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Distribution, Abundance, Status, and Phytogeography of Log Ferns (Dryopteris: Woodsiaceae) in Arkansas

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DISTRIBUTION, ABUNDANCE, STATUS AND PHYTOGEOGRAPHY OF LOG FERNS (*DRYOPTERIS:* WOODSIACEAE) IN ARKANSAS

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ABSTRACT

A study of the distribution, abundance, status, and phytogeography of the six taxa of Log Ferns (*Dryopteris:* Woodsiaceae) that are known to occur in Arkansas was conducted from 1981-1986. Five of these ferns are generally quite rare in Arkansas. Except for *D. marginalis*, all exist in Arkansas as small, peripheral populations that are marginal, outlier populations to the west and south or west and north of their metropolis. Two sterile, triploid hybrid taxa (*D.* X *australis* and *D.* X *leedsii* each occur at only one locality, and there with but one of their parent taxa. The population of the putatively sterile hybrid *D.* X *australis* has a large number of juvenile plants that were not asexually produced by rhizome expansion. The microhabitat of *D.* X *australis* is suggested to favor gametophyte establishment. It is speculated that some level of pseudomeiotic spore production and/or apogamy may be involved in the production of numerous juvenile sporophytes.

INTRODUCTION

The ferns in the homosporous fern genus *Dryopteris,* commonly known as Wood Ferns, Shield Ferns, and Log Ferns, are conspicuous in eastern North America, are well collected, and well studied ferns that occur at outcrops, forests, and swamps (Carlson and Wagner, 1982; Montgomery, 1982; Montgomery and Paulson, 1981; Small, 1938). The plants are medium to large in size. Fronds are wintergreen, 2-3 times pinnate, 0.5-2 m in length, with one to eight fronds per plant. Generally no more than one-half of the fronds of a plant are sporiferous. The frond petiole contains 3-6 vascular traces. The indusium is reniform; spores are bilateral, saccate, and 30-60 micrometers in longest axis. Of the 36 taxa in the genus, two-thirds are hybrids. Although the basic species are distinct, hybrids plants are generally indistinct, intermediate, and thoroughly baffling to the non-specialist taxonomist (Dowell, 1908; Tryon and Britton, 1966); therefore, they are collected out of proportion to their occurrence and abundance (Wagner, 1971). Although the occurrence of the hybrids initially rendered the taxonomy of the genus to a level near chaos, it offerred unusually rewarding opportunities for biosystematic study in the 1950s-1970s, when relative nomenclatureal stability was reached (Lellinger, 1984).

The 15 sexual taxa in North America include nine diploids and six polyploid taxa (Carlson and Wagner, 1982). The taxa display a diverse array of distributional patterns, primarily temperate, boreal, and arctic affinities. Vicarious affinities suggest that the major source of North American diversity was perhaps eastern Asia, with high latitude migration during the Tertiary or during interglacial periods during the Pleistocene. Pleistocene glaciation may have played a major role in the origins of the polyploid taxa by creating conditions that brought sexual taxa together, and thusly, facilitating hybridization. Whenever in close proximity, hybridization frequently results in the production of plants of hybrid origin (Carlson, 1979; Tryon, 1986). The hybrids are readily distinguished in the field by 1) comparison of frond morphology which is typically intermediate, 2) by their general rarity of plants to the more abundant "typical" form of plants at that locality, and in the laboratory, 3) by recognition of abortive spores that vary in size and shape of the hybrids compared to the uniform size and shape of spores of the "typical" plants.

The 13 northern sexual taxa are known to form 29 different hybrids out of a possible 78. These hybrids plants often are quite persistent and may in fact out number the plants of their parental sexual taxa in some locations (Carlson, 1979). Consequently, the ecologic staying power of the hybrids may in fact exceed that of the parent sexual taxa, resulting in populations of hybrid plants where one or both parent taxa are no longer present, a condition referred to as "hybridization by remote control" by Wagner (1943). The relative abundance of hybrids, their intermediate morphology, the extent of inter-connectedness of the hybrids (shairing genomes of 1-4 sexual taxa) have resulted in an extensive literature reporting on the floristics and taxonomic status of *Dryopteris* in the state, regional, and national literatures.

Studies that have aided appreciably in our understanding of the genus include comparative foliar morphology (Wagner, 1971), gametophyte ecology (Cousens, 1975; Cousens and Horner, 1970), spore morphology (Barringtin *et al.,* 1986; Crane, 1953, 1955, 1956, 1960; Reed, 1954; Whittier and Wagner, 1971), spore abortion (Wagner and Chen, 1965; Wagner *et al.,* 1986), cytology (Hickok and Klekowski, 1973; Manton and Walker, 1953; Walker, 1969; Wagner, 1971), flavinoid chemistry (Scora and Wagner, 1954; Widen *et al.,* 1975), and more recently, electrophoresis of foliar proteins (Euw *et al.,* 1980; Gastony, 1986). The systematic research has led to the postulation of a number of comprehensive theories on the reticulation of diploid, triploid, tetraploid, pentaploid, and hexaploid cytomorphotypes into a genus-wide compilospecies involving repeated events of hybridization and polyploidy (Lovis, 1977; Wagner, 1971, 1983; Wagner and Wagner, 1980). Taxonomic and systematic efforts are currently aimed at relating North American taxa with those taxa to the east in Europe and to the west in Japan and China. Ecologic efforts must address the character of the local population and those environmental conditions or events which favor hybridization, polyploidy, and must address the means by which sterile hybrid plants out-number sexual taxa in the local population (Carlson, 1979; Nickrant *et al.,* 1978, Wagner and Whitmire, 1957).

Six taxa in the genus *Dryopteris* occur in Arkansas. Taylor and Demaree (1979) and Taylor (1984) reported four taxa, including three sexual species and one sterile hybrid. Field study by the authors and by others resulted in the addition of one sexual species and one sterile hybrid taxa to the flora, the location of additional populations of the rarer taxa, and a clearer depiction of the distribution of the genus in Arkansas (Peck and Peck, 1986; Peck *et al.,* 1987a, b). The existence of *Dryopteris* as generally rare, local, and disjunct in Arkansas is a condition similar to that found for *Dryopteris* in other southern states (Small, 1938). In that the genus *Dryopteris* in Arkansas occurs primarily as a series of small, local, isolated populations, peripheral to or disjunct from the metropolis of the taxa to the east in the southern and northern Appalachians, the field status of plants and populations of Arkansas *Dryopteris* was surveyed and inventoried to summarize our current knowledge of their distribution, abundance, and status in Arkansas.

MATERIALS AND METHODS

Herbarium specimens were inspected to complete the survey initiated by W. C. Taylor. Field search was conducted to relocate known populations of rarer taxa and to locate additional populations. Field census

was conducted on populations of each taxa by census of all plants within a 10 m sq plot, a size that circumscribed all plants of all populations of the rare taxa. For more abundant taxa, sample plots of the same dimensions were established. A plant was defined as a shoot apex; excavation was conducted to determine whether vegetative expansion of plants into colonies was evident for selected plants in close proximity. Plants were scored as fertile (sporiferous) adults, sterile adults, and juvenile sporophytes. Spores were collected for subsequent study. A literature review was conducted to interpret phytogeographic relations of Arkansas taxa and to compare them with taxa in neighboring states and the southeastern United States.

Table 1. Comparison of ploidy level, genome code, U.S. range, and Arkansas status of Log Ferns *(Dryopteris)*.

Dryopteris Taxon	Ploidy Level	Genome Code	U. S. Range	Arkansas Status Habitat	# Co.	Comments
goldiana	2n	GG	NEUS	mesic, rocky woods	0	not known ARK.
ludoviciana	2n	LL	SEUS	swamps	1	one locality
marginalis	2n	MM	NEUS	xeric, rocky woods	34	frequent & abundant
carthusiana	4n	IISS	NEUS	mesic, rocky woods	2	two localities
celsa	4n	GGLL	SEUS	acid, wooded seeps	4	ten localities
X australis	3N	GLL	SEUS	acid, wooded seeps	1	one locality
X leedsii	3N	GLM	SEUS	mesic, rocky woods	1	one locality

RESULTS AND DISCUSSION

Results are presented in summary tables with biosystematic, habitat, and phytogeograhic data in Table 1 and census data in Table 2.

Dryopteris carthusiana (Villars) H. P. Fuchs

The Spinulose Woodfern (Table 1), known earlier as *Dryopteris spinulosa* (O. F. Muell.) Watt, is a circumboreal, amphiatlantic plant that is an allotetraploid (4n = 164) denoted by the genome code IISS (Manton and Walker, 1953). It reaches its southwestern periphery of its range in Arkansas. Although found in swampy woods and moist wooded slopes in eastern North America, it is restricted in habitat in Arkansas, being found at one locality in each of two counties in Arkansas (Peck, 1986a, 1986b). This taxa occurs in Arkansas with not much more than two dozen plants (Table 2). This taxa may be at considerable risk in Arkansas (Table 2) in that few juvenile plants were recorded. Approximately three out of five plants are sporiferous, but no evidence of currently successful reproduction was noted.

Dryopteris celsa (Palmer) Small

The Log Fern (Table 1) is a North American endemic that is an allotetraploid (4n = 164) denoted the genome GGLL (Walker, 1959, 1962, 1969; Britton, 1972). The epithet means "elevated", referring to the habit of the plant to occur on nurse logs in swamps and seeps. The parents of this taxon are two sexual diploids *(D. goldiana* × *D. ludoviciana)*. The ranges of these taxa do not overlap today; it seems likely that during Pleistocene glaciation plant migration, the two ranges combined and hybrids were formed. The sterile, diploid hybrids (genome code GL) underwent polyploidy to become the present day fertile taxon GGGLL. Today *D. celsa* occupies a range latitudinally and altitudinally intermediate between its parents (Wagner, 1972). It occurs from New Jersey (Montgomery, 1975) to its southwestern periphery in Arkansas, Louisiana (Thomas *et al.*, 1973), and Texas, being rare, infrequent, and discontinuous across that range (Wagner, 1972). A completely disjunct segment of the range occurs in the Great Lakes region of Michigan (Wagner *et al.*, 1969) and New York (Wagner and Wagner, 1965).

The Texas population has long been misnamed as *Dryopteris cristata* (L.) Gray (Correll, 1955; Correll and Johnson, 1970; Correll, 1972; Correll and Correll, 1972). There is occurs in Bowie Co. at the margin of a bog near Texarkana, where it was collected on 27 Oct 1925 by E. J. Palmer (*29404*, MO, GH) and misnamed. The Texas plant is *D. celsa*.

Table 2. Census data from 10 m sq plots established within 25 populations of Log Ferns *(Dryopteris)*.

Dryopteris Taxon	County	Plots n	Apices/ Plot n	Juvenile Apices n	%	Nonfertile Adults n	%	Fertile Adults n	%
goldiana	Webster	4	28	0	0	0	0	28	100
ludoviciana	Bradley	2	35	31	89	0	0	4	11
marginalis	Garland	1	28	0	0	0	0	28	100
	Logan	4	27	0	0	4	15	23	85
	Montgomery	1	30	0	0	4	13	26	87
	Polk	4	30	0	0	1	3	29	97
	Stone	1	31	0	0	4	13	27	87
	Van Buren	1	38	0	0	4	11	34	89
carthusiana	Logan	1	14	0	0	6	43	8	57
	Stone	1	12	0	0	4	25	8	75
celsa	Garland	1	16	0	0	5	31	11	69
	Montgomery	1	30	0	0	4	13	26	87
	Polk	1	12	0	0	2	17	10	83
X australis	Garland	1	321	297	93	0	0	24	7
X leedsii	Van Buren	1	10	0	0	4	40	6	60
Totals		25	662	328		42		292	
Species Means (n=13)			25	2	8	3	12	20	80
Hybrids Means (n=2)			166	148	90	2	1	15	9

D. cristata is found north of the unglaciated region, and has been excluded from the southern Mississippi Valley (Thomas, Wagner, and Mesler, 1973).

In Arkansas, *D. celsa* was discovered 24 May 1925 by B. C. Marshall (*9*, US) at York Springs, located south of Imboden, Lawrence Co.; specimens were sent to W. Maxon, who correctly identified the plant. That population is now extirpated, with the area being heavily pastured; the spring marker now acts as a cenotaph marking the location. It was subsequently located at four populations in Polk County (*Moore, McWilliams, Iltis 52040*, US, MO; *Peck 84705*, LRU, MICH, MIL), two populations in Montgomery Co. (*Peck 84705*, LRU, MIL, MICH), and one population in Garland Co. (*Peck 84680*, LRU, MICH, MIL). At none of the extant populations are either parental sexual species present. *D. goldiana* is not known from Arkansas, occurring to the north of Arkansas in Iowa and Missouri (Iffrig, 1979); its genes are present in Arkansas only as an expression of its derived hybrid taxa *D. celsa*. The other parental taxa, *D. ludoviciana* does not occur in Arkansas, but is geographically separated from *D. celsa*.

This taxa occurs as small populations (Table 2), without juveniles, but with most plants sporiferous. Although conditions are generally good for gametophyte growth, based on the generally moist substrate, no indication of gametophyte establishment or sporophyte recruitment was noted. These populations are thus ecologically fragile.

Dryopteris ludoviciana (Kunze) Small

The Louisiana Log Fern (Table 1) is a fertile, sexual diploid (2n = 82) denoted by genome LL (Walker, 1959). Geographically, it is a North American endemic. Its epithet refers to its initial discovery in Louisiana, although the plant is clearly more abundant in Florida, from where it was renamed erroneously as *D. floridanum*. The plant frequents swamps and damp woods on the Atlantic Coastal Plain and Gulf Coastal Plain of the Southeastern United States. It was recently located in Arkansas (*Sundell & McIntyre 2864*, UAM; *Peck & Peck 84641*, LRU, MICH, MIL). The Arkansas population is the fourth located west of the Mississippi River (Peck *et al.*, 1985; Peck *et al.*, 1985); the three other populations are 350 km disjunct from the Arkansas population in

Bradley Co., being found earlier in Louisiana (one population) and Texas (two populations). The Arkansas population is the most northwestern population of this taxon. This taxa differs in population structure from other fertile species of *Dryopteris* in Arkansas. Juvenile sporophytes were found (Table 2); however, few sporophytes plants are sporiferous. Substrate conditions are generally favorable for gametophyte establishment. Although vegetative expansion is likely, no evidence of connections among plants could be found. It thus seems likely that sexual reproduction of this taxa occurs in Arkansas, but that it is slowly successful in producing plants that live long enough to reach reproductive maturity. Conditions for this plant may be close to its tolerance limits, but may not be limiting reproductive phenomena. Drought conditions or cold weather may hinder the survival of sporophytes more than the successful maturation from spore to gametophyte to sprorophyte.

Dryopteris marginalis (L.) A. Gray

The Marginal Shield Fern (Table 1) is a fertile, sexual diploid (2n = 82), denoted by genome code MM (Manton and Walker, 1953). It is a North American endemic that frequents rocky, wooded slopes and ravines. It occurs in 34 counties in the northwestern one-half of Arkansas in the Ozark and Ouachita mountains. It is the only widespread and abundant *Dryopteris* taxa in Arkansas. Populations of this taxa (Table 2) are often quite extensive, consisting of hundreds of plants, most of which are fertile, but consist of surprisingly few juvenile plants. It is not clear why this plant is so much more widely distributed and locally abundant than the other plants based on reproductive structure of its populations. Although its habitat is abundant, conditions on dry rocks can hardly be thought of as being highly conducive to fern reproduction. Characterization of the microhabitat which does lead to successful establishment of new plants might well be very informative to the reproductive biology of this genus.

Dryopteris × *australis* (Wherry) Small

The Southern Wood Fern (Table 1) is a sterile hybrid, being a triploid (3n = 82 + 41) denoted by the genome code LLG. It is the backcross hybrid (Wagner and Musselman, 1982; Walker, 1962) between the fertile allotetraploid *D. celsa* (LLGG) and the fertile diploid *D. ludoviciana* (LL). *D.* × *australis,* first discovered in 1927 in Alabama (Small, 1938; Wherry, 1937, 1961), is a North American endemic that occurs across the southeastern United States. The Arkansas population was the eighth known in North America; Arkansas was the fifth state known to have this taxa: North Carolina (two populations), South Carolina (one population), Alabama (two populations), and Louisiana (two populations). Both Louisiana populations are now extripated; the Arkansas population, the third located west of the Mississippi River, is now the only extant population west of the Mississippi River. Since its discovery in Arkansas, one population each was located in Georgia, Tennessee, Virginia, and Mississippi (pers. comm., W. Wagner and C. Werth, 1988). In Arkansas, it occurs in Garland Co. (*Orzell 1429,* UARK; *Peck & Peck 84680,* LRU, MICH, MIL). The Arkansas population co-occurs with one parental taxa, *D. celsa* (Orzell and Peck, 1985; Peck *et al.,* 1985), with the other parental taxa *(D. ludoviciana)* not present in Arkansas except 200 km distant in Bradley Co. The nearest population of *D.* × *australis* occurred 50 km to the south in Louisiana; presently, the nearest extant population occurs 500 km to the southeast in Mississippi.

The population structure of this taxa in Arkansas is quite unexpected (Table 2). Far more juvenile plants were found at one population of this "sterile" hybrid than for all populations of all fertile species combined. The local substrate was moist, but it was equally moist at locations where *D. celsa* occurred, but where juveniles were not encountered. These juveniles were not produced by vegetative expansion from existing plants: connections were not encountered. Some plants were small and appeared to have gametophyte tissue attached. It seems reasonable to speculate that these plants may have originated from spore production that in some way was not "sterile", possibly by pseudomeiotic reduction (De Benedictitus, 1969; Morzenti, 1962; Whittier, 1970), producing good spores, and apogamy of gametophytes to produce sporophyte plants. Alternatively, they may represent arrested development of plants that initiated colonization at the time of the successful adult plants, but have been held back by unknown genetic, physiologic, or developmental phenonema. This requires additional study to clarify whether either of these alternative explanations is sufficient and valid for this population.

Dryopteris × *leedsii* Wherry

Leeds' Wood Fern (Table 1) is a sterile, triploid (3n = 41 + 41 + 41) hybrid taxa endemic to North America. Its genome code is GLM. It is the backcross hybrid (Wagner and Wagner 1965, 1966; Walker, 1962) between the fertile allotetraploid *D. celsa* (GGLL) and the fertile diploid *D. marginalis* (MM). It frequents steep, rocky, wooded slopes, seeps, and swamps. Significantly, the Arkansas population was the first discovered, and was designated the type locality of the taxon (Wagner and Taylor, 1976). Six populations are now known from four states in North America: Arkansas (one population), Maryland (two populations), New York (two populations), and Pennsylvania (one population). Its distribution is sympatric with its parental taxa, being distributed along the interior highlands of southeastern United States.

In Arkansas, it occurs in Van Buren Co. (*Palmer 33216,* NY, US; *Demaree 10039,* US; *Moore 350441,* NY, US; *Taylor 2597,* SIU; *Wagner & Wagner 74164,* MICH; *Redfearn 29403,* SMS; *Peck & Peck 84721,* LRU, MICH, MIL) at a moist, rocky, wooded slope where only one *(D. marginalis)* of its two parental taxa occurs. It was discovered by E. J. Palmer on 30 Mar 1928; its taxonomic status was problematic, being often called the "Palmer" *Dryopteris.* The plants were inspected by Demaree in 1932, and D. Moore, in 1935. The importance of the plant was realized in the early 1960s, but it could not be relocated. An exciting tale of its eventual rediscovery in 1972 by Taylor and Demaree has been recorded by Wagner and Taylor, 1976; Taylor, 1982). This hybrid has occupied the same location for over 60 years; it is over 600 km disjunct from its nearest population. Based on discussions with Demaree, Taylor, and Wagner, the present status of the population is unchanged, or a few apices less than when first discovered (Table 2). Juveniles were never seen; from limited inspection,the plants appear to have a connection, suggesting that the population is the vegetative expansion of one plant.

CONCLUSIONS

The wood fern genus *Dryopteris* is represented in Arkansas by plants that have limited capability to quickly replace themselves. Consequently, the long-term persistence of plants is extremely important to the continued success of that population. Populations of the fertile, sexual species generally did not have juvenile sporophytes present: only *D. ludoviciana* had juveniles, and that population was characterized by having the fewest number of fertile sporophytes, suggesting that adult survivorship is limited. Based on these observations, all collectors should take great care never to collect entire plants of this fern. One frond is sufficient to obtain a confirmation of its identity and voucher its presence by deposition in an herbarium. It is quite important to continue to search for and document any new populations of this genus in Arkansas. Arkansas populations are peripheral to the range of all of these taxa, and provide outstanding opportunities to conduct studies of local population dynamics of these ferns.

The population structure of the "sterile" triploid hybrid *D.* × *australis* is astounding. It consists of very large fertile adults surrounded by a large number of immature, juvenile sporophytes. The moist conditions of the seepage area certainly would enhance the opportunity for any good spores of this sterile taxa to have a chance to establish a gametophyte and produce a sporophyte. The moist conditions would enhance gamete transfer, and certainly would not hinder apogamy. It is possible that pseudomeiotic reproduction occurred and that unreduced spore mother cells developed into giant spores, and gave rise to gametophytes and sporophytes. The genetic constitution of these juveniles is intriging, as to their ploidy level and the identity of the genomes that they carry. Alternatively, the juveniles might be as old as the adult plants, but are suppressed in development by unidentified factors. The alternative that the juveniles represent vegetative expan-

sions from the adults was ruled out by excavation. Additional study is essential to ascertain the ecologic and reproductive events which led to this peculiar structure of a population of a sterile hybrid.

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LITERATURE CITED

BARRINGTON, D. S., C. A. PARIS, and T. A. RANKER. 1986. Systematic inferences from spore and stomate size in the ferns. Amer. Fern J. 76:149-159.

BRITTON, D. M. 1972. The spores of *Dryoteris clintoniana* and its relatives. Can. J. Bot. 50:2027-2029.

CARLSON, T. M. 1979. The comparative ecology and frequencies of interspecific hybridization in Michigan woodferns. Mich. Bot. 18:47-56.

CARLSON, T. M. and W. H. WAGNER. 1982. The North American distribution of the genus *Dryopteris*. Contr. Univ. Mich. Herb. 15:141-162.

CORRELL, D. S. 1955. Pteridophyta. Vol. 1(1), *in* C. L. Lundell, Flora of Texas. University Press in Dallas, Southern Methodist University, Dallas, Texas.

CORRELL, D. S. 1972. A manual of the vascular plants of Texas I. Additions and corrections. Amer. Midl. Nat. 88:490-496.

CORRELL, D. S. and H. S. CORRELL. 1972. Aquatic and wetland plants of southeastern United States. GPO, Washington, DC. 1777 pp.

CORRELL, D. S. and M. C. JOHNSTON. 1970. Manual of the vascular plants of Texas. 1881 pp. Texas Research Foundation, Renner, Texas.

COUSENS, M. 1975. Gametophyte sex expression in some species of *Dryopteris*. Amer. Fern J. 65:39-42.

COUSENS, M. and H. T. HORNER. 1970. Gametophyte ontogeny and sex expression in *Dryopteris ludoviciana*. Amer. Fern J. 60:13-27.

CRANE, F. W. 1953. Spore studies in *Dryopteris*, I. Amer. Fern. J. 43:159-169.

CRANE, F. W. 1955. Spore studies in *Dryopteris*, II. Amer. Fern J. 45:14-16.

CRANE, F. W. 1956. Spore studies in *Dryopteris*, III. Amer. Fern J. 46:127-130.

CRANE, F. W. 1960. A key to American *Dryopteris* species based on characteristics of the perispore. Amer. Fern J. 50:270-275.

DEBENEDICTUS, V. M. M. 1969. Apomixis in ferns with special reference to sterile hybrids. Ph.D. dissertation, Uni. Mich., Ann Arbor, MI.

DOWELL, P. 1908. New ferns described as hybrids in the genus *Dryopteris*. Bull. Torrey Bot. Club 35:135-140.

EUW, J. V., M. LOUSANSAMA, T. RIECHSTEIN, and C. J. WIDEN. 1980. Chemotaxonomy in *Dryopteris* and related fern genera. Review and evolution of analytic methods. Stud. Geobot. 4:275-311.

GASTONY, G. J. 1986. Electrophoretic evidence for the origin of fern species by unreduced spores. Amer. J. Bot. 73:1563-1569.

HICKOK, L. G., and E. J. KLEKOWSKI. 1973. Abnormal reductional and non-reductional meiosis in *Ceratopteris:* alternatives to homosporous meiosis in *Ceratopteris:* alternatives of homozygosity and hybrid sterility in homosporous ferns. Amer. J. Bot. 60:1010-1022.

HICKOK, L. G. and E. J. KIEKOWSKI. 1975. Chromosome behavior in hybrid ferns: a reinterpretation of Appalachian *Dryopteris*. Amer. J. Bot. 62:560-569.

IFFRIG, G. F. 1979. The distribution of *Dryopteris goldiana* and *D. marginalis* in Missouri. Amer. Fern J. 69:29-30.

LELLINGER, D. 1984. Ferns of North America. Smithsonian Institution, Washington, D.C.

LOVIS, J. D. 1977. Evolutionary patterns and processes in ferns. Pp. 229-415, *in* R. D. Reston and H. W. Woolhouse (eds.) Advances in Botanical Research 4:229-415. Academic Press, NY.

MANTON, I., and S. WALKER. 1953. Cytology of the *Dryopteris spinulosa* complex in eastern North America. Nature 171:1116-1118.

MONTGOMERY, J. D. 1975. *Dryopteris celsa* and *D. clintoniana* in New Jersey. Amer. Fern J. 65:65-69.

MONTGOMERY, J. D. 1982. *Dryopteris* in North America. Part II: the hybrids. Fiddlehead Forum 9(4):23-30.

MONTGOMERY, J. D., and E. M. PAULTON. 1981. *Dryopteris* in North America. Fiddlehead Forum 8(4):25-31.

MORZENTI, V. M. 1962. A first report on pseudomeiotic sporogenesis, a type of spore reproduction by which "sterile" ferns produce gametophytes. Amer. Fern J. 52:69-78.

NICKRENT, J. D., L. J. MUSSELMAN, L. A. PITCHFORD, and D. W. SAMPSON. 1978. The distribution and ecology of *Dryopteris* in southeastern Virginia and adjacent North Carolina. Amer. Fern J. 68:45-51.

ORZELL, S., and J. H. PECK. 1985. Southern woodfern, *Dryopteris* × *australis*, new to Arkansas. Proc. Ark. Acad. Sci. 39:144.

PECK, J. H. 1986a. *Dryopteris carthusiana* in Arkansas. Proc. Ark. Acad. Sci. 40:94.

PECK, J. H. 1986b. Second locality for *Dryopteris carthusiana* in Arkansas. Amer. Fern J. 76:28-29.

PECK, J. H., S. ORZELL, E. SUNDELL, and C. J. PECK. 1985. *Dryopteris ludoviciana* and *D.* × *australis* new to Arkansas. Amer. Fern J. 75:71.

PECK, J. H., and C. J. PECK. 1986. Additions to the pteridophyte flora of Arkansas. Ark. Nat. Plt. Soc. Occ. Pap. 6:1-4.

PECK, J. H., C. J. PECK, and W. C. TAYLOR. 1987a. Checklist of the pteridophyte flora of Arkansas. Ark. Acad. Sci. Biota Surv. Checklist No. 47. 4 pp.

PECK, J. H., C. J. PECK, and W. C. TAYLOR. 1987b. Update on the pteridophyte flora of Arkansas. Proc. Ark. Acad. Sci. 41:113-114.

PECK, J. H., E. SUNDELL, and C. J. PECK. 1985. Louisiana Log Fern *(Dryoptera ludoviciana)* new to Arkansas. Proc. Ark. Acad. Sci. 39:144.

REED, C. F. 1954. Spores, sporangia, and indusia of the genus *Dryopteris* in North America, north of Mexico. Bartonia 27:47-56.

SCORA, R. W., and W. H. WAGNER. 1964. A preliminary chromatographic study on Eastern American *Dryopteris.* Amer. Fern J. 54:105-113.

SMALL, J. K. 1938. Ferns of the Southeastern United States. Science Press, Lancaster, PA. 517 pp.

TAYLOR, W. C. 1982. Dr. Demaree and the Palmer *Dryopteris.* SIDA 9:287-289.

TAYLOR, W. C. 1984. Arkansas ferns and fern allies. Milwaukee Public Museum, Milwaukee, WI.

TAYLOR, W. C., and D. DEMAREE. 1979. Annotated list of the ferns and fern allies of Arkansas. Rhodora 81:503-548.

THOMAS, R. D., W. H. WANGER, and M. R. MESSLER. 1973. Log fern *(Dryopteris celsa)* and related species in Louisiana. Castanea 38:269-274.

TRYON, R. M. 1986. The biogeography of a species, with special reference to ferns. Bot. Rev. 52:117-156.

TRYON, R., and D. M. BRITTON. 1966. A study in the variation in the cytotypes of *Dryopteris spinulosa* Rhodora 8:59-92.

WAGNER, F. S. and L. J. MUSSELMAN. 1982. The occurrence of the southern woodfern, *Dryopteris* × *australis* (Wherry) Small. Castanea 47:182-190.

WAGNER, W. H. 1943. Hybridization by remote control. Amer. Fern J. 33:71-73.

WAGNER, W. H. 1971. Evolution of *Dryopteris* in relation to the Appalachians. Pp. 147-192, *in* P. C. Holt (ed.) The distributional history of the biota of the southern Appalachians. Part 2: Flora. Virginia Polytechnic Inst. & St. Univ. Research Div. Monograph No. 2.

WAGNER, W. H. 1972. Disjunctions in homosporous vascular plants. Annals Missouri Bot. Gard. 59:203-217.

WAGNER, W. H. 1983. Reticulistics: the recognition of hybrids and their role in cladistics and classification. Chapter 8, *in* N. I. Platnick and V. A. Funk. Advances in cladistics, Vol. 2. Columbia Univ. Press, NY.

WAGNER, W. H., and K. L. CHEN. 1965. Abortion of spores and sporangia as a tool in the detection of *Dryopteris* hybrids. Amer. Fern J. 55:9-29.

WAGNER, W. H., and W. C. TAYLOR. 1976. *Dryopteris* × *leedsii* and its westernmost station. Sida 6:224-234.

WAGNER, W. H., and F. S. WAGNER. 1965. Rochester area log ferns *(Dryopteris celsa)* and their hybrids. Proc. Rochester Acad. Sci. 57-71.

WAGNER, W. H., and F. S. WAGNER. 1980. Polyploidy in pteridophytes. Pp. 199-214, in W. H. Lewis. Polyploidy: biological relevance. Plenum Press, NY.

WAGNER, W. H., F. S. WAGNER, and D. J. HAGENAH. 1969. The log fern *(Dryopteris celsa)* and its hybrids in Michigan — a preliminary report. Mich. Bot. 8:137-145.

WAGNER, W. H., F. S. WAGNER, and W. C. TAYLOR. 1986. Detecting abortive spores in herbarium specimens of sterile hybrids. Amer. Fern J. 76:129-140.

WAGNER, W. H., and R. S. WHITMIRE. 1957. Spontaneous production of a morphologically distinct, fertile allopolyploid by a sterile diploid of *Asplenium ebenoides.* Bull. Torrey Bot. Club 84:79-89.

WALKER, S. 1962. Further studies in the genus *Dryopteris:* the origin of *D. clintoniana, D. celsa,* and related taxa. Amer. J. Bot. 49:497-503.

WALKER, S. 1962. The problem of *Dryopteris leedsii.* Amer. J. Bot. 49:971-974.

WALKER, S. 1969. Identification of a diploid ancestral genome in the *Dryopteris spinulosa* complex. Brit. Fern. Gaz. 10:97-99.

WHERRY, E. T. 1937. Southern occurrences of *Dryopteris clintoniana.* Amer. Fern J. 27:1-5.

WHERRY, E. T. 1961. Supplementary notes on *Dryopteris* hybrids. Amer. Fern J. 51:33-35.

WHITTIER, D. P. 1970. The rate of gametophyte maturation in sexual and apogamous species of ferns. Phytomorphology 20:30-35.

WHITTIER, D. P., and W. H. WAGNER. 1971. The variation in spore size and germination in *Dryopteris* taxa. Amer. Fern J. 61:123-127.

WIDEN, C. J., D. M. BRITTON, W. H. WAGNER, and F. S. WAGNER. 1975. Chemotaxonomic studies on hybrids of *Dryopteris* in eastern North America. Can. J. Bot. 33:1554-1567.