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The status of *Gymnocarpium heterosporum* and *G. robertianum* in Pennsylvania

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In 1935, Katherine Schneider made the first discovery of what she identified as the limestone oak fern, *Gymnocarpium robertianum* (Hoffm.) Newm., in Blair County, Pennsylvania (Wherry, 1942a). This significant find was not disclosed until 1941, when she and Elsie Canan located a larger colony of plants nearby and arranged to have the site verified by E.T. Wherry. At the time, this finding was regarded as the most remarkable disjunct occurrence of any species for the state of Pennsylvania (Wherry, 1942b); an honor that later went to *Montia chamissoi* (Ledeb. ex Spreng.) Greene (Wherry, 1964). Nevertheless, the Blair County site still maintained the presumed distinction of being the southernmost locality known for *G. robertianum* in North America (Ogden, 1981), with the nearest stations being 260 miles to the northwest in St. Clair County, Michigan and 300 miles directly north in Frontenac County, Ontario (Sarvela *et al.*, 1981).

The small number of herbarium specimens originating from the Blair County site indicates that it was a well-kept secret indeed, with only a handful of botanists who made collections there (Table 1). Most gave general directions to it as either "2 miles northwest of Hollidaysburg," "3 miles northwest of Hollidaysburg," or "3.5 miles north of Duncansville." Thomas Darling, Jr. visited the site on August 25, 1956, and the specimen that he deposited at the Smithsonian (US) provides the most detailed locality information: "among limestone rocks on northwest-facing talus slope near quarry, approximately 2 miles northwest of Hollidaysburg, near point where Burgoon Creek intersects Beaverdam Branch of Juniata River, Blair County." The most recent date of collection is August 10, 1957, when the site was visited by L.K. Henry (Table 1). No herbarium specimens taken from there since that date were located.

In his study of *Gymnocarpium* in North America, Wagner (1966) recognized two tetraploid ($n = 80$) species, *G. dryopteris* (L.) Newm. and *G. robertianum*, both with a broad distribution that extended from the Pacific coast to the Atlantic, predominantly in the north temperate regions. Wagner (1966) also first documented the occurrence of diploid ($n = 40$) plants, *G. dryopteris* var. *disjunctum* (Rupr.) Ching, referred to here (based on discussions in Pryer & Haufler, 1993) as *G. disjunctum* (Rupr.) Ching. This species is restricted to northwestern North America (Alaska, Alberta, British Columbia, Washington, Oregon, Idaho, Montana and Wyoming). Root (1961) observed a prevalence of plants in the Great Lakes region with abortive spores and a frond morphology seemingly intermediate between that of *G. dryopteris* and *G. robertianum*. Wagner (1966) applied the name *G. heterosporum* W.H. Wagner to these widespread putative hybrids. The holotype that Wagner (1966) selected for this intermediate taxon was among the specimens that previously had been identified as *G. robertianum* from Blair County, Pennsylvania (Table 1). His cytogenetic analysis of the type population was extremely interesting in that the plants were not tetraploid, as was expected, but were triploid

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TABLE 1. Herbarium specimens of *Gymnocarpium heterosporum* (originally identified as *G. robertianum*) from Blair County, Pennsylvania.

Collector	Collection Date	Herbaria ²
E.D. Canan	September 20, 1941	CM
W.H. Wagner, Jr.	September 20, 1941	MICH ³ (2 sheets), PAC, VPI
E.T. Wherry	September 20, 1941	PENN, PH, VPI
E.T. Wherry	June 5, 1942	US
T. Darling, Jr.	August 25, 1956	GH, MICH, UC, US
L.K. Henry	August 10, 1957	SFS

²Abbreviations from Holmgren *et al.*, 1981

³Location of holotype of *G. heterosporum*

(chromosome pairing average: $33.5_{II}+52.5_{I} \approx 120$ chromosomes). Wagner (1966) suggested that *G. heterosporum* might have originated from a cross between *G. disjunctum* and *G. robertianum*, and that it had become established from Alaska to the Great Lakes region as an apomictic species by means of a unique spore mechanism.

Sarvela's (1978) worldwide synopsis of *Gymnocarpium* included three taxonomic modifications that pertain to the genus in North America. First, he split what had hitherto been called *G. robertianum* into two taxa: *G. robertianum s.s.*, confined to eastern North America (Newfoundland to the Great Lakes region), and *G. jessoense* (Koidz.) Koidz. ssp. *parvulum* Sarvela, occurring from the Great Lakes region westward to Alaska. The distinguishing features of these two tetraploid taxa have been elaborated upon by Sarvela *et al.* (1981), Pryer *et al.* (1983), and Pryer (1990). Second, Sarvela (1978) established the name *G. Xintermedium* Sarvela to refer to the widespread intermediate taxon with abortive spores that was first observed by Root (1961). Sarvela (1978) proposed that the type specimens of *G. heterosporum* from Blair County represented a rare taxon, distinct from the hybrid plants that he referred to *G. Xintermedium*. Recent enzyme electrophoretic work suggests that *G. Xintermedium* is tetraploid and was derived from a cross between *G. dryopteris* and *G. jessoense ssp. parvulum* (Pryer, unpubl. data). In North America, the geographic ranges of *G. Xintermedium* and *G. jessoense ssp. parvulum* are completely sympatric and are included almost entirely within the western portion of the widespread distribution of *G. dryopteris*. The intermediate morphological and phytochemical characteristics of *G. Xintermedium* were investigated by Pryer *et al.* (1984). Third, Sarvela's (1978) interpretation of *G. heterosporum* was that it had originated from a cross between *G. robertianum* and *G. jessoense ssp. parvulum*. At that time, Sarvela presumed that *G. jessoense ssp. parvulum* was diploid and so this interpretation of the origin of *G. heterosporum* was supported by Wagner's (1966) triploid chromosome counts from the type locality. However, when it was later discovered that *G. jessoense ssp. parvulum* was actually tetraploid (Sarvela *et al.*, 1981), Sarvela (1980) acknowledged that the parentage of these triploid plants was still unresolved.

There is a persisting conflict in the Pennsylvanian botanical literature as to the correct identity of the Blair County plants. According to Wherry *et al.* (1979) they are *G. heterosporum*. Wiegman (1979) also calls them *G. heterosporum*, but he includes *G.*

robertianum as a synonym. In 1985, the Pennsylvania Department of Environmental Resources designated these plants as endangered in the state under the name *G. robertianum* and there was no mention of *G. heterosporum*. In this study, specimens originating from the Blair County site (Table 1) were examined with a view to resolving the question of their identity. The spore condition of ferns, i.e. abortive spores vs. well-formed spores, is often a good indicator for distinguishing between recent hybrids and stable species, respectively (Wagner *et al.*, 1986). All of the specimens in Table 1 had fronds that were either sterile or, if fertile, had been collected too early or too late in the season to adequately demonstrate their spore condition. A deliberate effort was made to search for closed sporangia on fertile specimens that had been collected late in the season. The few that could be found were gently removed with the moistened tip of an insect pin, placed in Hoyer's mounting medium on a glass slide, and induced to release their contents (cf. Wagner *et al.*, 1986). In all cases, the contents included indistinguishable sporangial matter along with blackish, abortive spores.

Fronds of *G. robertianum* typically exhibit dense to moderate glandularity on the rachis, lower, and upper blade surfaces. They generally are narrowly triangular and have stalked second basal pinnae; fertile fronds produce light brown, kidney-shaped spores (Sarvela *et al.*, 1981; Pryer *et al.*, 1983; Pryer, 1990). The specimens from Blair County (Table 1) have all of these morphological attributes of *G. robertianum* except that the fertile fronds have abortive spores. Since Wagner (1966) obtained only triploid chromosome counts from this site, it is likely that plants of the hybrid *G. heterosporum* occurred there exclusively at that time.

An enzyme electrophoretic, cytological, and morphological investigation of the *Gymnocarpium dryopteris* complex (Pryer & Haufler, 1993) led to a significant discovery that has a direct bearing on the possible origin of *G. heterosporum*. In that study, it was determined that most plants formerly called *G. dryopteris* and occurring within the unglaciated regions of Ohio, West Virginia, Pennsylvania, Virginia, and North Carolina are diploid ($n = 40$). These plants form the basis of a new species to be called *G. appalachianum* Pryer & Haufler. This species and the western *G. disjunctum* are the diploid progenitors of the widespread allotetraploid *G. dryopteris* (Pryer & Haufler, 1993). *Gymnocarpium appalachianum* is distinguished from *G. dryopteris* by its significantly smaller spores and subtle, but notable, morphological characteristics of the pinnae, pinnules, and pinnulets of mature, fertile fronds (Pryer & Haufler, 1993). The only known occurrences of *G. appalachianum* in Pennsylvania are from Bedford County (Table 2), which lies immediately south of Blair County. The present-day distribution of *G. appalachianum* is completely separate from that of *G. robertianum* (Fig. 1). It is conceivable, however, that in the past (e.g. during the Wisconsinan glaciation) the ranges of these two species might have overlapped and provided them an opportunity to come into close proximity and produce the very rare triploid hybrid *G. heterosporum*.

As mentioned earlier, the hybrid specimens from Blair County (Table 1) strongly resemble *G. robertianum*. When closely examined, however, they also have some of the subtle characteristics of the pinnae, pinnules, and pinnulets of *G. appalachianum*. For example, the following basal pinnae characters on the holotype of *G. heterosporum* can also be found on well-developed fronds of *G. appalachianum* (cf. Fig. 2 in Wagner, 1966 with Fig. 9 in Pryer & Haufler, 1992): i) stalked basal basicopic pinnules, ii) basal acroscopic pinnules with basal pinnulets shorter than second basal pinnulets, and iii)

TABLE 2. Verified herbarium specimens of *Gymnocarpium appalachianum* from Pennsylvania.

BEDFORD CO.: 5 mi. s of Hyndman, 5 May 1951, W.E. Buker s.n. (CM); 2 3/4 mi ssw of Hyndman, 16 Jun 1948, D. Berkheimer 9803 (CM); Wolfsburg, Raystown Branch of Juniata River, 3 Jul 1988, K.M. Pryer, J. Klein, & J. Kunsman 940 (CAN).

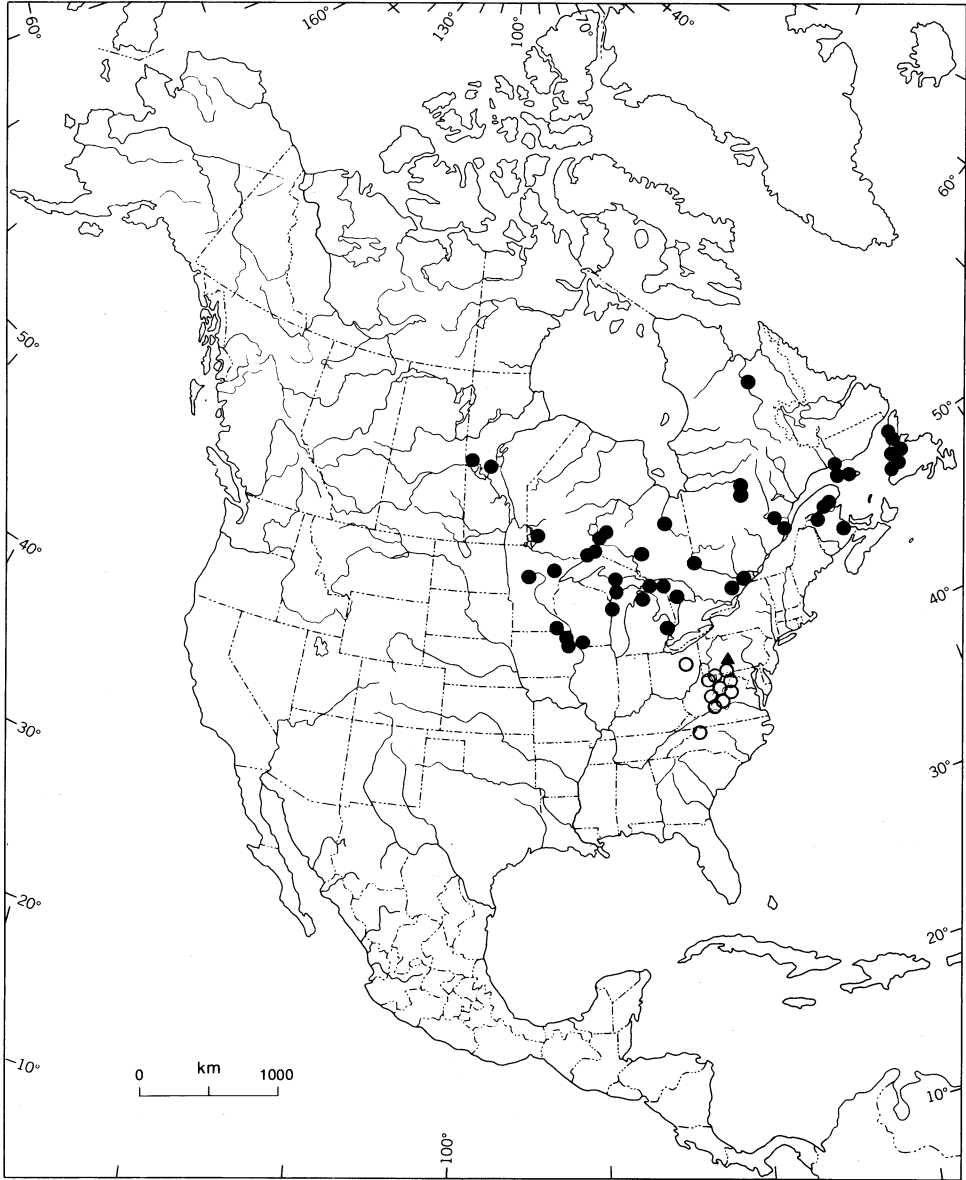


FIG. 1. Known North American distributions of *Gymnocarpium appalachianum*, *G. heterosporum*, and *G. robertianum*. Closed circles = *G. robertianum*. Open circles = *G. appalachianum*. Triangle = *G. heterosporum* (originally identified as *G. robertianum*; site was in Blair County, Pennsylvania and is now extirpated).

second basal basiscopic pinnules with basal pinnulets shorter than second basal pinnulets. In the Dryopteridaceae, the morphology of triploid hybrids tends to be more like that of the tetraploid parent that medial between the parental taxa (Barrington, 1986; Werth *et al.*, 1988). Therefore, it is not surprising that *G. heterosporum* is more similar to *G. robertianum* than it is to *G. appalachianum* in its overall morphological aspect.

On 9 November 1955, Wherry wrote to Thomas Darling, Jr.:

I went to the locality of the Limestone oak fern a few weeks ago. It is in good shape, not disturbed by man. . . . One can then walk along a road leading to a limestone quarry, and if anyone ever asked what I was doing I would say examining the rock formations and not mention the fern which is a weed anyway. . . . The map shows two village names, Canaan and Eldorado, nearby. I never found Canaan (probably an abandoned railroad station), but Eldorado is now an expanding suburban development, fortunately a safe distance away.

Attempts made by Kunsman (1984) to relocate the limestone oak fern colony in Blair County were in vain. In a recent letter, Thomas Darling, Jr. provided me with a copy of the Hollidaysburg quadrangle on which Wherry had pinpointed the exact locality (map now deposited in the Archives Collection of the Library of the Academy of Natural Sciences of Philadelphia). I visited the area in 1988 with John Kunsman and we confirmed that the site had been greatly altered by expanded quarry activities and the construction of a four-lane highway that cuts right through what must once have been the northwest-facing talus slope on which the ferns grew. We scoured the small west-facing patch of woods that still remains but unfortunately to no avail. Finally, when the mystery of the Blair County hybrids seems so near to being solved, the plants, and perhaps the taxon, have been obliterated and sadly we may never have the pleasure nor the satisfaction of better understanding them.

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SHORTER NOTE

Clarifying the History of *Polypodium australe* Fée Reported from San Clemente Island, California. – In 1980, Whitmore (pers. comm. to RML) contended that labels must have been switched at the University of California Botanical Garden on a plant from San Clemente Island which had been determined as *P. australe* (Lloyd & Hohn, Amer. Fern J. 59:56-60, 1969). Most recently, Haufler and Windham (Amer. Fern. J. 81:22, 1991) excluded *P. australe* from the Flora North America treatment of *Polypodium* because, “Lloyd & Hohn refer to a specimen made from the Botanical Garden plant rather than an original Raven collection. In fact, the only Raven collection they do discuss is one of *P. californicum* obtained at the same time and place as the Botanical Garden plant” and “Because no plants collected from natural habitats have been identified as *P. australe* . . .”

On the contrary, Peter Raven brought RML three living rhizomes of *Polypodium* which he collected on San Clemente Island (SC1, SC2, SC3). These rhizomes were potted and placed in Lloyd’s personal collection of exclusively western North American *Polypodium* which was housed in the courtyard of the Life Science Building at Berkeley and not at the UC Botanical Garden. Following the initial discovery of the *P. australe* characteristics of SC3, Lloyd wrote Raven for more details on their exact collection locations. He replied on 21 November 963: “Interesting! 1 and 3 are from canyons in the vicinity of Wilson Cove, 2 is from a deep canyon leading to the west side of the island below Middle Ranch. 1 is equal to the cited collection 17341, 2 to 17329.” Thus, although there are not vouchers for Raven’s collections, the herbarium specimen referred to (*Lloyd & Hohn*, 4420, UC) was taken directly from SC3.

Observations published by R. H. Roberts (Brit. Fern Gaz. 12:69-74, 1980) on the differentiation of *P. australe* from *P. macaronesticum* prompted one of us (FAL) to examine the features of the San Clemente Island plants anew. Could it be that these plants were actually *P. macaronesticum* rather than *P. australe*? Given the common habitats involved (offshore islands southwest of a continental coast with a Mediterranean