OAK FERNS *GYMNOCARPIUM DRYOPTERIS* AND RELATED TAXA IN THE PACIFIC NORTHWEST...AND BEYOND

From: Ed Alverson, The Nature Conservancy, 1820 Roosevelt Blvd., Eugene OR 97404
[ed.r.alverson@ci.eugene.or.us]

The oak ferns, *Gymnocarpium* Newman, are a small genus (about 8 species worldwide) in the fern family Dryopteridaceae with a wide distribution around the northern hemisphere in North America, Europe, and Asia, mostly in temperate regions. With bi- or tri-pinnate, triangular-shaped fronds arising from creeping rhizomes, the plants form large clonal patches in the understory of moist conifer forests. Traditionally, the North American taxa have been treated as two species, the glandular *Gymnocarpium robertianum* (Hoffmann) Newman, and the glabrous *Gymnocarpium dryopteris* (L.) Newman. However, the treatment published in 1993 in *Flora of North America* recognizes five species in North America. Where did all these species come from? It turns out that *Gymnocarpium dryopteris*, as traditionally circumscribed, is now recognized to comprise three species, of which two are distinct diploids, and the third, an allotetraploid derived from hybridization between the two diploids. This is, after all, a familiar tale in fern evolution, but because of their complex patterns of morphological variation, it was necessary for researchers to utilize other characters - such as chromosome numbers, spore characters, and isozyme banding patterns- to reveal the full story.

The first piece of critical data that suggested that *G. dryopteris* might be more than one taxon was a 1966 paper by W.H. Wagner Jr. Whereas all previous chromosome counts of *G. dryopteris* from Europe and North America had been tetraploid, with *n=80*, Wagner found plants growing along Denny Creek, east of Seattle near Snoqualmie Pass, that were diploid, with *n=40* pairs of chromosomes at meiosis. Wagner documented that ploidy in *Gymnocarpium* was expressed in spore size, and that coastal diploids had markedly smaller spores than the widespread tetraploids. He also noted that some plants with apparently malformed spores might be triploid hybrids. The diploid populations were recognized by Wagner and by other workers as representative of one end of a gradient of morphological variation, with the Pacific Northwest diploids (to which the name "*disjunctum*" applied) representing the robust, finely dissected extreme. However, there was a great deal of variation, and in some areas (such as Alaska and the Yukon), all points of the morphological and spore size gradient were found to occur. Wagner was "inclined to agree that var. *disjunctum* should probably merit recognition" (Wagner, 1966) Arthur Cronquist, in *Vascular Plants of the Pacific Northwest* (1969), noted Wagner's findings but did not adopt the name "var. *disjunctum*" for the coastal northwest plants (Hitchcock et al. 1969, Hitchcock and Cronquist 1972).

In the 1970's, Jaakko Sarvela, from the University of Helsinki, Finland, undertook a global study of *Gymnocarpium* (Sarvela 1978, Sarvela 1980). He treated "*disjunctum*" as a subspecies of *G. dryopteris*, and in the 1980 paper described a "hybrid subspecies", *Gymnocarpium dryopteris* ssp. x *brittonianum* Sarvela, representing the specimens with malformed or abortive spores. A triploid chromosome count, provided by Prof. Britton, was a key piece of evidence needed to demonstrate that these were indeed hybrids between a diploid and a tetraploid.

Wagner (1966) had found abortive spored hybrids occurring across northern North America, as far eastward as Nova Scotia, which was most puzzling, because the diploid parent, "ssp. *disjunctum*", was only known from the western portion of North America. How could hybrids occur so far from their likely point of origin?

Kathleen Pryer, a graduate student of Prof. Britton, further investigated the systematics of the North American oak ferns in her 1981 MS thesis. In addition to confirming the relationship between spore size and ploidy in *Gymnocarpium*, she also undertook a chromatography study of the North American taxa, which not only showed distinctions between *G. disjunctum* and *G. dryopteris*, but also showed the hybrid *G. x brittonianum* to be largely (though not completely) additive of the profiles of the two putative parents (Pryer et al, 1983). Still, the pieces did not all fit cleanly together. Of particular note was the emerging realization that there were actually two clusters of triploid hybrids, one in western and one in eastern North America, with a marked gap in the hybrid distribution in central Canada (despite the continuous presence of the tetraploids across Canada).

Fortunately for our story, Pryer continued her *Gymnocarpium* studies even after completing her MS degree. A more extensive study of herbarium material revealed another cluster of small spored plants -putative diploids- in the Appalachian Mountains of Pennsylvania, West Virginia, and Virginia. This, in fact, was the key piece of evidence that previous workers had missed - there was not one, but two areas of diploid oak ferns in North America, one area in the west, and one in the east. Furthermore, if one only compared the eastern diploids with the western diploids, they were clearly distinct in many respects. The Appalachian diploids , which Pryer and her co-worker Chris Haufler named *Gymnocarpium appalachianum* Pryer & Haufler, were petite compared to the robust western diploids. Furthermore,

Pryer found consistent differences between the two diploids in the patterns of frond morphology. Finally, isozyme analysis showed a clear separation between western and eastern diploids, with an average Nei's genetic identity of 0.274, comparable to the average value for congeneric fern species (Pryer and Haufler, 1993). It was primarily the presence of triploid hybrids, along with the tetraploid *G. dryopteris*, that muddled the morphological distinctions between the western and eastern diploids.

The implications of these findings are several. First, our western North American diploid should clearly be treated as a distinct species from *G. dryopteris*, using the name *Gymnocarpium disjunctum* (Rupr.) Ching. The blurring of boundaries between *G. disjunctum* and *G. dryopteris* is due to the presence of triploid hybrids with malformed spores, but because these hybrids are presumable sterile, there is no avenue for gene flow between these two species so they are reproductively isolated. Second, *G. dryopteris* is an allopolyploid, and presumably a rather ancient polyploid, formed at some time in the past when the ranges of the two diploid taxa came together (perhaps under different climatic conditions than today), allowing the species to hybridize. The primary hybrids were sterile diploids, but one or more hybrid individuals underwent chromosome doubling to produce a fertile tetraploid species. Third, the abortive-spored members of the *G. dryopteris* complex could represent one of two different hybrid combinations - *G. dryopteris* x *G. disjunctum* (represented by the type of *G. x brittonianum* [Sarvela] Pryer & Haufler), or *G. dryopteris* x *G. appalachianum*. Unfortunately there is no easy way to distinguish these two hybrid combinations with herbarium material. However, it is likely that the hybrids in western North America represent the former, while hybrids in eastern North America are primarily the latter (Pryer and Haufler, 1993).

There is one piece of this story in the Pacific Northwest that is still unresolved. In Pryer and Haufler (1993), the records for *G. dryopteris* in Oregon and Washington (where *G. disjunctum* is the primary representative of the complex) are based on unpublished spore measurement data from specimens at WTU and ORE that I provided to the authors. I documented certain individuals that had longer spores than typical *G. disjunctum*, although their total spore "volume" was less than typical *G. dryopteris* and readily distinguished from the latter taxon. Pryer and Haufler chose to treat these "long spored" individuals as representatives of *G. dryopteris*, but I disagree with that conclusion on the basis of spore "volume". As such, I do not believe that *G. dryopteris* should be cited as a member of the flora of Washington or Oregon until its presence is confirmed by a tetraploid chromosome count.

In the west, *G. dryopteris* is generally a Rocky Mountain species, and the places where it would most likely occur in Washington is in Pend Oreille Co., where the hybrid *G. x brittonianum* has apparently been documented. Botanists working in the Rocky Mountain region of British Columbia, Alberta, and adjacent portions of Idaho and Montana have the greatest challenge in naming *Gymnocarpium* taxa, because both western species, plus the hybrid *G. x brittonianum*, are common in this region. Workers in this region should study the illustrations of oak fern frond morphology in Pryer and Haufler (1993). However, the best (and possibly only) method to identify oak ferns with certainty in this region is to collect voucher material with mature spores, and examine the spores under a microscope.

References

Hitchcock, C.L., A. Cronquist, M. Ownbey & J.W. Thompson. 1969.
Vascular Plants of the Pacific Northwest. Part I: Vascular Cryptogams, Gymnosperms, and Monocotyledons. University of Washington Press, Seattle.

Hitchcock, C.L. and A. Cronquist. 1972.
Flora of the Pacific Northwest. University of Washington Press, Seattle.

Pryer, K.M. & D.M. Britton. 1983.
Spore studies in the genus *Gymnocarpium*. *Can. J. Bot.* 61(2):377-388.

Pryer, K.M., D.M. Britton, & J. McNeill. 1983.
A numerical analysis of chromatographic profiles in North American taxa of the fern genus *Gymnocarpium*. *Can. J. Bot.* 61(10):2592-2602.

Pryer, K.M. & C.H. Haufler. 1993.
Isozymic and chromosomal evidence for the allotetraploid origin of *Gymnocarpium dryopteris* (Dryopteridaceae). *Systematic Botany* 18(1):150- 172.

Sarvela, J. 1978.
A synopsis of the fern genus *Gymnocarpium*. Ann. Bot. Fenn. 15:101-106.

Sarvela, J. 1980.
Gymnocarpium hybrids from Canada and Alaska. *Ann. Bot. Fenn.* 17:292-295.

Wagner, W.H. Jr. 1966.
New data on North American oak ferns, *Gymnocarpium*. *Rhodora* 68:121-128.