NOTE ON SOME CHARACTERS IN FERNS
SUBJECT TO MENDELIAN INHERITANCE

BY IRMA ANDERSSON
THE JOHN INNES HORTICULTURAL INSTITUTION, MERTON, SURREY

THOUGH many natural hybrids have been described by various writers and innumerable new forms of such species as Scolopendrium vulgare, Athryrum Filix-foemina and Polystichum angulare have been the result of fertilization, when spores of different varieties have been sown together (LOWE 1895), very few attempts at a genetical analysis have been made. This is the more astonishing as modern fern genera, e. g. Scolopendrium, Athryrum, Polystichum and Asplenium, as represented in some private collections, exhibit many features which are regarded as criteria of comparison and used as a basis for phyletic seriation in Ferns (e. g. BOWER 1923). Among such features the architecture and venation of the leaf are considered to be of importance. The contour, texture and venation of the expanded leaves in Ferns show great difference in detail. Various order of branching, outline of segments, their relation to one another and to the main rachis are features which offer easily observed criteria of comparison. (BOWER 1923).

At the present stage of our investigations only a few facts are available to demonstrate that the characters referred to above, together with others used in the systematic treatment of Ferns, are determined by factors which behave as Mendelian units. The experiments have, however, proceeded far enough to draw certain conclusions and to justify a preliminary note.

MATERIAL AND MODE OF CULTURE.

The original plants were obtained mainly from the collection of Mr. H. STANSFIELD of Manchester. To obtain hybrids of known parentage it was found convenient to use the transparent culture medium which previously had proved to be suitable for the rearing of prothallia. Spores were therefore sown on a thin film of agar with KNOP'S solution in petri dishes under sterile conditions. Before the
production of archegonia each single prothallium was transferred to a separate petri dish. In order to ensure cross-fertilization, when the archegonia were open the petri dish was filled with KNOP's solution and prothallia with antheridia of the proposed male parent were added. Twelve hours is usually long enough to effect fertilization. The solution with the male prothallia is then removed. The hybrid usually appears a week or two after, and, when the root and cotyledon are well developed it is transferred to soil. The prothallium of Polystichum angulare and Scolopendrium vulgare is at first either male or asexual. This stage is followed by a period of growth after which the archegonia appear at the usual place. When the archegonia are ready for fertilization the antheridia are as a rule empty. This applies to the normal regularly formed more or less heartshaped prothallium. It is therefore often necessary to keep a prothallium for a considerable time in order to secure self-fertilization, as new lobes or outgrowths must develop, which are covered with antheridia. For the purpose of self-fertilization of single gametophytes the prothallia are therefore best transferred to soil after they have been cultivated separately in dishes and have grown to a considerable size. The pots must be covered with glass, and water must be given from above when the prothallia are ready for fertilization.

EXPERIMENTS WITH POLYSTICHUM ANGULARE.

The plants used in this investigation were bred from a variegated sporophyte with the familiar characteristics of the Polystichum angulare type, but with pinnules rather less regular in shape, owing to the amount of white tissue. The family, originally raised for the purpose of elucidating the inheritance of variegation, showed a simple segregation in respect to the characters which will be here described. Four types of plants could easily be distinguished (Fig. 1): plants similar to the original parent (No. 00) i. e. typical Polystichum angulare (type I) and plants similar to these as regards the shape of the pinnules, but different owing to the imbricated position of the pinnae and pinnules (type II); another form (type III) with truncated fronds which usually terminate in a short hornlike protrusion of the rachis, with pinnae of various lengths, each with from three to seven pairs of pinnules and usually terminating in one that is fanshaped. The pinnules are more or less cuneate-flabellate, palmately lobed and toothed. Type IV is similar to type III, but has pinnae and pinnules im-
bricated. The number of pinnae and pinnules is the same as in type III.

**Experiment 1.** Spores from the original sporophyte No. 00 were sown on soil and a family raised consisting of 158 plants of type I, 50 plants of type II, 63 plants of type III and 14 plants of type IV. The expectation on a 9 : 3 : 3 : 1 basis is practically realised, the cal-

![Fig. 1. Polystichum angulare. A type I, B type II, C type III, D type IV. E side-view of frond of type IV, + the protruding rachis.](image)

culated ratio being, 159,75 : 53,25 : 53,25 : 17,75. Some of these plants were kept for breeding purposes, i.e. Nos. 01—051.

**Experiment 2.** Spores from 24 sporangia were sown on agar, the content of each single sporangium in a separate dish, and the prothallia in each dish were allowed to fertilize i. se. All together 278 plants were raised, of which 152 plants were of type I, 55 plants of type II, 52 plants of type III, 14 plants of type IV and 5 plants which belonged either to type III or IV, but could not be placed with certainty. The expected ratio was 156,32 : 52,11 : 52,11 : 17,37. The distribution of the
four types in each sporangium was the same. Some of these sporophytes were bred from (see table); the figures enclosed by brackets indicate the No. of the sporangium from which the plant was derived. The figures outside the bracket is the number of the present sporophyte.

**TABLE 1. Showing Distribution of the Types of Sporophytes in \( F_2 \) from a Heterozygous Polystichum angulare Plant.**

| Reg. No. of Parent-Sporophyte | Type of Parent-Sporophyte | Type I | Type II | Type III | Type III or IV | Type IV |
|------------------------------|---------------------------|--------|---------|----------|---------------|--------|
| 01                           | I                         | 56     |         |          |               |        |
| 04                           | »                          | 120    | 41      |          | 48            |        |
| 011                          | »                          | 50     | 17      | 15       |               | 5      |
| 024                          | »                          | 30     | 12      |          | 10            |        |
| (83)18                       | »                          | 46     |         |          |               |        |
| (84)3                        | »                          | 30     |         |          |               |        |
| (36)1                        | »                          | 89     | 28      |          |               |        |
| (71)11                       | »                          | 28     | 7       |          |               |        |
| (92)16                       | »                          | 70     | 13      |          |               |        |
| (35)8                        | »                          | 16     |         | 7        |               |        |
| (10)4                        | »                          | 17     | 7       |          | 5             |        |
| (10)6                        | »                          | 24     | 5       |          | 3             |        |
| (84)17                       | »                          | 40     | 15      | 16       |               | 5      |
| (92)12                       | »                          | 29     | 9       |          | 11            |        |
| 021                          | II                        |        | 13      |          |               |        |
| 037                          | »                          |        | 100     |          |               |        |
| 051                          | »                          |        | 77      |          |               |        |
| 02                          | »                          |        |         | 154      |               | 49     |
| 03                          | »                          |        |         | 311      |               | 108    |
| 017                          | »                          |        | 20      |          |               | 6      |
| 028                          | »                          |        | 71      |          |               | 26     |
| (83)15                       | »                          |        | 17      |          |               | 6      |
| (84)9                        | III                       |        |         | 82       |               |        |
| 014                          | »                          |        |         | 18       | 1             | 6      |
| 018                          | »                          |        |         | 30       |               | 12     |

*Experiment 3.* Descendants raised from the four types in experiments 1 and 2 gave families, the details of which are set out in the table. Type III and IV are not so easily distinguished when the plants are small, and in some families which had to be discarded early, plants of these types have been counted together.

*Experiment 4.* Spores from separate sporangia were sown on agar and each prothallium transferred to a separate dish and in some
of the dishes the prothallia were self-fertilized. Others had subsequently to be transferred to soil, where, after self-fertilization, they have given rise to one or more sporophytes. 22 of the 78 gametophytes thus self-fertilized gave sporophytes of type I, 20 gave type II, 18 gave type III and 18 gave type IV, the expected ratio being $20:20:20:20$. Of these self-fertilized gametophytes gave rise, moreover, to more than one sporophyte. In all, 79 sporophytes were thus derived, the largest number to be grown from one prothallium being 11 sporophytes. All the sporophytes derived from the same gametophyte were alike and prove the purity of the gametophyte.

The assumption of two independent factors, their equal distribution at reduction division (Exp. 4) and recombination at fertilization is, in spite of the small numbers, substantiated. One factor determines the shape of fronds, pinnae and pinnules and the other determines the position of pinnae and pinnules, (i.e. the length of rachis, imbrication of pinnae and pinnules).

The presence of variegation in the sporophytic or gametophytic generation has no effect on the ratio in which the types occur.

**EXPERIMENTS WITH SCOLOPENDRIUM VULGARE.**

*Dwarfness.* A muricate form of *Scolopendrium vulgare*, var. *crispum nanum*, the fronds of which only attain a length of 3—4 cm., was found to be a homozygote. Dwarfness is recessive to tallness. (For other varieties possessing characters which reduce the size of the plant see below.)

*Branching.* That various types of branching of the fronds found among varieties of *Scolopendrium vulgare* are recessive to non-branching is evident from several experiments. Furcated and multifid varieties (Fig. 2 E—H) crossed with the *vulgare* type (Fig. 2 A) have always given unbranched hybrids. In one experiment the var. *spirale* φ (Fig. 2 C), possessing unbranched fronds not exceeding 10 cm. in length and having the basal parts very much undulate and with torsion of the apex, was crossed with the var. *ramocristatum* φ, a multifid and non-undulate variety (Fig. 2 E—F). $F_1$ had the common *vulgare* type of frond and in $F_2$ a segregation occurred into 67 plants of *vulgare* type, 25 plants of *spirale* type, 20 plants of *ramocristatum* type and 5 plants like *ramocristatum* but with undulation and torsion of the fronds (Fig. 2 I), the calculated ratio being $65.79 : 21.93 : 21.93 : 7.31$.

Further, the regularly *multifid* (Fig. 2 E—F) or *palmate* type is
probably dominant to the irregularly multifid one (Fig. 2 G—H). One heterozygous regularly multifid plant segregated into 61 plants of the former type and 21 plants of the latter.

The projecting lobes of the margin on fronds of var. sagittatum projectum (Fig. 2 D) have been shown upon crossing to be recessive to the vulgare type of frond. The former variety crossed with palmately or irregularly furcated varieties has also given hybrids of vulgare type.

Crispate or undulate fronds are recessive to the vulgare type, e.g. in one experiment where the variety crispum fertile (Fig. 2 B) used as a ♀, was crossed with the vulgare type, $F_1$ was vulgare and in $F_2$ a segregation occurred into 57 vulgare type and 19 crispum fertile type. For the segregation in $F_2$ from the cross between var. ramocristatum and var. spirale see above.

The inheritance of entire leaf and incised leaf has been studied by LANG (1923), who showed that a segregation of 3 entire-leaved to one incised-leaved took place in $F_2$. This has been confirmed in my experiments with similar types, the difference being that the variety used by me was at the same time homozygous for undulation. The $F_2$ consisted of 65 entire-leaved plants and 20 incised-leaved plants. $F_3$ from one of the entire-leaved plants gave 55 entire-leaved and 17 incised-leaved plants.

Murication of the upper surface of the frond is dominant to smooth surface. Sporophytes homozygous in this respect are muricate from the first leaf. Those heterozygous attain the character gradually.

The development of the ridge inside the margin on the under side of the frond is formed by the protrusion of certain layers of the undersurface (Fig. 3 A—C). In some plants this protrusion is so well developed that it forms a transparent membrane which stands away from the frond (Fig. 3 A and G). This particular form of frond is dominant to the smooth form. Strictly speaking the hybrids may be said to be intermediate, as the first fronds are devoid of this margin. The feature gradually develops on later fronds (Fig. 3 B—C), but always to a less degree than on the homozygotes (Fig. 3 A, homozygous

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Fig. 2. Scolopendrium vulgare. A vulgare-type, B crispum fertile, C spirale, D sagittatum projectum, E—F under and upper side of frond of regularly multifid type. G—H upper and under side of fronds of irregularly multifid type. I the double recessive obtained in $F_3$ from $C \times E—F$ types. K—L type with the costa developed into the hornlike terminal protrusion, $M$ underside of frond of young plant of $K—L$, showing the cup-like structure, $N$ underside of frond of similar type with wing-like structure. All reduced approximately to the same scale.
Fig. 3. _Scolopendrium vulgare_. A—D undersurface of fronds representing plants of an $F_1$ family, A—C with ridge, D without ridge. E frond of $F_1$ from a muricate _vulgare_ type $\times$ a regularly multifld variety (both with sori on the undersurface), showing sori on the upper surface. F frond of a variety with incisions between the sori which face each other. G upper side of frond of a multifld variety with the transparent membrane round the edge, showing position of sori.
NOTE ON SOME CHARACTERS IN FERNS

plant). The homozygous plant starts from the first leaf with this peculiar margin. Thus the $F_1$ in one experiment, when the plants were young, consisted of 78 plants without ridge and 27 plants with ridge. When the plants were fully grown the ratio was 27 with ridge (Fig. 3 A), 45 with ridge less developed (Fig. 3 B—C) and 33 without ridge (Fig. 3 D). The calculated ratio, $26.25 : 52.50 : 26.25$ would no doubt have been obtained if the plants had been kept longer, as there were too many of the still non-ridged and too few heterozygous ridged. Subsequently another lot has been raised of the same family, consisting, when scored young, of 29 plants without ridge and 13 plants with ridge. Twelve prothallia in the former family were kept isolated and each one self-fertilized. 5 prothallia gave sporophytes without ridge and 7 gave sporophytes with ridge from the first frond. These homozygous sporophytes with ridge have a special appearance as the development of this peculiar margin seems correlated with contraction of the whole lamina. This occurs to such an extent that the fronds only attain a length of about 15 cm., and a width of 15—20 mm. They show excrescences and folds of the upper surface and margin and the dark leathery part of the frond is in strong contrast to the projecting transparent membrane-ridge of the underside. Plants in this family heterozygous for margin show serration of the edge, where the ridge is developed.

The position of the sorus is often altered as a consequence of the development of this membrane-ridge. A dislocation of part of the sorus is effected if the ridge crosses the sori. In the multifid types, with transparent membrane round the edge of the frond, the sori mostly follow the inside of the fold thus produced and are exposed towards the upperside of the frond (Fig. 3 G). The displacement of the sori from the underside of the frond to the upperside is further characteristic of a regularly multifid form without well developed membrane. The best example is found, however, in the hybrid between a regularly multifid variety without marginal fold and the muricate *vulgare* type, also without fold, both having the ordinary position of the sorus on the undersurface of the frond. The hybrid, which is muricate, has typical *vulgare* type fronds, but with sori on the upper side of the fronds from the edge towards the costa (Fig. 3 E). This feature is probably not correlated with murication as it does not appear in the typical *muricatum* plants of the family raised here. This peculiarity is also found in certain *vulgare* type plants. Furthermore, the deep incisions on the fronds of certain varieties, which give them a more or less
pinnate appearance, occur between the sori which face each other. The result is the exposure pictured in Fig. 3 F. Further investigation is needed as to the development of this as well as other characters, and the relation of these processes to each other in conjunction with the analysis of the factorial constitution.

This applies also to another character, i.e. the development of the costa into a hornlike terminal protrusion, a process combined with transformation of the apex of the frond into a large, more or less cup or winglike structure on the under side of the frond (Fig. 2 K—N). A structure, probably homologous, is found in another variety. Here the fronds terminate abruptly, the costa forms the hornlike protrusion, but the rest of the apex of the frond is merely turned back towards the undersurface. The character in question has been found to segregate, but its relation to other characters is not at present clear.

**Fertility.** Reciprocal hybrids have in all experiments been alike. They are all very soriferous, the spores being normally developed. The only instance of sterility, i.e. the non-appearance of sori, met with up to the present time, occurred in the crispate plants in $F_2$ from the cross *vulgare* type $\times$ var. *crispum* fertile (see above). Fronds of these plants are thinner in texture than normal fronds and it is possible that older plants will become fertile.

**EXPERIMENTS WITH ATHYRIUM FILIX-FOEMINA.**

**Branching.** The extra branching of fronds and pinnae, characteristic of *crested* varieties, is dominant over the typical *Athyrium Filix-foemina* type of frond. In one experiment the crested var. *grandiceps* gave 37 *grandiceps* plants and 10 of the type. A less tasseled form, but with clearly furcated pinnae gave 43 furcated plants and 14 plants of the type. Other plants have been homozygous for furcation.

**Shape of pinnules.** The regular shape of the pinnules is recessive to the irregular. A sporophyte with pinnules varying in shape from lanceolate to flabellate, with regular or irregular outline, often with dilated or bifid apex, gave 72 plants with irregularly developed pinnules and 27 plants with regularly developed pinnules.

Very distinct degrees of laciniation of the pinnules occur, the more laciniated types being recessive to the less laciniated. On the laciniated plants pinnules or whole pinnae are often found similar to those of the next (dominant) type. This phenomenon occurs so frequently in plants of a certain family and its derivatives, that it may be said to
Fig. 4. Athyrium Filix-foemina. A frond of a sporophyte of the var. Frizelliae, a aberrant pinna, b characteristic pinnae. B—E fronds representing types of descendants derived from frond A. F—G fronds of two other types of descendants in the same family, F showing pinnae like B and D, G showing pinnae like C and E.

be the rule. The genotypical constitution of the different parts of the laciniated types in question has not yet been determined, owing to the
non-development of sori. It is interesting to note in this connection that Benedect (1924) found in budsports of the Boston fern, that the more advanced types of leaf division were not thrown by once pinnate types, but only by varieties with a higher degree of division.

The genotypical constitution of a sporophyte of Athyrium Filix-foemina var. Frizelliae (Fig. 4 A), another structural mosaic, is, however, available for investigation, as all parts of the plant are copiously soriferous. The chief characteristic of the var. Frizelliae is that the pinnae branch immediately on the rachis, producing a short rounded, or a solid leafy, semi-circular, flabellate-formed pinna. This parallel form to Nephrolepis Duffi has thus two transformed parts instead of the single pinna, one covering the other. The fronds end in a rather larger terminal pinna of the same form. A particular frond (Fig. 4 A) of our sporophyte showed some pinnae like that illustrated (part a of frond), alongside of pinnae characteristic of var. Frizelliae, (part b of frond). Spores from pinna a and from part b were gathered separately. From pinna a a family was raised (Fig. 4 B—G) consisting of 119 plants, of which 48 plants had exactly the same type of pinna as pinna a (Fig. 4 B). The family derived from part b consisted of 97 plants, of which 16 had exactly a-type of pinna. Both families also contained plants with solely Frizelliae-type of pinna (like part b and Fig. 4 D), and some plants which had the first fronds with pinnae like a and subsequently developed fronds with pinnae representing transitional stages from a-type to Frizelliae-type (Fig. 4 F). Some, or all of these latter plants had a mixture of both types on the same frond. In the family raised from the a-pinna 56 such plants occurred and in the other family 19. In both families the three types also occur with shortened rachis and imbricated pinnae and pinnules (Fig. 4 C, E, G). The proportion of the types derived from the two parts of the frond indicates that a genotypical difference existed between the two parts.

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