THE MORPHOLOGY AND CYTOLOGY OF
POLYSTICHUM × POTTERI HYBR. NOV.
(= *P. ACROSTICHOIDES × P. BRAUNII*)

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ABSTRACT

The hybrid between *Polystichum acrostichoides* and *P. braunii* is common but overlooked in Vermont. Based on a qualitative analysis, the hybrid is structurally intermediate for most traits, but character states are not predominantly medial or nearer to those of tetraploid *P. braunii*. Indusia of the hybrid are much larger than those of either progenitor, suggesting a summation of development programs for indusial development. Stomates of the triploid hybrids are intermediate and nearer to those of *P. braunii* in size, but those of diploid *P. acrostichoides* are unexpectedly larger than those of tetraploid *P. braunii*. Chromosome counts confirm that the hybrid is commonly triploid, and that non-homologous pairing is high, as reported for other *Polystichum* hybrids (mean number of bivalents is 21.7). The hybrid is described and named as *P. × potteri*.

Key Words: *Polystichum*, hybrid, fern morphology, Vermont

INTRODUCTION

During the past few years botanists have frequently encountered the hybrid between *Polystichum acrostichoides* and *P. braunii* at Vermont stations where both parents are common. Review of herbarium materials has yielded a set of these hybrids from the northern Appalachians, all determined as *P. braunii*. This hybrid now appears to be common, at least in the Green Mountains, but overlooked because it shares several features, notably a similar lamina dissection, with its tetraploid progenitor, Braun's Holly Fern (*P. braunii*). In this paper, I provide basic structural, cytological, ecological, and geographical documentation for the hybrid. Since I argue that commonly occurring entities in nature need names, I am

also providing an epithet, type designation, and Latin description.

The first and only previous report of the native hybrid between *Polystichum acrostichoides* and *P. braunii* was by Thompson & Coffin (1940). It was based on a single small sporophyte that they encountered in Smuggler's Notch, Vermont during the summer of 1937. Thompson and Coffin used 18 characters to evaluate the hybrid. They reported that the hybrid shared seven character states with *P. acrostichoides* and three with *P. braunii*. Of the seven character states reported as intermediate, three were nearer to *P. acrostichoides*, three were medial, and one was nearer to *P. braunii*. One character state was not intermediate (leaf length was shorter than that of either progenitor). This relatively early report provided no information on cytology or variation in spores or sporangia.

Morzenti (1962), in developing her ideas on pseudomeiotic sporogenesis, described the cytology of a *Polystichum acrostichoides* × *P. braunii* hybrid from the garden of Harold Rugg (at Hanover, New Hampshire), thought to be a derivative of the plant discovered by Thompson and Coffin. At meiosis the Rugg plant had 41 bivalents and 82 univalents (two of four sets of chromosomes pairing). Assuming that the *P. acrostichoides* parent was diploid ($x = 41$) and the *P. braunii* parent was tetraploid ($x = 82$) (Löve et al., 1977), the origin of the Rugg plant must have been via an anomalous cytological pathway. Morzenti suggested that the Rugg plant was tetraploid (rather than triploid as expected) because *P. acrostichoides* had contributed an extra set of chromosomes, either from a tetraploid sporophyte or, according to Morzenti (1962), from "duplication of the normal diploid genome of that species in the hybrid" (for instance, via an unreduced gamete). The tetraploid plant from Rugg's garden had some sporangia that yielded 16 giant, viable spores. These giant spores yielded gametophytes with spermatozoa and archegonia, but no sporophytes.

SYSTEMATIC TREATMENT

Polystichum × potteri Barrington, *hybr. nov.* = *Polystichum acrostichoides* (L.) Roth × *P. braunii* (Spenner) Fée.

DIAGNOSIS: Hybrida sterilis e Polysticho acrostichoide atque P. braunii prodiens, ab illo differt foliis pinnatisectis vix supra medium

latissimis apicem versus non contractis, carenti foliis laxis sine sporangiis; ab hoc petiolis et pinnis basalibus longioribus. Indusia hybridae indusiis parentium grandiora.

HOLOTYPE: Vermont, Orange Co., Strafford, Beacon Hill; low ledges in shady maple woods above Chadsey residence, *Barrington 939:* VT.

PARATYPES: The Appendix provides citations of the numerous paratypes.

Stem prostrate, short-creeping, branching at irregular intervals, bearing a single whorl of rigidly ascendent leaves. Leaves long-petiolate, chartaceous to coriaceous; lamina long-lanceolate, narrowed to a truncate base, apically attenuate, but not abruptly narrowed into the fertile apical portion (Figure 1); lamina dissection twice-pinnate, but the distal half of most pinnae merely pinnatifid to pinnatisect (Figure 2); basal acroscopic pinnules of most pinnae crenate to pinnatifid, one-third to twice again as long as the nearest more distal pinnules; pinnules crenate and long-spinulose, ascendent along the pinna-rachis (costa axis attached at 50–60 degrees from the pinna-rachis). The distal half or two-thirds of each lamina with approximate sori, (lax trophophylls not seen). Indusia irregularly crenate-margined, ca. 1.0 mm in diameter. Sporangia commonly but not always indehiscent; tapetal remnants clinging to sporangium interior. Spores irregular, pale.

Indument of petioles and rhizome apex a dense cover of broad-lanceolate, amber to stramineous scales with a few short marginal setae and scurf like that of the rachis. Rachis scurf abaxially lanceolate to long-lanceolate, amber to stramineous, weakly to heavily short-setate, more or less descendent along the rachis; adaxially filiform and stramineous. Leaf-surface indument abaxially well developed, of long (ca. 0.7 mm) very narrow-lanceolate scurf.

ETYMOLOGY: *Polystichum* × *potteri* is named for the late Henry Potter of West Rutland, Vermont, lifelong student of the Vermont fern flora and one of the state's finest naturalists, who was still active last field season at 94.

I have found it useful to develop a set of categories for the qualitative character states encountered in the hybrids. Relative to those of its progenitors, hybrid character states are necessarily of three sorts:
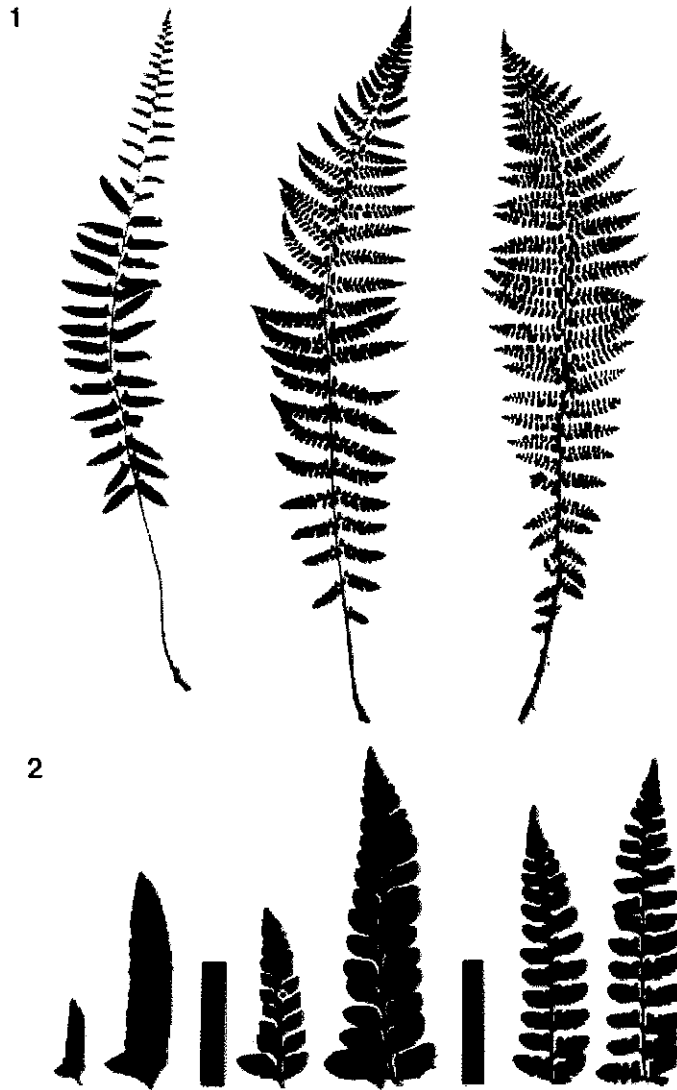
Figures 1 and 2:   Figure 1.   Leaf silhouettes of *Polystichum* species: from left to right, *P. acrostichoides* (*Barrington #1123*, original leaf length 63 cm). *P.* × *potteri* (*Barrington #939*, original leaf length 77 cm), and *P. braunii* (*Barrington #1138*, original leaf length 66 cm).

Figure 2.   Pinna silhouettes of *Polystichum* species (left pinna of each pair from three-quarters up lamina, right pinna from center): from left to right, *P. acrostichoides* (*Barrington #1123*), *P.* × *potteri* (*Barrington #939*), and *P. braunii* (*Barrington #1138*). Bars = 2cm.

shared with one of the progenitors, intermediate, or anomalous (that is, neither shared nor intermediate). Intermediate character states are more or less variable between the two progenitors. The less variable intermediate states are either medial (clustered at the mean between the progenitors) or nearer one or the other of the two progenitors.

Twenty-two qualitative characters were scored for the two species and their hybrid (Table 1). Comparison of the hybrid with its progenitors revealed that the hybrid shared five character states with *Polystichum braunii,* but only two with *P. acrostichoides.* Thirteen character states were intermediate between the two progenitors: three of these were nearer *P. acrostichoides,* eight were medial, two were nearer *P. braunii,* and one was variable. A single character state, indusium diameter, was anomalous -—it was larger than that of either progenitor. In sum, the characters assessed were variable in their expression relative to the two progenitors.

An Anderson hybrid index (Anderson 1936, 1949) was computed for *Polystichum* X *potteri,* using the qualitative character states (Table 1). Contrary to Anderson's usual approach, the index was computed for the composite characters diagnostic of the group of hybrids as a whole and not for the individual character states of each hybrid. Based on the hybrid index, the hybrid is intermediate and slightly closer to *P. braunii* than to *P. acrostichoides* (57th percentile, given *P. braunii* is the 100th percentile).

An Anderson hybrid-index score was computed for the sporophyte from Rugg's garden that was presumably the source of Morzenti's tetraploid count. (Only characters available from the herbarium sheets were possible to score.) The MICH collection was at the 42nd percentile, and the GH collection was at the 41st percentile; that is, both were slightly closer to *P. acrostichoides* than were the triploid plants of the hybrid. The Thompson & Coffin specimen at GH was scored at the 61st percentile, that is similar to the composite index for the hybrids.

Guard-cell measurements, which were done to corroborate ploidy-level information derived from cytology, yielded unexpected results. Guard-cell pair length and width of the diploid species were a bit larger than those of the tetraploid species, rather than a bit smaller (Table 2). Guard-cell measurements of the triploid hybrids

Table 1. Structural features of *Polystichum* × *potteri* and its progenitors compared (Anderson Hybrid Index scores in parentheses: 0 = shared with *acrostichoides*; 1 = intermediate and nearer *acrostichoides*; 2 = medial; 3 = intermediate and nearer *braunii*; 4 = shared with *braunii*.)

Character	*acrostichoides* (a) (all 0)	hybrid	*braunii* (b) (all 4)
Petiole length	long	intermediate, nearer a (1)	short
Lax trophophylls	present	shared with b (4)	absent
Attitude of fertile leaves	stiffly ascendent	shared with a (0)	laxly ascendent
Lamina texture	coriaceous	medial (2)	herbaceous to chartaceous
Evergreenness	evergreen	intermediate, nearer a (1)	deciduous to unevenly evergreen
Lamina base width	nearly = medial width	medial (2)	one third the medial width
Point of maximum lamina width	near lamina base	medial (2)	above the middle of the lamina
Lamina dissection medial	1-pinnate to 1-pinnate, pinnatifid	intermediate, nearer b (3)	1-pinnate, pinnatisect
Angle of costae	45°	medial (2)	80°
Stomate length	long	intermediate, nearer b (3)	short
Rachis-scale setae	present	intermediate, nearer a (1)	rare
Rachis-scale texture	dull	intermediate, various (2)	lustrous
Adaxial rachis scales	narrow-lanceolate to lanceolate	shared with b (4)	filiform

Table I. Continued

Character	acrostichoides (a) (all 0)	hybrid	braunii (b) (all 4)
Abaxial lamina scurf size	small	medial (2)	large
Abaxial lamina scurf shape	filiform	intermediate, nearer a (1)	narrow-lanceolate
Lamina scurf frequency	rare	medial (2)	abundant
Fertile lamina portion	contracted	shared with b (4)	not contracted
Receptacle shape	round to elongate	shared with b (4)	round
Sorus proximity	confluent	medial (2)	remote
Receptacle sclerenchyma	abundant	shared with b (4)	weak
True indusium diameter	small	not intermediate (not indexed)	small
True indusium shape	entire	medial (2)	crenate
Anderson Hybrid Index Totals	0	48	84

Table 2.   Guard-cell pair measurements in μm for *Polystichum* $\times$ *potteri* and its progenitors (n = 30 guard cell pairs measured for each sporophyte)

	PARENTS AND PUTATIVE TRIPLOIDS		
Locality	*acrostichoides*	hybrid (putative triploids)	*braunii*
Wheelock			
DSB #	1172	946	1175
mean length (s. d.)	54.1 (3.48)	51.3 (3.45)	49.0 (2.67)
mean width (s. d.)	40.6 (1.93)	34.0 (2.36)	31.8 (2.81)
Strafford			
DSB #	1185	939 (holotype)	1183
mean length (s. d.)	52.6 (3.20)	51.1 (3.20)	47.7 (3.79)
mean width (s. d.)	37.9 (2.57)	32.3 (2.13)	31.2 (1.98)
Barnard			
DSB #	1144	1097	1119
mean length (s. d.)	54.4 (4.09)	48.0 (2.82)	46.7 (3.10)
mean width (s. d.)	37.1 (2.54)	31.0 (2.16)	31.0 (1.85)
Mean for all sites			
mean length (s. d.)	53.6 (0.97)	50.0 (1.83)	47.8 (1.14)
mean width (s. d.)	38.6 (1.88)	32.5 (1.52)	31.2 (0.38)

	PUTATIVE TETRAPLOID		
Rugg s. n. (GH)		Rugg s. n. (MICH)	
mean length (s. d.)	59.8 (5.36)	mean length (s. d.)	64.0 (4.43)
mean width (s. d.)	12.5 (0.78)	mean width (s. d.)	42.0 (2.26)

were nevertheless intermediate and nearer to those of *Polystichum braunii*. Guard-cell dimensions of the Rugg collections at GH and MICH (both presumed to be vouchers for Morzenti's tetraploid hybrid) were larger than those of any other plants in the sample (Table 2).

One unusual structural variant was seen among the hybrids collected in Vermont. The basal pinnae in most leaves of *Barrington 1155* (VT) are the same length as the widest pinnae in the blade, but the next few pinnae acropetally are irregular in length: some are short like those at the base of *Polystichum braunii* leaves; others are long like those of *P. acrostichoides*.

GEOGRAPHY & ECOLOGY

Polystichum × *potteri* is known from Quebec, Nova Scotia, New Brunswick, New Hampshire, Vermont, New York, and Pennsylvania. In Vermont the hybrid is found in cool, wet forests from 1000 to 3000 feet. The hybrids are often found in ice-carved notches and on wet, steep, rocky slopes—both habitats characterized by unstable, thin-soiled substrates. Both parents are present at all of the Vermont stations known to the author.

Polystichum braunii has a circumboreal distribution (Hultén, 1962). Compared with other circumboreal ferns, it is relatively northern in distribution. For instance, in Europe it is confined to the maritime parts of Scandinavia and montane regions, and in western North America it is entirely coastal and northern. In Vermont *P. braunii* is limited to wet, disturbed substrates in forests at altitudes above 1000 feet. In contrast, *P. acrostichoides* is endemic to North America. It is a common species of woodlands in eastern North America where it is best developed on wooded, thin-soiled slopes, which are frequently disturbed. The hybrid between the two was encountered in Vermont at fairly high altitudes where *P. braunii* (near its lower limits) and *P. acrostichoides* (near its upper limits) occupy the same habitat.

Eight of the 14 Vermont sites yielded only a single hybrid sporophyte despite careful searching, whereas two sites had two sporophytes each, one had five, one had ten, and one had twenty-four. Some of the sporophytes at these sites are clustered and appear to be part of a single clone, suggesting that vegetative reproduction increases numbers of plants in populations. However, the large populations are for the most part well spread out over the terrain, from which I infer that they are separate genets, not ramets derived from branching of stems.

CYTOLOGY & SPORE VARIATION

Seventeen sporophytes yielded cytological preparations with univalents. The three sporophytes yielding counts were triploids with univalents and various numbers of bivalents ranging from 19 to 26 (Table 3; Figure 3–6). During early anaphase the bivalents are slow to separate, resulting in the characteristic early anaphase figures

Table 3. Chromosome number and pairing behavior in *Polystichum × potteri*

Barrington Collection Number & Sporocyte Letter	Univalents	Bivalents	Trivalents
939A	71	26	0
939B	81	21	0
942A	74	23	1
942B	77	23	0
942C	87	18	0
942D	79	22	0
1094A	85	19	0
Mean	79.1	21.7	0.14
(s. d.)	(5.73)	(2.69)	(0.37)

also illustrated in European work on *Polystichum* hybrids (Manton and Reichstein, 1961; Sleep and Reichstein, 1967). Chromosome segregation is irregular in meiosis, so that micronuclei are common in the resultant spores.

The spores resulting from meiosis are for the most part wrinkled and irregular in shape. Giant spores resulting from inclusion of all the meiotic nuclei in a single cell, like those observed by Morzenti (1962), were common in some of these triploid hybrids (*Barrington 909* VT). Indehiscent, pale, collapsed sporangia are useful in field identification of the hybrids, but indusia only rarely fail to evert as in *Dryopteris* hybrids (Wagner and Chen, 1965). Some of the sporangia of the hybrids open as the summer progresses; the proportion of sporangia which open varies with the sporophyte. Pale bits of tapetal material which cling to the interior of the opened sporangia of the hybrid, but which are absent from those of the parents, are diagnostic. These tapetal remnants were seen in all herbarium specimens of hybrids at VT.

DISCUSSION

Polystichum × potteri has been largely overlooked because it superficially looks so much like its tetraploid progenitor, *P. braunii*. Lamina dissection is probably the single most important character used in determining northeastern North American specimens of *Polystichum* and, in this character, the hybrid is intermediate and nearer *P. braunii*.

Intermediacy of sterile hybrids, assumed to be F_1s only, often

serves as the basis for hypothesizing hybrid ancestry of plant line-
ages (Wagner, 1983), but scoring of hybrids is often based on intui-
tion rather than on character analysis. Hybrids between tetraploids
and diploids are commonly expected to approach the tetraploid in
structure because the tetraploid is genetically represented twice, but
the diploid only once. However, all of the various possible character
states are represented among the characters surveyed in the present
hybrid. Although medial states are most common, they only
account for about one-third of the characters, and only two charac-
ters are intermediate and nearer *Polystichum braunii*. Since structu-
ral features are elaborated by various genetic systems, most of them
polygenic, a complex array of character states is to be expected in
hybrids. A quantitative analysis of the character states of progeni-
tors and hybrids would serve as the basis for a better understanding
of hybrid character states in *P.* × *potteri*.

The Anderson-hybrid-index scores for the Rugg specimens (GH,
MICH) were closer to *Polystichum acrostichoides* than was the
composite hybrid-index score. Though these data are qualitative,
(and the tie of the tetraploid count to these Rugg specimens is
circumstantial) they suggest that an extra set of chromosomes from
P. acrostichoides resulted in leaf characteristics more like those of
the diploid species. The hybrid-index score for the Thompson &
Coffin specimen suggests that it was a triploid, and consequently
probably not from the same plant as the Rugg collections (contrary
to Morzenti, 1962).

The original qualitative scoring of the hybrid (Thompson and
Coffin, 1940) differs from the present one in showing more charac-
ters shared with the progenitors and fewer medial character states.
Their emphasis was on contrasting the contribution of the progeni-
tors and not on the expression of each of the characters they used.

The unusually large indusium size of the hybrid is particularly
interesting because it is a novel character state not found in the
progenitors. In this case the larger size of the hybrid indusia suggests
that the parental genomes have been summed to program for a
longer developmental period, generating a larger indusial flange
(that is, the round top, not the stalk). The precise developmental
sequences in both parents could be compared to investigate this
idea. Indusium size is important in characterizing species of *Polysti-
chum* in Mexico (Smith, 1981), so that transformations in this par-
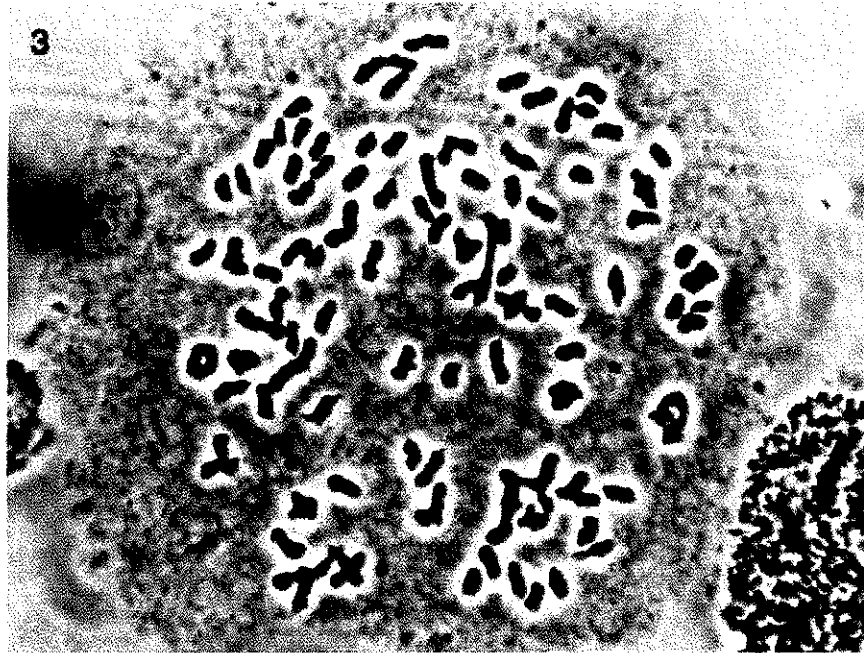
Figures 3 and 4: Figure 3. Late prophase of meiosis I (79I and 22II), *Barrington #942*, 1050X. Figure 4. Camera lucida drawing of sporocyte in figure 3.

5

6
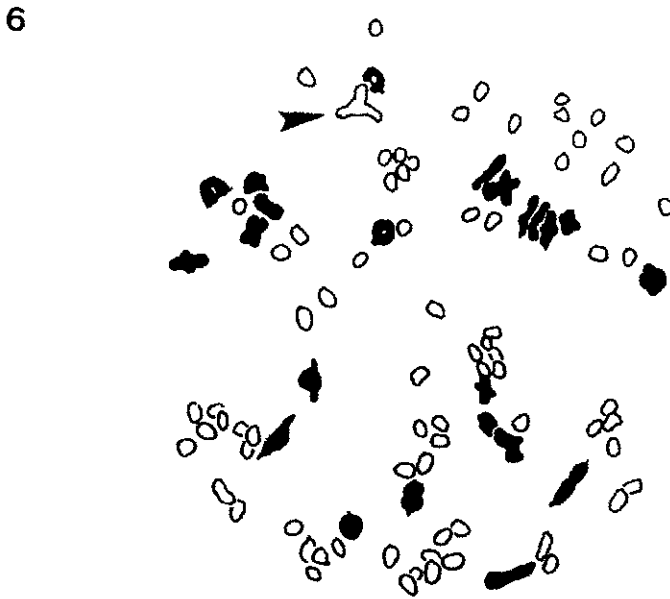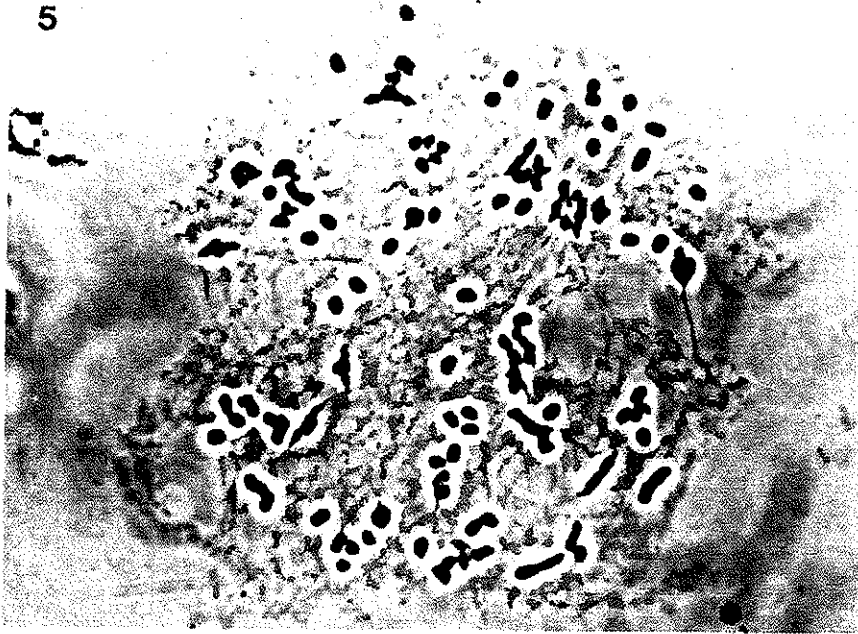
Figures 5 and 6:   Figure 5.   Metaphase of meiosis I (74I, 23II, 1III indicated with arrow), *Barrington #942*, 800X.   Figure 6.   Camera lucida drawing of sporocyte in figure 5.

ticular character are possibly important in considering the evolution of the genus as a whole.

The irregular pinnae of *Barrington 1155* can be interpreted as a result of mixed developmental programs from the two parents: broad basal pinnae determined by the *Polystichum acrostichoides* program, followed by pinnae of various lengths resulting from compromises betwen the two parental programs. In contrast, normal hybrids evidence an orderly progression of compromises between the two parental programs, resulting in leaves with regular pinna development intermediate between that of the two parents. Random prevalence of one parental developmental program over another has been invoked to explain a class of irregular features found in hybrids (Barrington, 1985).

The most intriguing character is the stomate size of the three entities. The reasonably good inverse correlation of stomate length with ploidy level known for the species and the triploid hybrid is counter to that demonstrated in classical studies (e.g., Wagner, 1954). Perhaps the diploid progenitor or progenitors of *Polystichum braunii* are both characterized by stomates that are much smaller than those of the native eastern North American *P. acrostichoides*. The large stomate size of the Rugg collections, presumably vouchers for the tetraploid, suggest that the presence of an extra *acrostichoides* genome has an unusual effect on the determination of stomate size.

The contrast between the present triploid chromosome counts and the tetraploid count first reported for this hybrid is remarkable. The hybrid apparently arises most often as a result of fusion of normal gametes of the two parents. A fertile hexaploid race of *Polystichum × potteri* may possibly be found, as was a fertile tetraploid population for *Asplenium ebenoides* (Wagner, 1954). Such a plant, backcrossing to *P. acrostichoides*, could have generated the tetraploid documented by Morzenti. No fertile hexaploid hybrids have yet been encountered; all of the large sample of sporophytes recently collected in Vermont are presumed to be sterile triploids, since they all show pale tapetal remnants inside the sporangia. Thus, Morzenti's original hypothesis for the origin of the tetraploid is the simplest, given our present understanding of the hybrid.

Many *Polystichum* hybrids form more bivalents than would be expected as a result of pairing of homologous chromosomes (by

definition the result of homoeologous pairing), ranging from an average of 11 (range 6–24) in European *P. braunii* × *lonchitis* (Lovis, 1977) to 26 (range 19–33) in Californian *P. dudleyi* × *munitum* (Wagner, 1973). In *Cystopteris*, Vida (1974) has reported a similar high number of bivalents in the apomictically generated diploid cytological race of *C. fragilis*. Lovis inferred from these data that *Polystichum* and *Cystopteris* polyploids are segmental allopolyploids, that is they share "valuable complex linkages" common to both ancestors, but are otherwise chromosomally divergent. The present hybrid adds to the list of hybrids with unusual levels of pairing. This high level of pairing is of potential interest, since the other polystichums hybridizing with *P. braunii* are much less divergent morphologically. Lovis (1977) reported that Sleep saw similar high levels (overall range nine to 25) of bivalents in synthesized hybrids of *P. acrostichoides* with *P. lonchitis, P. munitum,* and *P. setiferum.*

The origin of *Polystichum braunii* remains an interesting and unsolved problem. None of the five hybrids involving *P. braunii* in Europe and North America shows a full set of bivalents, so that no diploid from these regions is implicated as a progenitor. Though no conclusive information is available from eastern Asia, the close structural similarity to *P. makinoi,* a diploid, suggests that the ancestry of *P. braunii* is Asian.

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APPENDIX

Exsiccatae for *Polystichum* × *potteri* Barr.

(Specimens determined by D. H. Wagner, Univ. of Oregon, which I have not seen are indicated as det. DW. All others—those at GH, NHN, VT, and YU—are paratypes except for the holotype, *Barrington 939.*)

CANADA: (all det. DW) **Nova Scotia.** Inverness Co.: near Harvard Lakes, *A. Prince & C. Atwood 1442* (DAO). Co. indet.: Folleigh, *M. Malte s. n.* (CAN 216749). **New Brunswick.** York Co.: Keswick, *J. Brittam 26,* (GH). **Quebec.** Brome Co.: Water-

loo, *Br. Marie-Anselm s. n.* (DAO). Montmorency Co.: Montmorency Falls, *Macoun 69235 p. p.* (CAN).

UNITED STATES: **New Hampshire.** Coos Co.: White Mountains, quite high, *E. Tuckerman s. n.* in 1843 (GH). **Vermont.** Caledonia Co.: Sutton, W slope of Mt. Hor, *Barrington 777, Zika 3386, 3390* (VT); Wheelock, E face of Mt. Ide, near summit, *Barrington 944, 945, 946, 947, 948, 949, 950, 1084, 1085, 1167* (VT). Chittenden Co.: Underhill, Nebraska Notch, *Barrington 904, 912, 928* (VT); Underhill, base of the chin of Mansfield, *Pursh s. n.* in 1838 (GH). Essex Co.: Brighton, W side of Rt. 114 near Morgan town line, *Barrington 834, Zika 4130* (VT). Lamoille Co.: Eden, Access Road to Belvidere Serpentine Mine, *Hickey 906* (personal herbarium R. James Hickey); E side of Rt. 100 near Lowell town line, *Barrington 909, 959* (VT); Stowe, *F. Bumstead s. n.* (YU); Cambridge, Smuggler's Notch, *Barrington 918* (VT), garden specimen from Smuggler's Notch, *R. H. Thompson & R. L. Coffin s. n.* in 1940 (GH), *J. Churchill s. n.* (MO 1055822, det. DW). Orange Co.: Braintree, *J. Bates 496* (YU); Brookfield, E side of Brookfield Gulf, 1200 feet, *Barrington 1081, 1082, Zika 7196, 7199* (VT); Strafford, Beacon Hill, *Barrington 939* (holotype), *940, 941, 942, 943* (VT). Orleans Co.: Westmore, E side of Mt. Hor, 1500 feet, *Zika 7348* (VT); Town indet., Willoughby Mt., *J. Churchill s. n.* (MO 1055821, det. DW). Rutland Co.: Sherburne, Shaw Hill Brook ravine, 1550 feet, *Barrington 750* (VT); W slope of Wolf Hill, *Barrington 749a* (VT). Windsor Co.: Barnard, Barnard Gulf, *Barrington 1091, 1092, 1093, 1094, 1096, 1097, 1098, 1099, 1100, 1103, 1105, 1106, 1116, 1125, 1131, 1134, 1135, 1140, 1143, 1148, 1151, 1153, 1155, 1157* (VT); same locality, *E. Kittredge s. n.* (MO 993604, det. DW); Cavendish, W side of Proctorsville Gulf, *Barrington 898* (VT); Sharon, Honey Brook Ravine, *Barrington 990* (VT); Woodstock, *Miss Strong s. n.* (HNH). **New York.** (all det. DW) Delaware Co.: Arkville, *P. Wilson s. n.* (NY). Co. indet.: Ox Clove, Catskill Mts., *C. Lown s. n.* (NY). **Pennsylvania.** Sullivan Co.: Ganoga Glen, *H. Pretz 3922, 3923a,* (MICH, det. DW). Wayne Co.: Scott Twp., NE side of Schrawder Mt., 1 mi N of Island Lake, *W. Dix s. n.* (US, det. DW); NE slope of Shrawder Mt., *E. Wherry s. n.* (GH; US, det. DW). Starrucca, Lake Shehawken, *W. Dix s. n.* (GH); Sterling, *R. C. Harlow s. n.* in July, 1939 (GH), in July 1941 (GH), Gas Hollow, 2 mi. from Jericho (GH).