THE PRESENT STATUS OF HYBRIDITY AMONG THE PTERIDOPHYTES[1]

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Abstract: Hybrids are known in 62 out of the 270 recognized genera of ferns and fern allies. To date 552 pteridophyte hybrids have been recorded in literature.

The hybrids known to occur in 55 genera are discussed, out of 253 whose chromosomes were counted 29 were diploids, 129 were triploids, 76 tetraploids, 14 pentaploids and 5 hexaploids, in other words almost 90% were polyploids.

Of the 255 spores studied 84% were sterile, but 16% were fertile.

Hybridization, along with gene mutations, chromosome rearrangements and polyploidy, is regarded as a key genetical mechanism in bringing about species diversity. The factors extant in the environment, including various types of isolation, naturally fix or discard the products formed by the four above-mentioned processes.

Hybridization is now regarded as a very common phenomenon in the plant kingdom. There are many thousands of references to crossing as summarized by Knobloch (1956, 1959, 1962, 1963, 1968, 1972). If the literature of botany can be trusted, there are *about* 23,675 known interspecific and intergeneric hybrids among flowering plants (Knobloch, 1972). As more investigations are made, some of the alleged hybrids will be found to be spurious but, on the other hand, others will surely be added.

In view of the fact that no tally has been made of fern hybrids existing among the 10,000 known taxa in this group, it was thought that such a tally might be instructive. Three hundred and forty-three research papers and books have been consulted and the results of this search, started four or five years ago, can now be summarized. Some of the genera listed below are those given by the various authors and are not necessarily considered valid by other workers.

Adiantum: There are twelve known hybrids in this genus of which ten have had their chromosomes counted. Two are diploids, four are triploids, three are tetraploids and one is a pentaploid. Five of the ten were assayed for fertility and all five are sterile. Only three were studied morphologically and all are intermediate in appearance between their parents.

Aleuritopteris: Two crosses are listed in the literature but neither one was analyzed by the authors.

Anemia: Fifteen hybrids are known thus far of which only two were counted. One is diploid and one is tetraploid. Nine of the fifteen were examined for fertility and all nine are sterile. The eight studied morphologically are all intermediate in appearance.

Arachniodes: None of the seven crosses were counted. Of the four assayed for fertility, all are sterile. No other observations were made.

(1) It is a pleasure to dedicate this paper to my friend Dr. Charles DeVol.

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Aspidotis: The single known hybrid in this genus (formerly placed in the genus *Cheilanthes*) is fertile and is intermediate in appearance.

Asplenium: It is probably not surprising that in this large genus there have been about one hundred and ten hybrids recorded. Seventy-seven have been counted. Eight are diploids, thirty-five are triploids, thirty-one are tetraploids and three are pentaploids. Of the fifty assayed for fertility, forty-five are sterile. Of twenty-two examined morphologically, seventeen are intermediate and five display a resemblance to one or the other parent.

Athyrium: There are seventeen known crosses in this genus of which only one has been counted and that is a triploid. Twelve were examined for fertility and all are sterile. Five were looked at morphologically and three are intermediate whereas two displayed dominant characteristics.

Blechnum: There are five crosses in this genus. Two have been counted; one being a triploid and the other a tetraploid. Of three assayed for fertility, all are sterile. Only one was discussed for appearance and it is intermediate.

Bolbitis: The one cross here is a tetraploid. It was not otherwise analyzed.

Botrychium: In the grape ferns, there are four crosses known. One was counted and is a tetraploid. The spores of one were examined and they are apparently capable of germination. Two were looked at morphologically and both are intermediate.

Byrsopteris (*Arachniodes?*): The one cross here is sterile and was not otherwise discussed as far as cytology are concerned.

Cheilanthes: There are, apparently, eighteen crosses here of which sixteen have been counted. Fourteen are triploids and two are tetraploids. Of ten assayed for fertility, all are fertile (the apogamous condition, so prevalent in this genus, is apparently conducive to the production of viable spores). Both of those examined for morphology are intermediate.

Coniogramme: One of the two crosses known was counted and it is a tetraploid. Fertility was not considered by the authors. One of the two was examined otherwise and it is intermediate in appearance.

Cornopteris: Only one of the two crosses was counted and it is a triploid. Neither cross was further analyzed.

Cyathea (Sensu Holttum): The one cross known was not analyzed for the points we are considering here.

Cyclosorus: Six crosses have been recorded and six have been counted; three are triploids and three are tetraploids. All six are mostly sterile. Three of the six have been commented upon for morphology and all three resemble one or the other of the parents.

Cyrtomium (*Phanerophlebia*): All three crosses have been counted and all are triploids. None were otherwise commented upon by the authors consulted but it is known that there is some fertility in the crosses.

Cystopteris: Six crosses are known here. Five have been counted. One is a diploid, two are tetraploid and two are hexaploids. Three were considered for fertility and of these two are fertile and one is sterile. The morphology of the three studied showed that two are intermediate and one shows dominance.

Danaea: The one cross here is a triploid and it is sterile.

Diplazium: On the eleven crosses known, three were counted. Two are diploids and one is a tetraploid. Six were assayed for fertility and all are sterile. The two examined for morphology are intermediate.

Doodia: The one cross was not further analyzed.

Doryopteris: None of the three crosses were counted and none were considered for fertility. Two of two are intermediate in appearance.

Dryopteris (also see related *Thelypteris):* There are approximately seventy-seven different hybrids in this genus. Fifty-four were examined cytologically and of this number seven are diploids, twenty-three are triploids, eighteen are tetraploids, five are pentaploids and one is a hexaploid. Fifty were assayed for fertility with forty-five being considered sterile and five fertile. Of the twenty-four otherwise commented upon, thirteen are intermediate and eleven resemble one or the other parent.

Equisetum: The small horsetail genus has a surprising fifteen crosses within its confines but none of these were counted. Of the nine looked at for fertility, all are sterile. Two of the six examined are intermediate and four exhibit dominance.

Eriosorus: Of the four known crosses, two were counted, both being hexaploids. The spores of two were examined and both exhibited enough abortion to be considered sterile. Two were looked at morphologically and one is intermediate and one resembles one of the parents.

Grammitis: The one cross in this genus was not analyzed.

Gymnocarpium: The one hybrid is triploid, sterile and intermediate in appearance.

Hymenophyllum: There are five filmy fern hybrids listed but none has been assayed.

Hypolepis: Of the eight known crosses, only one has been counted (tetraploid). None were examined for fertility and of the five considered morphologically, three are intermediate and two display some degree of dominance.

Isoetes: One cross is known and it is considered fertile.

Lepisorus: The one cross here is a triploid but was not further examined.

Leptopteris: One hybrid is known but no further information is provided.

Lindsaya: None of the three known crosses were counted. The one assayed for fertility is sterile and the one considered morphologically is intermediate.

Lonchitis: On the one known hybrid, no information is provided.

Lunathryium: Neither of the two crosses were counted or otherwise analyzed.

Lycopodium: Only two of the thirteen crosses have been counted: one is a diploid and the other one is a pentaploid. Six were assayed for fertility and all six are at least partly fertile. The morphology of eight was determined and of these five are intermediate and three resemble one or the other parent.

Microlepia: Of the two crosses here, one was counted. It is a triploid. The fertility is not known. Only one of the two was examined for morphology and it is said to be intermediate in appearance.

Osmunda: None of the three crosses have been analyzed cytologically. One was examined for fertility and it is sterile. One was compared with the parents and found to be intermediate.

Pellaea: Three of the eight crosses were counted. One is a diploid and two are triploid. Spores of three were checked and two were found to be capable of germination and the third one is sterile. Five were assayed for morphology and all are apparently intermediate in appearance.

Phyllitis: There are eight hybrids here of which seven were counted: one is a diploid, three are triploids and three are tetraploids. These eight crosses are exclusive of those involving the genus *Asplenium.* Other pertinent data is not given on any of the eight hybrids.

Pityrogramma: None of the thirteen *different* crosses were counted. As in the genus *Asplenium* and elsewhere, there are actually more crosses in the literature than given here. Our rule is that when different names are given to the same "cross", they are all lumped together as one cross. This point will be discussed briefly later. None of the thirteen were considered for fertility and of two looked at morphologically, both are intermediate.

Plagiogyria: There are three hybrids in this genus but no pertinent information is otherwise provided.

Pleopeltis: The one cross here was counted as a pentaploid.

Pleuroderris: The one hybrid is sterile and intermediate.

Marsilea: One cross is known; it is thought to be sterile.

Polypodium: Of the seventeen crosses known, eleven were counted: five are triploids, three are tetraploids and three are pentaploids. The spores of eleven were examined and found to be aborted. Two were examined morphologically and both are intermediate.

Polystichum: Of the forty-six hybrids known, eighteen have been counted. Of these three are diploids, twelve are triploids and three are tetraploids. Of the twenty-five examined for fertility, twenty-four are sterile. Eight were assayed for their morphology and five were found to be intermediate and three displayed dominance.

Psilotum: The one known cross was not analyzed in detail by the person reporting it.

Pteris: Thirteen of the twenty-two hybrids were counted: two are diploids, nine are triploids and two are tetraploids. Nine of the twelve examined for fertility are sterile and three are fertile. Two were examined morphologically and both are intermediate.

Schizaea: There is one cross in this genus. It was not analyzed for fertility or morphology.

Selaginella: Neither of the two crosses noted were counted but both are listed as sterile. One of the two is intermediate and one shows dominance.

Tectaria: No pertinent data was given on the one cross in this group.

Thelypteris: Five of the nine crosses were counted with four being triploids and one being a tetraploid. Eight were assayed for fertility and all are sterile. Five were examined morphologically and all are intermediate.

Woodsia: Only two of the nine crosses were counted and both were triploids. Three of the five examined for fertility are sterile and four of the six looked at morphologically are intermediate.

Woodwardia: One of the two crosses was counted and it is a triploid. It is also sterile and intermediate. The characteristics of the other hybrid are unknown.

The number of genera listed above totals fifty-five. Actually other genera are involved in intergeneric crosses such as *Camptosorus, Ceterach, Pleurosorus, Notholaena, Dictyogramme, Jamesonia* and *Quercifilix* making a total of sixty-two. If we accept the number 270* as the total number of fern genera, then the sixty-two genera involved in hybridization represents less than one quarter of the possible genera. It is almost inconcenivable that more genera are not involved. A somewhat better

* Number of genera less the indicated synonyms per list supplied by Dr. W. H. Wagner, Jr. of the University of Michigan. It is well-known that there is still considerable disagreement on the delimiting of certain families and the proper disposition of some genera.

picture emerges when we note that sixty-three percent of the thirty-one families of ferns (Wagner, above) are involved in hybridization.

According to our compilation above, there are five-hundred and fifty-two pteridophyte hybrids recorded in the literature. Because of their varying genotypes, it is not known just how many crosses are possible but certainly there would be more than the number indicated above, especially when one considers that there are over ten thousand taxa in the group as a whole. Our number of hybrids should, therefore, be considered as a conservative figure.

The more interesting aspects of our study are concerned with the cytology, fertility and morphology of the recorded hybrids. In regard to the former category, 46% or 253 have had their chromosomes counted with the following results: twenty-nine are diploids, one hundred and twenty-nine are triploids, seventy-six are tetraploids, fourteen are pentaploids and five are hexaploids. The diploids are crosses between two diploid taxa, the triploids can be combinations from a diploid with a tetraploid or rarely from two diploids, one of which possesses an unreduced spore, gametophyte and egg, the tetraploids could arise from two tetraploid parents or from two diploid parents followed by doubling, the pentaploids might have arisen from a cross between a tetraploid and a hexaploid and the hexaploids from crosses between two hexaploids or from a cross of two fertile triploids followed by doubling. From the figures quoted above, it is obvious that the majority of fern hybrids are not diploid in nature. In fact, almost ninety per cent are polyploid.

Forty-seven percent of the total number of crosses or two hundred and fifty-five were assayed for the appearance of their spores and two hundred and thirteen or eighty-four percent are sterile. The concept that hybrids are sterile is a common one and the above figure more or less bears this out but the sixteen percent fertile hybrids should, I hope, prevent us from ever again making the generalization that *all* hybrids are sterile. Morzenti (1967) studied this matter in *Asplenium plenum* and was able to prove that certain spores of an otherwise sterile hybrid were able to produce gametophytes. On the basis of her study, it may be that some of our sterile hybrids do occasionally produce viable spores. The nature and causes of sterility are beyond the scope of this paper. One theory is that some spores, because of independent assortment within the spore mother cells in the sporangium may be deficient for part of the necessary genetic material and therefore inviable.

The concept of dominance was postulated by Mendel over a hundred years ago. Subsequent to his discovery, it was found by others that certain hybrids were intermediate in morphology. One hundred and thirty-seven of the total fern hybrids in our study were commented upon by the authors morphologically and of this number ninety-nine are intermediate and thirty-eight resemble one or the other of the parents. The multiple allele hypothesis can explain both dominance and intermediacy in that the state achieved depends upon the number and kinds of genes involved and the types of enzymes produced by the DNA and RNA of the genes. Also to be considered is the phenomenon of linkage. Linked genes (on the same cnromosome) tend to assort together and we obtain a preponderance of parental types and a low incidence of recombinants. Linked and unlinked genes in the various taxa involved in crosses, together with the effect of multiple alleles, could account for the varying morphology observed.

The frequency with which specific hybrids were formed has not been studied by us. It is thought that actual hybrid swarms occur in many groups such as in the *Pteris* group; and *Dryopteris*×*boottii* is not uncommon within the range of its

parents. On the other hand, ×*Asplenophyllitis confluens* was rare and is now extinct.

The proper naming of hybrids has been a controversial subject. It is however covered somewhat in the International Code of Botanical Nomenclature. Many of the fern hybrids are listed as a formula with the two parents connected by an ×sign. Others are given a name followed by the formula. Both of these methods are permitted under the code. Successive crosses of the same two taxa are however given different names by some of our authors. For example the hybrid *Pityrogramma*×*albicans* Domin (=*P. chrysophylla* (Sw.) Link×*P. calomelanos* (L.) Link) involves the same two taxa as *P.*×*hybrida* Domin, *P.*×*consimilis* Domin, *P.*×*intermedia* Domin, *P.*×*lutea-alba* Domin and *P.*×*mira* Domin. No study was made by us of this group but presumably the different named hybyids varied morphologically. A similar situation exists in the genus *Aneimia*. The Code, cited above, suggests differing forms of the same cross be designated as nothomorphs.

One final aspect of our admittedly incomplete study is concerned with the subject of intergeneric crosses. There are slightly more than twenty such hydrids in the fern literature; *Asplenium* crosses with *Camptosorus, Ceterach, Pleurosorus* and *Phyllitis, Athyrium* crosses with *Cornopteris, Cheilanthes* with *Notholaena, Coniogramme* with *Dictyogramme, Eriosorus* with *Jamesonia, Phyllitis* with *Ceterach, Dictyoxiphium* with *Tectaria* and *Tectaria* with *Quercifilix*. There are those who would argue that, in the above cases, a merging of genera is indicated in appropriate taxa and that there are no such crosses possible. If one glances at the list of intergeneric hybrids listed in Knobloch (1972) one, I feel, must come to the conclusion that there is enough genetic harmony between taxa of related genera to allow for such hybridizations.

LITERATURE CITED

Knobloch, I. W., 1956. Estimate of the number of hybrids in the plant animal kingdoms *in* Handbook of Biological Data, Wm. Spector, ed.

_____, 1959. A preliminary estimate of the importance of hybridization in speciation. Bull. Torr. Bot. Cl., **86**(5): 296-299.

_____, 1962. Hybrid fertility: animals, plants, *in* Growth, P. L. Altman and D. S. Dittmer, eds.

_____, 1963. The extent of hybridization in the *Gramineae*. Darwiniana, **12**: 624-628.

_____, 1968. A check list of crosses in the Gramineae. 176 pp., Stechert-Hafner Service Agency, New York.

_____, 1972. Intergeneric hybridization in flowering plants. Taxon, **21**: 97-103.

Morzenti, V. M., 1967. *Asplenium plenum:* a fern which suggests an unusual method of species formation. Amer. J. Bot., **54**: 1061-1068.