruffling series, and will be considered in order.

Reversions of the Primary Sports of *Bostoniensis*

Before the reversions of the primary sports of *bostoniensis* are dealt with, it will be worth while to consider the possible reversion of *bostoniensis* itself. *Bostoniensis* differs from the wild species, *exaltata*, from which it must have originated, in certain vegetative characters—it has laxer, broader, more numerous leaves—and also in producing only abortive sporangia. The wild species is abundantly fertile, and the spores germinate readily. In *bostoniensis*, however, the sporangia abort at an early stage, apparently before the tetrad division. The resulting sporangia are small and shriveled, but there are usually enough of them to produce fruit dots of considerable size and the gross appearance of fertility.

Of the actual reversion of *bostoniensis* to a fertile condition there is no authentic record. There have been many attempts on the part of florists to produce plants by planting the soral material and there have been a few reports of success, but the reports have told nothing of the condition of the plants from which the spores (?) were obtained, *i.e.*, whether the original plant had first reverted in reproductive and vegetative characters as well, or whether the fertile spores were a chance production on a plant otherwise like ordinary *bostoniensis*.

There is nothing inherently improbable in either of the above suggested contingencies. An approximation to vegetative reversion may frequently be seen in plants which have been grown in untoward conditions of light, temperature, and food. In these plants the leaves assume a stiffer, more erect habit, decidedly suggestive of the appearance of the wild species but without its condition of spore fertility. Favorable conditions cause a return to the normal *bostoniensis* characters. It may be noted, however, that real reversion might occur frequently in florists' establishments without being observed, because the difference in appearance between the sterile and the fertile sori is not calculated to attract the attention of the average grower, and also because a reverted plant would probably be discarded as undesirable.

The primary progressive sports of *bostoniensis*, as listed in the revised chart, comprise four types: (1) Division sports, *Piersoni* and *Anna Foster*; (2) Dwarf sports, *Scotti* and *Giatrasi*; (3) Ruffled sports, *Harrisi* and *Roosevelti*; and (4) a "fish-tail" or forked-leaf form, *Gretnai*. The possible and actual reversions may be best considered under the same categories.

Piersoni. The history of *Piersoni* is illuminating. I am indebted for the following facts to J. C. Trevillian, who has been in charge of the fern houses at F. R. Pierson's Tarrytown establishment since and before the origin of *Piersoni*, the first of a long line of Pierson varieties.

The first break from the once pinnate form came as a small two-leaved

runner in a stock bed of *bostoniensis*. Both the first two leaves were twice pinnate. This small plant was set apart and most carefully cherished. As proved by later developments, it was worth many times its weight in gold. Its third leaf must have been a disappointment, for it represented a return to the once pinnate form and may therefore be considered the original example of reversion. Thenceforward the original *Piersoni* plant and the thousands of progeny of this variety have always shown a mixture of leaf types: *viz.*, typical twice pinnate, once pinnate, and intermediates on which entire, lobed, and divided pinnae may co-exist. Even a single pinna may show all three grades of division (Pl. V, figs. 1-6).

Not only is there variation in leaf division on a single plant at any given time, but there seems also to be seasonal variation or possibly variation according to different cultural conditions. In April, 1916, a group of about fifty stock plants of *Piersoni* was observed in the John Lewis Childs Floral Park greenhouses which were almost completely in a once-pinnate condition. The plants were growing set out in rich soil in a well lighted bench. Most of them possessed only once pinnate leaves, but their identity was not possibly in doubt both because records had been kept of the planting and because of subsequent history. Three of these stock plants possessing only once pinnate leaves were selected for special observation with the thought that they might represent permanent reversion to a once pinnate condition. After being potted up at the Botanic Garden they were given good conditions of lighting, etc. The new leaves which followed were mainly of the twice pinnate type. Since then, all the plants of this origin kept at the Botanic Garden are predominantly twice pinnate, although cultural conditions have not been continuously at the optimum.

The experience with the Childs plants just described bears out a conclusion which Trevillian has reached after twenty years' experience with *Nephrolepis* varieties: *viz.*, that during the less favorable cultural conditions of winter, all the division varieties tend to produce more reverted leaves than in the more favorable six months from April onward. It is a well established fact that all *bostoniensis* varieties show a recognized slowing up in the number of new leaves produced during winter, and apparently associated with this is a tendency to produce leaves with less division. It may be concluded, then, that the maximum development of the special characteristics of any form depends upon an optimum of cultural conditions, and that it is therefore with *Nephrolepis* varieties partly a matter of season. The Childs plants above cited presented an extreme case of seasonal fluctuation.

The condition of *Piersoni* with respect to the amount of leaf division may be described as a state of "fixed instability." Taken as a whole, the variety represents a distinct and definite saltation from *bostoniensis*, but the jump or variation was not all the way to a stable twice pinnate type although the predominant leaf form throughout the year and normally at any

time of the year is twice pinnate. The amount of reversion noted in the Childs plants referred to above is exceptional. Twice pinnate leaves are usually in the majority at all times of the year. That the divided-leaf condition is fixed is well illustrated by the experience with the Childs plants just related. Although externally those plants had lost all indications of the twice pinnate character, continued cultivation showed that it had been only temporarily obscured. It seems a safe conclusion that the actual basis of the original *Piersoni* variation from *bostoniensis* must have been a protoplasmic change which maintained itself even though temporarily not evident in the gross characters.

The facts detailed thus far—the appearance of once pinnate leaves in *Piersoni* stock—represent no real regressive variation or reversion but rather fluctuation within the limits of the *Piersoni* type. There are, however, three possible types of unmistakable reversion which should be considered.

The occurrence of a complete and discontinuous reversion to a once-pinnate form is highly probable. The fact that there is no record of such a reversion does not alter the probability. The florist would not be likely to detect its occurrence. *Bostoniensis* is almost invariably grown wherever any of its varieties are in cultivation, and the appearance of a once pinnate plant among *Piersoni* stock ordinarily would be passed over as a misplacement of a *bostoniensis* plant. As will be described below, this type of permanent reversion is well known in other varieties.

Partial reversion to a condition of greater instability is postulated on the basis of the behavior of other varieties considered below. This change would result in a strain in which the number of twice pinnate leaves would be fewer than in the best strains.

The most interesting reversion attributable to *Piersoni*, or, indeed, to any other *bostoniensis* variety, is a plant of the *Piersoni* type of division, but one the exact origin of which is unfortunately shrouded in doubt. I obtained it from the New York Botanical Garden where it was being grown under the name of a totally different variety and species, *Nephrolepis hirsutula tripinnatifida*. Its earlier history is unknown, but two explanations of its origin are possible. It may represent a progressive twice pinnate sport from wild fertile *exaltata* of which the New York Garden has plants from several collections in Porto Rico; or it may represent a reversion in fertility from some plant of *Piersoni* which has been grown there for the nineteen or twenty years since its introduction. The latter explanation seems the more probable. In any event, it is unique among *Nephrolepis exaltata* forms in its fertility, and a particular interest attaches to it in the possible type of its spore progeny of which several separate sowings are being grown and will be reported on later.⁴

Anna Foster (Pl. V, figs. 7–12) represents a twice-pinnate form also in a

⁴ For purposes of reference and discussion, I have assigned the name "*fertilis*" to this form. Technically its name should read, *Nephrolepis exaltata bostoniensis* var. *fertilis*.

state of unstable division like that of *Piersoni* but even more pronounced. It was the first of all the Boston fern sports to be reported, but seems always to have been so unstable and so much less attractive than *Piersoni* that it never gained much general popularity. In well developed plants about half the leaves show the double pinnation, but this is never so completely developed as in good *Piersoni* leaves. The best leaves are partly once pinnate, and most of the divided pinnae are incompletely divided. At the present day, twenty years after its appearance, there has come down one strain attributable to *Anna Foster* which shows only an occasional twice pinnate leaf. Such a plant presumably represents reversion from the more completely divided original type.

Harrisi and *Roosevelti*. These two varieties, possessing almost identical leaf forms, may be dealt with together as far as possible reversions are concerned. No reversions are known. The conditions in this respect are almost exactly like those discussed in connection with the possible complete reversion of *Piersoni* to a once-pinnate form. Florists who grow the ruffled forms almost always grow *bostoniensis* as well, since the cultural conditions required are the same. If a complete reversion should occur, it would pass unnoticed or be interpreted as a chance *bostoniensis* plant accidentally associated.

Scotti. Exactly the same conditions prevail with *Scotti* as with *Roosevelti* and *Harrisi*. No reversions have been detected, not even occasional fluctuating leaves.

Gretnai. The fish-tail form, *Gretnai*, shows fluctuations in the degree in which its pinnae and leaf tip fork, but the character is always present to some extent. No complete reversion to the normal Boston-fern type has been noted.

Giatrasi. This fern represents one of the most distinct of all mutations from *bostoniensis* shown in the primary sports. *Piersoni*, while differently divided, has the same habit and size, and produces continually some similar leaves. *Giatrasi*, on the contrary, differs so markedly in size, habit of growth, and leaf characters that its separation as a "species" could easily be justified. Its leaves attain a length of no more than one third that of *bostoniensis*; the petioles are darker colored and wiry, those of *bostoniensis* being greenish and herbaceous; the pinnae are shorter in proportion, blunter, and wavier, the midribs are often sinuous, and the plant is notably slower in growth.

Giatrasi (Pl. VIII, fig. 2) does not produce any single fluctuating leaves, but it has produced as a runner sport (at the Giatras establishment) a form which may well be considered a reversion. This new form was introduced to the trade under the name of the "*New York*" fern (Pl. VIII, fig. 1). In characters it is intermediate between the Boston fern and *Giatrasi*, possessing in considerable degree all the characters of the latter fern except that it is considerably larger although never equalling *bostoniensis* (Pl. VIII, fig. 3) in

height. There is no indication of "fixed instability" here. Both *Giatrasi* and the "New York" fern are discontinuous and stable sports, without fluctuations *inter se*.

The case of the *New York* *Nephrolepis* emphasizes a fact true in general for reversions: complete return to all the characters of the parent form rarely if ever occurs. The original progressive variations were not mere fluctuating changes about a mean, but decided and permanent changes which must find their explanation in some cytological alteration of definite character.

Summarizing, we may note the following types of reversion among the primary progressive sports of *bostoniensis*:

1. A reduction in the stability of the original progressive change, as shown by a permanent decrease in the proportion of divided leaves in *Anna Foster* and probably also in *Piersoni*. It is possible that this type of reversion should be considered as a fluctuation.

2. A possible reversion (mutation) to a fertile condition, with the *Piersoni*-like form from the New York Botanical Garden as an illustration (Pl. V, figs. 13-17; Pl. VI, fig. 6).

3. A reversion (mutation) from a dwarf form to a size intermediate between the dwarf and *bostoniensis* (Pl. VIII).

N.B. The production of single atypic leaves does not constitute reversion but rather merely part of the normal variability of a given plant (Pl. V, figs. 1-17).

Reversions of the Secondary Sports of *Bostoniensis*

Reversions of superbissima (Pl. VIII, fig. 6).

The simplest examples of reversion among the secondary sports of *bostoniensis* have occurred in plants of the variety *superbissima*. This is a dwarfed sport from *Piersoni*, and differs from the latter form almost entirely in a foreshortening of the rachis and of the midribs of the pinnae. The actual amount of green tissue does not seem to be proportionately reduced. As a result of this brachytic type of dwarfing, the leaves have a crowded and congested appearance. In type of division and stability of leaf division, *superbissima* seems to be exactly like *Piersoni*. In the course of a year any given plant is sure to produce a good many once-divided leaves. Two distinct reversions have been noted and are represented by forms which have been continuously cultivated.

The first of these was introduced as a new variety by Pierson under the name of *viridissima* (Pl. VIII, fig. 5), given on account of its dark green color, presumably the result of the congestion of leaf tissue. This form is of the same size as *superbissima* and has the same rigid thick rachides, but is entirely once pinnate like *bostoniensis*. In other words, it represents a reversion in one of the two progressive characters of *superbissima*, that of leaf division. The plants of *viridissima*, as grown for some years, have

continued constant, and show no indication of fluctuating variations toward a more divided form.⁵ A second instance of this reversion has also taken place at the Brooklyn Botanic Garden in material of *superbissima* obtained originally from the city greenhouses of Fairmount Park, Philadelphia. So far it has not been sufficiently grown to allow an opinion as to its identity with Pierson's *viridissima*.

From *viridissima*, although no fluctuating variation has been observed, there has developed in at least two establishments a further reversion of stable character, in this case one of size. This new form (Pl. VIII, fig. 4), which has not received any name, is taller and laxer, thus intermediate in size and habit between *viridissima* and normal *bostoniensis*. It has not, however, made complete return to *bostoniensis* size but is comparable to the "New York" fern, described on a preceding page as a reversion from *Giatrasi*. Like that form, it is stable in its characters, and it may here be noted as a general observation that the mutations showing reduced size are invariably more stable than those presenting differences in amount of leaf division. This semi-dwarf mutation from *viridissima* was first noted by Trevillian in the Pierson establishment. Since then I have found it also in the greenhouses of Peter Wagner of Brooklyn.

From *superbissima* there has developed directly another reversion in size (Pl. VIII, fig. 7), but which has retained the double division of both *superbissima* and *Piersoni*. This also was first noted in the Pierson greenhouses where it has developed in *superbissima* stock more than once. It has also occurred in the greenhouses of John Lewis Childs at Floral Park, and likewise at the Brooklyn Botanic Garden. A description of the circumstances of this last occurrence is worth recording.

In a pot of *superbissima* which included three or four crowns, there developed in one crown two leaves considerably taller and looser in division. The crowns were then potted separately for observation. That containing the two taller leaves developed more of the same sort of leaves, becoming eventually intermediate in size between *superbissima* and *Piersoni*. Additional plants were raised from it of the same sort, and the form remained stable in further cultivation.

It should be noted here that the several reversions of this particular type have not resulted in exactly identical forms. The different plants are all intermediate between *superbissima* and *Piersoni* but there are some variations in height and shape of the segments.

Special interest attaches to the three reversionary forms above described because of their very definite character. Each represents a single return toward the original Boston-fern type. In all three cases the new forms were

⁵ Since the above sentence relating to *viridissima* was written, a further variation has taken place in this form, first noted in the summer of 1921. In the only plant of *viridissima* being maintained, what appears to be a definite return to the characteristics of *superbissima* has occurred, so that there is now no authentic plant of the original Pierson *viridissima* sport in the Botanic Garden collection.

immediately stable in their own type. That is, there was no tendency to fluctuate toward the parent forms. It is also of interest, as has been noted by Babcock and Clausen (*Genetics in Relation to Agriculture*, pp. 315, 316), that these changes in leaf form and size occur independently of each other, indicating that the protoplasmic basis of the changes is also distinct—"to factor mutations in vegetative reproduction."

Reversions from elegantissima-compacta.

The form *elegantissima-compacta* has given rise to more distinct reversions than any other variety. It may be recalled here that it, like *superbissima*, represents a doubly progressive sport from *Piersoni*, showing both increased leaf division and reduction in size. In its dwarf character it does not have the foreshortened and congested aspect of *superbissima*, and its leaves are somewhat more divided, being twice pinnate-pinnatifid (Pl. IX, fig. 2; Pl. X, figs. 1-3). This division is also considerably more stable than that of *Piersoni* or *superbissima*, although reverting leaves occur not infrequently, and consequently seasonal changes may also occur. These, however, do not affect the type of the plant, which continues year after year to hold the characters of the original variation. By analogy from *superbissima*, we should expect at least the two types of reversion found in that plant, the production of a taller twice-pinnate plant and of a once-pinnate form. As a matter of fact, both these expected forms and one other have developed.

The simplest form is a complete reversion to the once-pinnate condition, first found at the Pierson establishment and sold by them under the name "Dwarf Boston" (Pl. X, fig. 4). This form is of about the same size as the primary progressive sport *Scotti*, and under some conditions rather closely resembles this. It has typically, however, more the appearance of *bostoniensis* in leaf form and habit. It is stable in that no divided leaves are produced from it. As it is somewhat taller than *elegantissima-compacta*, it is to be considered also a reversion in size as well as in division.

Another distinct and definite reversion has been introduced under the name of "*John Wanamaker*" (or *Wanamakeri*) by Robert Craig of Philadelphia (Pl. X, figs. 13-18). This is an incomplete reversion in division in which some of the leaves are entirely once pinnate but considerably ruffled and wavy, while others are more or less lobed or even twice pinnate but also showing the ruffling. The leaves are taller and narrower than those of *elegantissima-compacta*, even when divided. The variety seems to represent reversion toward double division reaching only an intermediate condition. In its ruffled character it might be considered to present a progressive sport in this particular, but it seems more reasonable in this case to interpret this ruffling as a modification of leaf division.

This same form has arisen several different times at the Pierson greenhouses and also at Giatras's place in West Hoboken. These different examples of this mutation vary a little in form and size, but are, in general, very like each other.

A plant of this type obtained originally at Pierson's and set out in an open stock bed at the Brooklyn Botanic Garden underwent an interesting change in that it returned entirely, in crown and runners, to apparently the original type of *elegantissima-compacta*. There might be reason for suggesting that the growth in an open bench had something to do with it except for the fact that in many thousands of plants grown under the same conditions at Craig's I did not see any similar break. The explanation is probably found in the possibility that the particular number which I obtained from Pierson did not really represent a stable sport or mutation but rather a fluctuation of a type which will be described below.

From the *Wanamaker* type there has developed at Pierson's a reversion to a completely once pinnate unruffled form, corresponding to "Dwarf Boston" in general appearance and size (Pl. X, fig. 5), but not sufficiently cultivated to warrant any general opinion as to its characters. It corresponds to the reversion from *viridissima* described above since it represents a second step back toward *bostoniensis*.

In addition to the above mentioned, Trevillian has also detected among the plants in his charge another *elegantissima-compacta* mutation which approaches *Piersoni* in characters, i.e., it is twice pinnate and tall. Two examples from Pierson's have been grown at the Botanic Garden (Pl. VI, figs. 2, 3). By reference to the illustrations it will be seen that there is some little difference in the shape and size of the ultimate segments of these two types. Both, however, are generally like the *Piersoni*-like reversions produced from *superbissima*, and, it may be added, like other similar reversions from progressive sports of a higher order of leaf divisions. A series of leaves of six of these types, produced by mutation from five different progressive sports representing several different grades of leaf division, is illustrated in Plates VI and VII. Thus figure 1, Plate VI, shows a reversion from *Smithi*, a four-pinnate form. Attention is called to the fact that the six types, although alike in division, vary noticeably in outline and carriage of the pinnae, in texture, and in minute characters.

When it is recognized that each of the twenty derivative mutations from *Piersoni* noted on the chart may give rise directly or indirectly to reversions of a *Piersoni* type, the possibilities of a confused tangle of forms, practically impossible to differentiate by description, will be realized. What explanation could the ordinary systematic examination of such a group of forms bring forth? Some systematists would explain the variation as a set of closely related intergrading forms, connecting the extremes as parts of one single "species." With fertile sexually reproducing forms, the suspicion of hybridism would certainly attach. Especially would this apply in such cases in which the reversion was intermediate in form and other characters. Obviously, if we may consider these vegetative mutations as analogous to variations among wild forms which appear similar, we may see adequate reason for caution in making generalizations regarding complexes of wild forms.

The reversions of *elegantissima-compacta* described above all belong to the category of stable forms, presenting distinct and definite changes in leaf form and division. The kind of reversion mentioned earlier in the paper as reduced stability of division ("fixed instability") has also occurred, and one case has been under continuous observation and cultivation for several years.

A plant of typical *elegantissima-compacta*, obtained directly from its place of introduction, the Pierson establishment, was one of the original group of *bostoniensis* varieties to be received in 1915, and in fact was designated "no. 1" in my accession series. With the other forms then at hand, it was planted out in open soil in a bench for reproduction by runners. Among its numerous progeny in that first cultivation was one small plant with leaves almost entirely once pinnate. In the spring of 1916 (March) this was planted in a large square pan for further propagation with the idea that it might prove to be a stable once pinnate reversion. At this time it consisted of six leaves (Pl. IX, fig. 1, shows a similar plant), entirely once pinnate with the exception of one which was shallowly lobed on some pinnae. By August the pan had become full of small plants which were separately potted and grown for eleven months. Although the stock crown had been almost completely once pinnate, these runner plants were in general like typical *elegantissima-compacta* in leaf division, with scattered once pinnate leaves mixed in. In July, 1917, the stock consisted of fourteen plants in four- and six-inch pots, but not in the best condition, owing to crowding. Three sorts of plants could be distinguished among them. One plant with fifteen or more leaves was almost entirely once pinnate, only one or two leaves showing any double division. There is little doubt that this represented the original once pinnate crown first detected, but this cannot be absolutely assured. Nine plants were mainly twice pinnate as in typical *elegantissima-compacta*, but each had one or more once pinnate leaves. Four plants had leaves practically without any reversion.

The cultural conditions had been the same for all, so that the modifications observed must have taken place as a result of internal changes. Examples of the three sorts were kept for further observation, but their subsequent behavior was the same. The plant with mainly once pinnate leaves continued once pinnate in its original crown, but the secondary crowns produced in the same pot by runners to the number of eight had leaves mainly of the twice-divided type of *elegantissima-compacta*. In other words, the original once pinnate crown, produced as a runner variation, retained its leaf characteristics as its own new leaves developed, but gave rise only to new plants with more divided leaves, either like typical *elegantissima-compacta* or, in some cases, with the less stable amount of division, but with no real modification of leaf form (Pl. X, figs. 6-12).

This behavior is worthy of emphasis because it has been found to be of frequent occurrence in the study of reversion among other division forms.

On more than one occasion and with diverse varieties, attempts to reproduce some reverting leaf type by setting out the new form in bench for vegetative reproduction have resulted in the continuance in the new crown of its new characteristics but with the reappearance in the runners derived from it either of the original form of division or of that form with some reduced stability. The larger size of the reverted crown is typical generally of reversions, both temporary and permanent sorts.

With these facts in mind, exception must be taken to the conclusion adopted by Boshnakian (Jour. Hered. 7: 233. 1916) and repeated by Babcock and Clausen (*Genetics in Relation to Agriculture*, fig. 130 and explanatory description), interpreting a series of four connected *Nephrolepis* runners which show differences in form as four different mutations. The series shows respectively (1) a four-pinnate variety, *magnifica*; (2) a derived once pinnate plant; (3) a third generation (?) plant with unstable division, and (4) another third generation (?) plant like *magnifica*. Similar series of runners have occurred in my cultures (Pl. IX) which on further cultivation have resolved themselves into the three types of plants cited above, viz., (a) second generation reverted crowns, usually only one; (b) third generation crowns, like the original variety in division and in stability of division; (c) other third generation crowns like the original variety but with more reverted leaves per plant. Unless the plants figured by Boshnakian were afterwards planted and found to continue distinct, it is not safe to cite them as so many mutations; rather, they seem to belong in the category of fluctuations. It has been my experience that while a plant of a divided variety may often produce occasional reverted leaves and sometimes a new runner plant with only reverted leaves, the production of a stable self-reproducing reversion, in other words a mutation, is most uncommon.

In general, any given division variety may be expected to produce in cultivation one of three types of plants. The most numerous—an overwhelming majority—will be of the form typical for the parent stock, the only modification being in occasional single reverting leaves such as occur in the stock plants themselves. Second, an occasional plant will be developed which will appear almost entirely reverted but which, on further reproduction, will develop new plants like those of the original form, or at most with some reduction in stability of division. Such plants would be classed as fluctuations. It is obviously important for growers in selecting crowns for propagation to avoid such undesirable stock plants. Very rarely, a third type of plant will appear, distinct not only in its own characteristics but also in its runner progeny, a real mutation. These are somewhat more common in the regressive direction than in the progressive.

There is a very interesting morphological problem involved in this matter of the production of new forms, whether of regressive or of progressive type. The problem can only be indicated here, but the main facts are worthy of note. It is a well known fact that the stolons of *Nephrolepis*

originate in association with the leaves, one stolon being paired with each leaf in branching from the crown-stem axis. It should not be difficult to determine whether there is any association between leaf variations on the original crown and runner variation on the paired stolon. For example, do the stolons paired with reverting leaves tend to produce new plants showing a reduction in stability of leaf division in a manner analogous to the behavior in variegated *Pelargonium*?

The problem is not as simple as might at first appear from the above statement, because the relation of stolon to old and new plants is not entirely simple. The stolon from an original stock plant may bear along its several feet of length a considerable number of plants arising as lateral buds, generally on short spur branches. When the new bud plants are taken up for potting, each one may retain some portion of the parental stolon capable of continued bud reproduction. The progeny of such a plant would then consist of new plants from the original parental stolon together with others from the new stolons of the bud plant, *i.e.*, "sisters" and "daughters." With the possibility of such complications, the doubts expressed with reference to the relationships of the series of four connected plants figured by Boshnakian will be readily appreciated.

A not infrequent anomaly in the behavior of the stolons is what appears as a dichotomy of a stolon in which one half becomes a leaf without any evident associated stem axis while the other half continues as a normal stolon. I have seen three successive leaves produced in this manner on one stolon. Sometimes the stolon growing point is lost with the formation of a single leaf, and the appearance is given of the transformation of a stolon into a leaf. I have made no determination of the stelar behavior in these cases.

Reversions of other secondary sports.

Only one other secondary sport of *bostoniensis* has been recorded as having given rise to a reversion of the mutation type, another Pierson variety, *elegantissima*. This is a variety much like *elegantissima-compacta* in leaf division, but lacking the dwarf character of that form. Robert Craig of Philadelphia has reported and introduced as a new variety, named *robusta*, a form which has almost complete agreement in characteristics with plain *Piersoni* (Pl. VI, fig. 5). If its origin is correctly given, it is to be grouped with the other *Piersoni*-like reversions which have already been discussed.

Summarizing the facts recorded for the reversions of the secondary sports, we find the reversionary behavior similar to that described for the primary forms.

1. Reduction in the stability of the original progressive change as shown in the degree of division and in the proportion of divided leaves was experimentally demonstrated. Furthermore, this reduction was shown in *elegantissima-compacta* to pass through an almost completely reverted

form, and then to return in the next generation either to the original typical form or to one with reduced stability of division. The point is, there are cases of apparent reversion in which the new (*i.e.*, reverted) form seems incapable of reproducing its new type. Its runner progeny do not "breed true" but return in different degrees to the form from which the reversion originally sprang. The possibility suggests itself that such unstable variations may correspond in kind to the variations noted as probably due to seasonal changes. It may be that as reverted leaves appear to be more frequent during winter, long continued observation might also show that the temporarily reverted runners, the sort incapable of reproducing their kind, may also have a seasonal frequency.

2. Discontinuous variation in a regressive direction affecting the leaf division has been found in a number of forms: in *elegantissima*, to *robusta*, a *Piersoni*-like form; in *elegantissima-compacta*, in two steps through *Wanamaker* and to a once-pinnate form; also in *elegantissima-compacta*, in one step, to "Dwarf Boston," once pinnate; in *superbissima*, to *viridissima*.

3. Discontinuous variation, reversion in size: in *elegantissima-compacta*, to *Wanamaker*, and to a *Piersoni* type; in *viridissima*, to a taller form, intermediate in size between *viridissima* and *bostoniensis*.

4. No evidences of reversion to a fertile condition have been noted.

The characteristics and behavior of reversions from tertiary and higher degree progressive sports of *bostoniensis* will be left to a future paper for description.

BROOKLYN BOTANIC GARDEN

EXPLANATION OF PLATES

PLATE V

Fluctuating reversion: pinnae showing range of fluctuation in three forms.

FIGS. 1-5. Pinnae from one leaf of *Piersoni*, ranging from typical twice pinnate division (fig. 1) through intermediate forms (figs. 2-4) to once pinnate type (fig. 5)

FIG. 6. Simple pinna from another leaf of the same plant of *Piersoni* as shown in figures 1-5.

FIGS. 7-10. Pinnae from one leaf of "*Anna Foster*."

FIGS. 11, 12. Pinnae of *Anna Foster*, taken from another plant.

FIGS. 13-17. Pinnae of fertile *Piersoni*-like reversion, var. *fertilis*, showing same sort of fluctuation as in true *Piersoni*.

PLATE VI

Regressive mutations: leaves of twice pinnate reversions from different progressive forms.

FIG. 1. From *Smithi*, a four-times-pinnate form.

FIG. 2. From *elegantissima-compacta*, itself twice pinnate, pinnatifid.

FIG. 3. Also from *elegantissima-compacta*, but a distinct form.

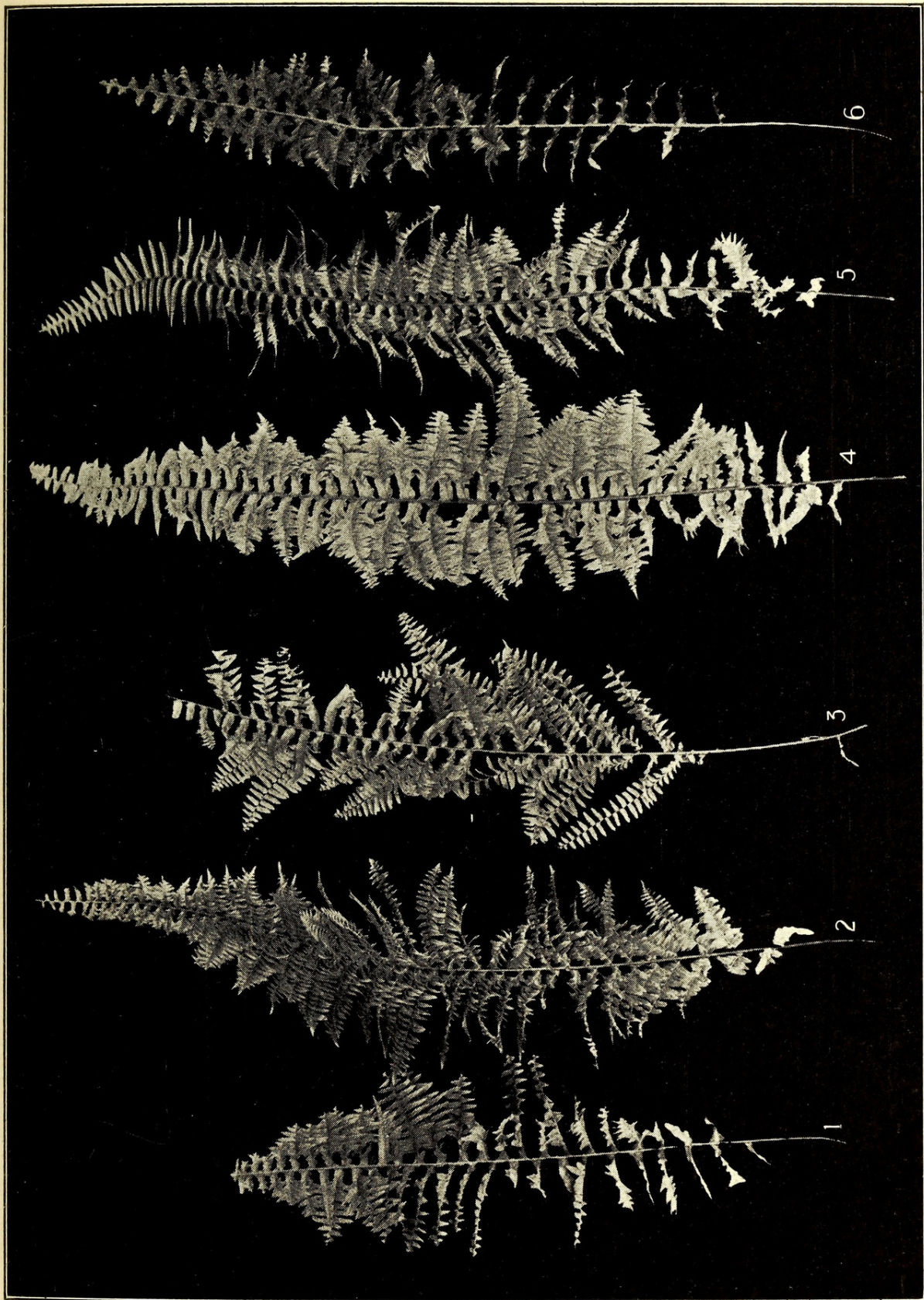
FIG. 4. From *superbissima*, a reversion in size (see also Plate VIII).

FIG. 5. *Robusta*, introduced by Robert Craig, Philadelphia; a reversion reported from *elegantissima*.

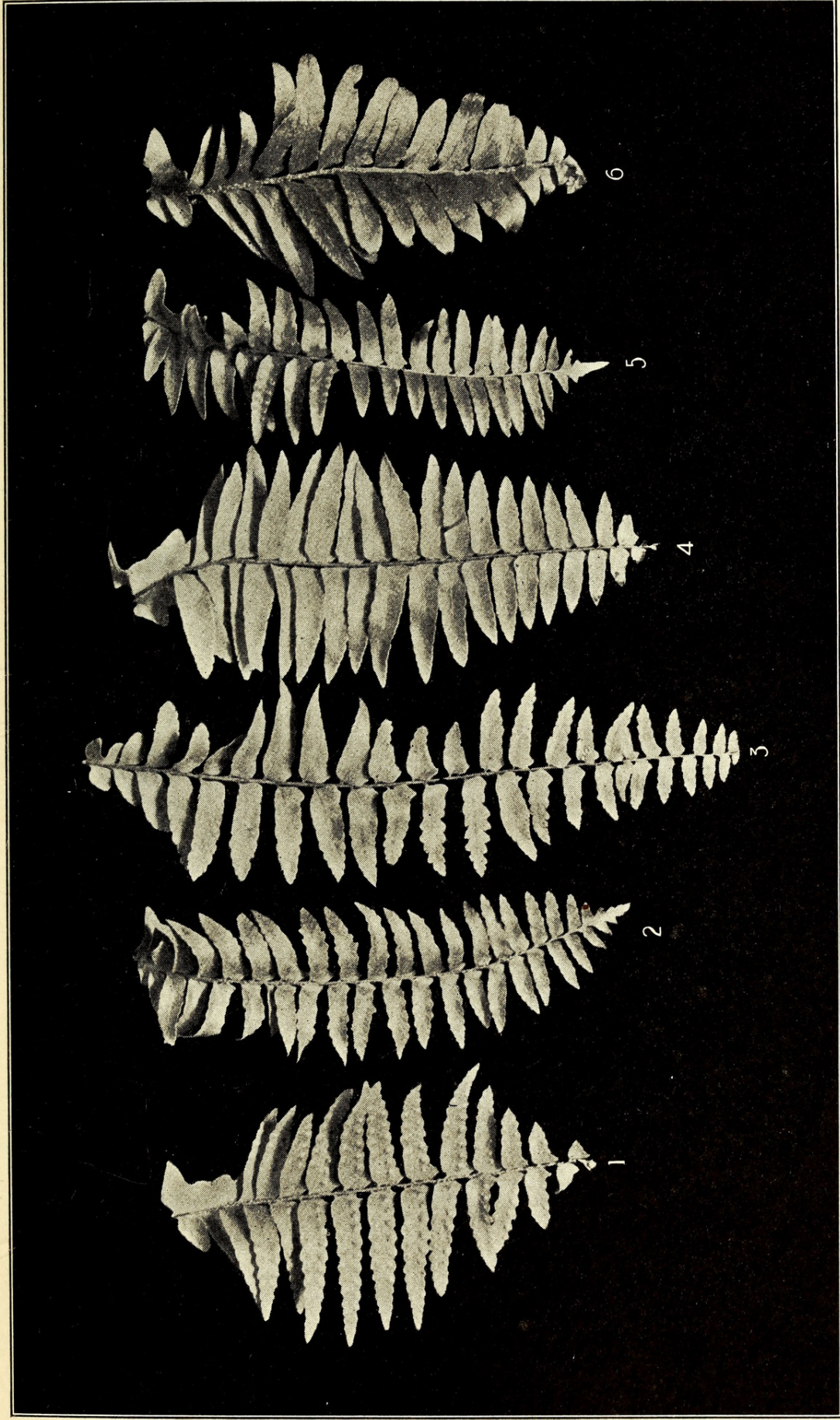
FIG. 6. Var. *fertilis*, possibly reversion from *Piersoni*.



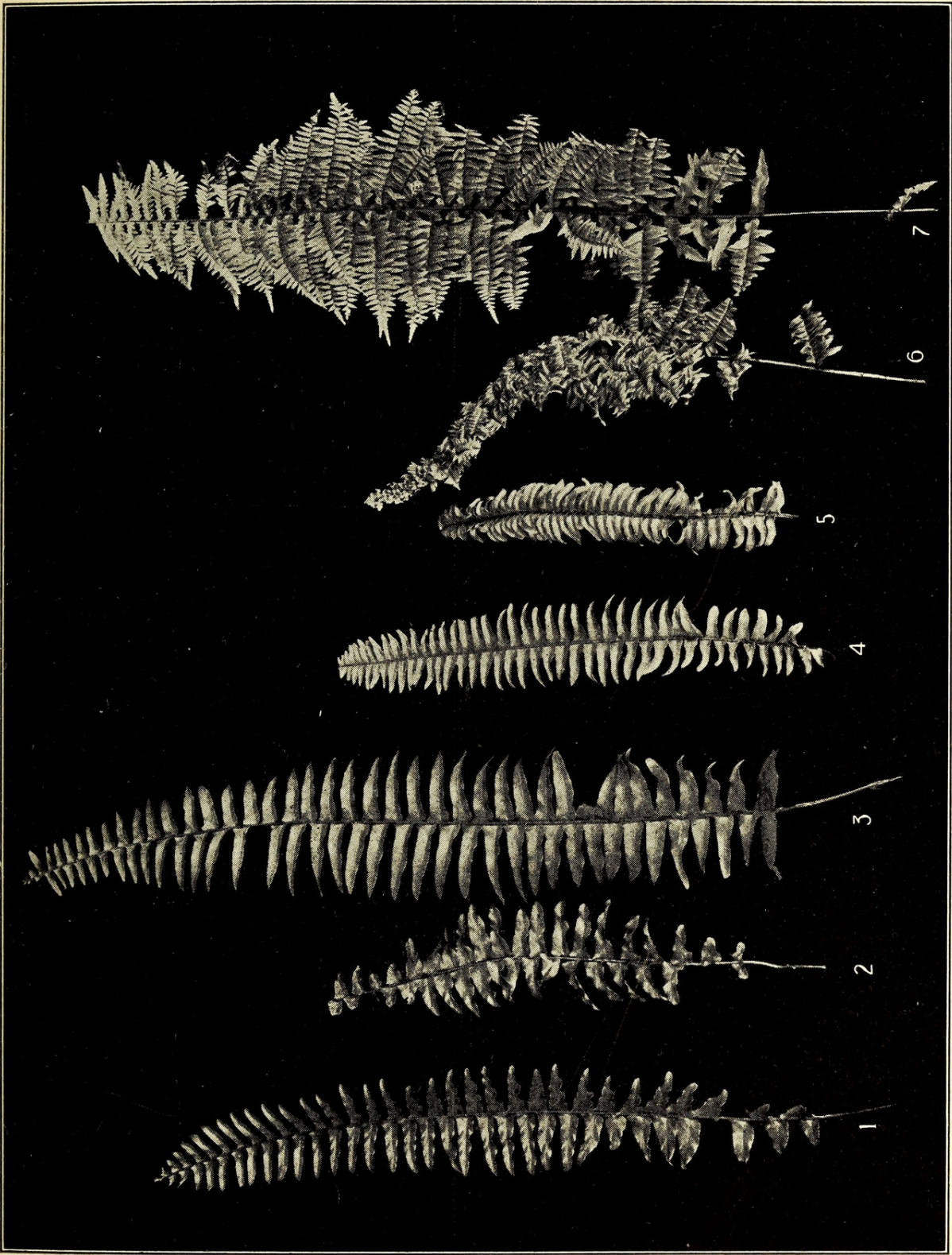
BENEDICT: VARIETIES OF NEPHROLEPIS



BENEDICT: VARIETIES OF NEPHROLEPIS



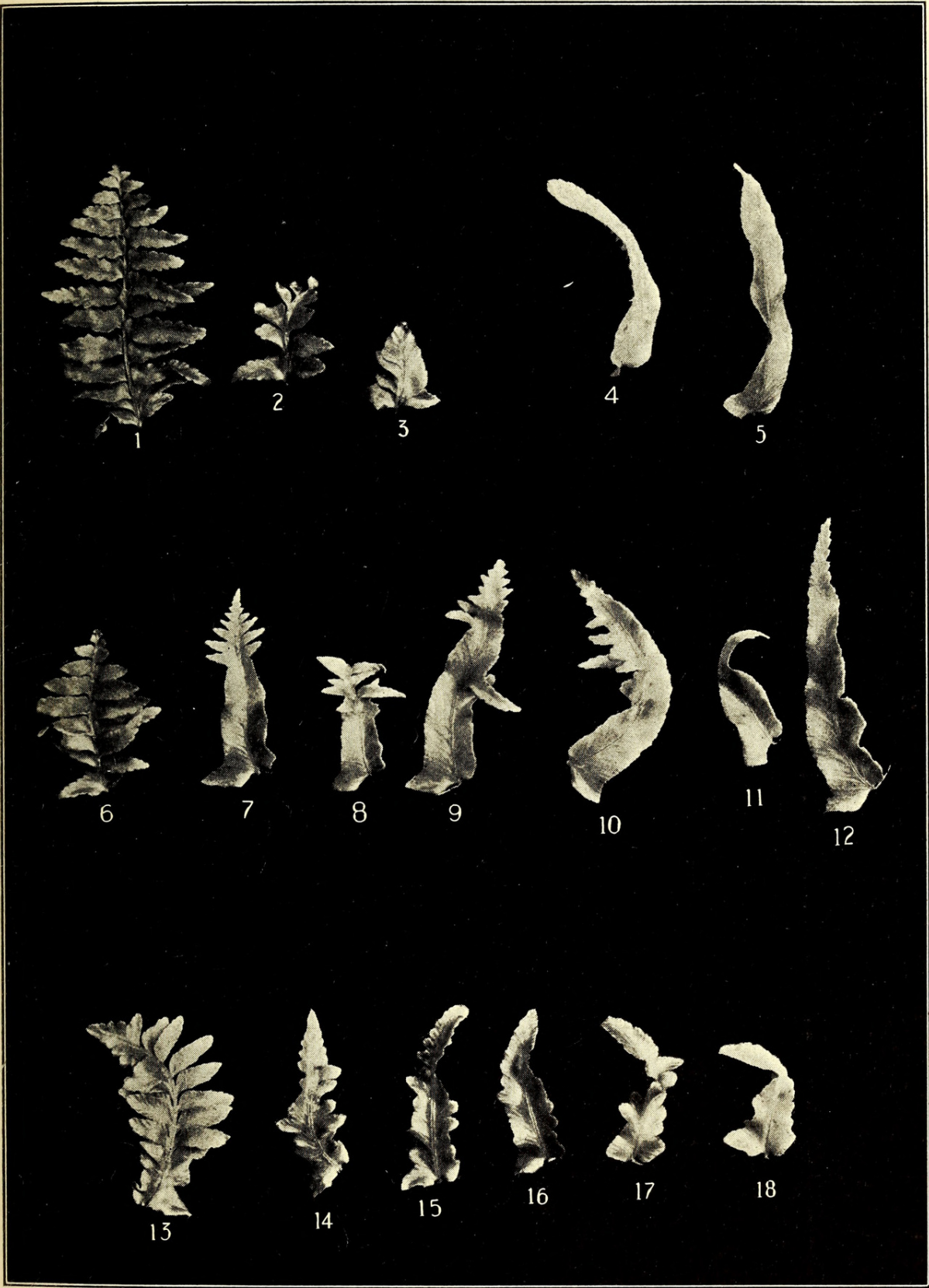
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BENEDICT: VARIETIES OF NEPHROLEPIS



BENEDICT: VARIETIES OF NEPHROLEPIS

PLATE VII

Regressive mutations: pinnae of leaves shown in Plate VI.

FIGS. 1-6. Represent respectively the same forms as shown in Plate VI, figures 1-6.

PLATE VIII

Regressive mutations: leaves of forms showing reversion in size and in division.

FIG. 1. "*New York*" fern, a regressive mutation from *Giatrasi* (fig. 2); introduced by George Giatras, West Hoboken, N. J.

FIG. 2. *Giatrasi*, dwarf primary sport from *bostoniensis*.

FIG. 3. *Bostoniensis*, for comparison to show intermediate size of *New York* fern.

FIG. 4. Unnamed reversion, from dwarf once pinnate *viridissima* (fig. 5).

FIG. 5. *Viridissima*, introduced by F. R. Pierson, Tarrytown, derived by reversion in division from twice pinnate *superbissima* (fig. 6).

FIG. 6. *Superbissima*.

FIG. 7. Unnamed reversion in size, but not in division, from *superbissima*.

PLATE IX

Fluctuating reversion: bud plants showing unstable regressive variation.

FIGS. 1, 2. Sister plants of an unstable strain of *elegantissima-compacta*. FIG. 1, entirely once pinnate, except for a few pinnae on one or two leaves which show double division. FIG. 2, plant showing typical form of *elegantissima-compacta*.

PLATE X

Fluctuation and mutation of *elegantissima-compacta*.

FIGS. 1-3. Pinnae from one leaf of *elegantissima-compacta*.

FIG. 4. Pinna of "*Dwarf Boston*," introduced by F. R. Pierson as a stable reversion from *elegantissima-compacta*.

FIG. 5. Unnamed once pinnate mutation from *Wanamaker* (see figs. 13-18).

FIGS. 6-12. Pinnae selected to show range of fluctuation in an unstable strain of *elegantissima-compacta* (see figs. 1, 2, Pl. IX).

FIGS. 13-18. Pinnae selected to show range of fluctuation in *Wanamaker*, a regressive mutation of *elegantissima-compacta* introduced by Robert Craig, Philadelphia.



Benedict, Ralph C. 1922. "The origin of new varieties of *Nephrolepis* by orthogenetic saltation." *American journal of botany* 9(3), 140–157.

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