Recent Taxonomic Changes for Oregon Ferns and Fern Allies

By EDWARD R. ALVERSON

Readers of Kalmiopsis were recently treated to a synopsis of taxonomic changes affecting flowering plants in Oregon (Chambers, 1992). The present article has been written to update readers on nomenclatural changes recently proposed for the seedless vascular plants, which include not only ferns, but also horsetails, club-mosses, and their relatives. Together these groups are often referred to as the ferns and fern allies. Many new names have been incorporated in the new Jepson Manual for California (Hickman, 1993), as well as the treatment of ferns and fern allies in Volume II of Flora of North America (FNA), due out in September 1993. Publication of the FNA treatment of ferns and fern allies at this time is most fortunate, for there has been a great deal of new and exciting biosystematic research in this group in recent years. As a result, even some fairly modern taxonomic references, such as Flora of the Pacific Northwest (Hitchcock and Cronquist, 1973), are now substantially out-of-date with regard to the ferns and their allies. Table 1 (page 22) lists name changes for Hitchcock and Cronquist (1973).

Several features of the ferns and fern allies have traditionally caused difficulties for taxonomists. One feature is the relative lack of substantial differences in spore-producing structures (i.e. the sporangia and associated indusia) among closely related species. While sporangia may differ substantially among genera (even this is not always the case), differences among related species are usually minor, if any. Typically morphological differences in congeneric ferns must be sought in vegetative characteristics. Compare this with flowering plants, where often the flowers and fruits are the primary focus of evolutionary selection and thus are the primary sources of useful morphological distinctions. Second, there are high levels of parallelism, or convergent evolution, among the ferns and fern allies. Convergent evolution is where two unrelated evolutionary lines share a common morphological feature that has evolved independently. Morphological parallelisms have made it particularly difficult to classify ferns at higher taxonomic ranks, such as genera and families.

Despite these inherent difficulties with traditional taxonomic evidence, many of the new changes in fern taxonomy are the result of careful analysis of morphology, with a focus on characters that are phylogenetically informative, rather than confusing. At the same time, fern systematists have recently employed the modern research methods now utilized by flowering plant systematists. These include scanning electron microscopy (especially to study spore ornamentation), chromosome counts, isoenzyme studies, and DNA analysis. These techniques are typically used together to corroborate or refute hypotheses based upon morphological evidence. All of the name changes described below are founded upon real, visible macromorphological evidence, though in some cases the differences may seem rather cryptic. In most cases, changes in interpretation have been confirmed by the use of these other types of chemical or micromorphological data. This article is organized by taxonomic level, first discussing changes at the family level, followed by new generic names, and last, changes in species' names.

The Demise of the Common Fern Family, the Traditional Polypodiaceae

A big change for readers most familiar with Flora of the Pacific Northwest (Hitchcock and Cronquist, 1973) is the splitting of the common fern family, Polypodiaceae, into a number of...
smaller, evolutionarily discrete family units. This is not a new interpretation, and the system adopted by The Jepson Manual and Flora of North America is not substantially different from that first presented nearly 50 years ago by the Chinese pteridologist R.C. Ching (Ching, 1940). It has become clear to pteridologists that the Polypodiaceae sensu lato contained a number of distinct evolutionary lineages without evident common ancestry. Much activity in recent decades has focused on gathering sufficient data to find agreement on exactly which groups represent distinct families, a difficult challenge when it is realized that the greatest diversity of ferns is found in poorly-collected tropical and subtropical regions. To some extent the traditional Polypodiaceae was a construct of temperate zone botanists. With recent botanical exploration and collecting in the tropics providing much additional data on tropical groups, there is now sufficient agreement on the natural groups or lineages that can be recognized at the family level. Though it is possible there will be a few “adjustments” in the future, it is safe to say that there is now general agreement toward the recognition of smaller, more discrete families.

Under the classification presented in The Jepson Manual and Flora of North America, the Polypodiaceae comprises only the genus Polypodium and its close relatives, most of which are tropical in distribution. Other families include the Aspleniaceae (represented in our flora by the genus Asplenium); Blechnaceae (Blechnum and Woodwardia); Dennstaedtiaceae (Pteridium); Dryopteridaceae (Athyrium, Cystopteris, Dryopteris, Gymnocarpium, Polystichum, and Woodwardia); Adiantaceae (called Pteridaceae in The Jepson Manual, with Adiantum, Aspidotis, Cheilanthes, Cryptogramma, Pellaea, and Pentagramma); and Thelypteridaceae (Phegopteris and Thelypteris).

The marsh ferns, Thelypteris, and wood ferns, Dryopteris, are good examples of unrelated lineages that in the past have been grouped because of similarities in frond outline and sorus characters. Both groups have reniform or kidney-shaped indusia. At one time they were combined into a single genus, but now they are placed in different families. Thelypteris species have two vascular bundles at the base of the petiole, hairs on the fronds, and base chromosome numbers of \(n=27\) to \(36\). Dryopteris species consistently have three or more vascular bundles in the petiole, no hairs on the fronds, and a chromosome base number of \(n=41\). These might not seem like major differences, but when compared with characteristics used to distinguish other fern groups, their magnitude and consistency suggest that the two lineages are not closely related.

New Names for Familiar Genera

Several of our familiar ferns and fern allies have been assigned new generic names. Most of these changes are a result of careful study of morphological and anatomical characters, and the data are strong enough that the splitting seems fairly well justified. One example is the familiar goldback fern, long known as Pityrogramma triangularis (Kaulf.) Maxon. The genus is primarily composed of a group of medium-sized tropical or subtropical species, such as \(P\). calomelanos (L.) Link, characterized by a yellow or white farinose indument on the underside of the fronds. Members of the western North American \(P\). triangularis complex possess the farinose indument, but are in many other ways anomalous in Pityrogramma. They are perhaps more closely allied to the group of genera related to Cheilanthes and Pellaea (Tryon and Tryon, 1982). In a review of the morphological, cytological, and chemical data, Yatskievych et al. (1990) concluded that differences between the \(P\). triangularis group and the typical species of Pityrogramma were so numerous that the common features, such as the yellow or white farinose indument, were probably the result of convergent evolution. They described the new genus Pentagramma for the western species of the \(P\). triangularis complex. Among the data supporting the separation of Pentagramma from Pityrogramma are the base chromosome number (\(x=30\) vs. \(x=29\)), characters of frond morphology and vein patterns, rhizome scales, number of vascular bundles in the stipes, and spore ornamentation. A study of the chemical constituents of the waxy farinose indument demonstrated that none of the major compounds found in Pentagramma are present in the species of Pityrogramma. While a full biosystematic study of the genus Pentagramma has not yet been conducted, it appears that only one taxon, \(P\). triangularis (Kaulf.) Yatskievych, Windham and Wollenweber ssp. triangularis, occurs in Oregon (Smith, 1980).

Clubmosses (Lycopodium sensu lato) are another group where recent workers have recognized segregate genera (Wagner and Beitel, 1992). Although the clubmosses share morphological similarities that immediately separate them from other groups of ferns and fern allies, Wagner and Beitel contend that groups
of lycopod species (typically treated as subgenera) have more differences among them than do different, related groups of ferns long recognized as distinct genera. Differences that separate major groups of clubmosses, which include anatomy, chromosomes, spores, life cycles, and ecology, are sufficient to recognize discrete genera.

In addition to the type genus, Lycopodium, the genera Diaphasiastrum, Lycopodiella, and Huperzia are also found in Oregon. Lycopodium now contains only the “typical” clubmosses, represented in Oregon by L. clavatum L., L. annotinum L., and L. dendroideum Michx. Hickey (1977) determined that L. dendroideum was the proper name for our taxon previously identified as L. obscurum L., which is restricted to eastern North America. The genus Diaphasiastrum is the group of species known as ground-cedar, represented in Oregon by D. complanatum (L.) Holub and D. sitchensis (Rupr.) Holub. The bog clubmoss, which occurs in Oregon primarily along the coast, will now be called Lycopodiella inundata (L.) Holub. While some will probably consider this a case of excessive splitting, I would urge botanical generalists to base their conclusions on the merits of the case rather than the difficulty of pronouncing new names.

The Mysteries of Reticulate Evolution

Many recently described species are members of allopolyploid species complexes (allo = different; polyploid = multiple sets of chromosomes). This type of evolution is common in ferns, and is initiated when two related but distinct species hybridize. Usually (though not always) the parents involved in formation of the hybrid are basic diploid species, with the standard two sets of chromosomes per cell. The initial hybrids are also diploid, and though they can grow into mature plants, they are unable to reproduce, because the spores they make are not viable because of genetic differences between the equivalent chromosomes that originated from each of the two parental species. These differences in chromosome

Huperzia miyoshiana

The last group of Oregon lycopods to consider are the fir clubmosses of the Lycopodium selago group, now placed in the genus Huperzia. These species are distinctive in that they produce gemmae in the upper leaf axils that disperse and grow into new plants. Hitchcock and Cronquist (1973) grouped all northwest plants into the single species L. selago. More recent research has shown that there are several other distinct species present in the Pacific Northwest, so the most up-to-date taxonomic of this group involves new generic and new species names. This group is represented in Oregon by Huperzia occidentalis (Clute) Beitel. It is found in northwestern Oregon in moist to boggy forests, where it often grows on rotting logs (Beitel 1986; Beitel and Mickel 1992). Huperzia occidentalis is distinguished from the other members of the H. selago complex by its broad, oblanceolate leaves that are spreading to reflexed, with papillate margins, and stems with marked annual constrictions (Beitel 1986). Other members of this complex, especially H. miyoshiana (Makino) Ching, may occur in northern Oregon. This species usually grows on rock outcrops or talus, has narrow, linear leaves that are spreading to ascending, is yellow-green in color, and has distinctive juvenile stems with recurved tips. These two species often produce sterile hybrids when they grow in proximity.
structure prevent the chromosomes from pairing and separating normally during meiosis (the type of cell division that occurs in the formation of spores.) An occasional abnormal cell division may occur in these sterile hybrids that results in doubling the chromosome set in a single reproductive cell. With double the complement of chromosomes, meiosis in the next generation of plants proceeds normally, because the duplicated chromosomes (which originated from the same parent) can pair with one another. When these fertile plants with double the chromosomes are able to reproduce sufficiently to sustain established populations, a new species is generated.

Fern taxa generated by this process are considered distinct species because they are reproductively fertile, morphologically differentiated, and reproductively isolated from the two original diploid parent species. Such species, when they have four sets of chromosomes per cell, are called allotetraploids. There can be allopolyploids with six sets of chromosomes (allohexaploid) or eight sets (allooctaploid) or more, although I am not aware of allopolyploid ferns in Oregon with more than four sets of chromosomes.

This type of speciation is referred to as reticulate evolution, because it represents the recombination of formerly divergent evolutionary lines into a third lineage that is a combination of the two parents. Given sufficient time, species that arise via reticulate evolution may spread to cover extensive geographic areas. In some cases, an allopolyploid may have a much wider geographic distribution than one or both of its diploid parent species. The reason for the success of established allopolyploids has been a subject of much discussion, but may be related to the ability of an allopolyploid to tolerate a wider range of conditions than either parent (Wagner and Wagner, 1980). Genetic characteristics of allopolyploids are generally expressed in an additive fashion, combining the features of both parents. Morphologically, this tends to be expressed as an intermediate condition. If one parent has fronds that are once-pinnate, and the other parent has fronds that are tripinnate, the allopolyploid will generally have fronds that are bipinnate. Where there are ecological differences between the two parents, allopolyploids may have the ability to occupy the habitats of both parent species as well as habitats that are intermediate between those of the parents. Thus an allopolyploid may be ecologically more versatile than either of its parents. While reticulate evolution may represent a sort of evolutionary cul-de-sac, allopolyploids can be very successful species, and even help to perpetuate genetic diversity by propagating a particular genetic line after one diploid parent has become extinct.

Some Examples of Reticulate Evolution in the Pacific Northwest

Like a surprise ending to a good detective novel, there is something satisfying about the discovery of a case of reticulate evolution where it has not been suspected. One case that has recently been brought to light is that of the northern maidenhair fern, *Adiantum pedatum* L. These maidenhair ferns are now understood to comprise an allopolyploid complex of two diploid species and one allotetraploid species (Paris and Windham, 1988). The currently accepted name for the representative present in Oregon and elsewhere in western North America is *A. aleuticum* (Rupr.) Paris (Paris, 1991). *Adiantum pedatum* proper is restricted to eastern North America. Both of these are basic diploid species, and though morphologically similar, they are distinguished by subtle characteristics of frond morphology. For example, the ultimate frond segments (pinnules) in *A. aleuticum* tend to be more elongate, with deeper and wider incisions on the upper (acroscopic) margin, compared to *A. pedatum*. Paris found that *A. aleuticum* also occurs in a few places in eastern North America within the general range of *A. pedatum*. In Vermont, populations of an allotetraploid originated from hybridization between *A. pedatum* and *A. aleuticum*, followed by chromosome doubling. This allotetraploid, named *A. viridimontanum* Paris, also provides corroborating evidence that *A. pedatum* and *A. aleuticum* are specifically distinct (Paris, 1991).

The oak ferns, *Gymnocarpium*, provide another example of reticulate evolution that was only recently deciphered. In this case, the well-known name, *Gymnocarpium dryopteris* (L.) Newm., applies to an allotetraploid species that is widespread across northern North America. The two diploid parents of *G. dryopteris* are found in the Pacific Northwest and the eastern U.S., respectively. *Gymnocarpium disjunctum* (Rupr.) Ching is the name of the northwest diploid, and the recently discovered eastern diploid has been named *G. appalachianum* Pryer and Haufler (Pryer and Haufler, 1993). The two diploid species are distinguished by subtle, but constant features of frond morphology. For example, in *G. appalachianum*, the second pair

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of pinnae is usually stalked, while in G. disjunctum it is always sessile. Unfortunately, the morphologically intermediate G. dryopteris tends to confuse the issue. With herbarium specimens, G. dryopteris can easily be distinguished from both diploid species by its significantly larger spores. In the field, identification can be more difficult, especially in regions such as the Pacific Northwest where G. dryopteris is sympatric with one of the diploids. In G. disjunctum, the first pairs of pinnae of the second and third pinnae are unequal in length; the lower, or basiscopic pinnae are longer. In G. dryopteris the first pairs of pinnae of the second and third pinnae are more or less equal in length. While G. disjunctum is by far the more common species in Oregon, there are apparently a few records of G. dryopteris in Oregon as well.

Patterns of reticulate evolution in Adiantum and Gymnocarpium are similar in many ways; there are also some significant differences. In Adiantum, the allotetraploid species is of limited distribution, and occurs only within the geographic area where the ranges of two diploid species overlap. In contrast, the allotetraploid in Gymnocarpium is very widely distributed, occurring in Europe as well as across North America. The two diploid species have relatively narrow geographic distributions that at present do not overlap. This evidence suggests that G. dryopteris originated at some time in the distant past, while A. viridimontanum is a relatively young species. It probably originated after the last ice sheet receded from northern North America, and has not had sufficient time to establish a wider geographic presence.

Several cases of reticulate evolution have been found in western North American species of polypody or licorice fern, Polypodium. This genus is a hotbed for reticulate evolution, and the P. vulgare L. complex in Europe was one of the first examples of reticulate evolution in ferns to be documented and described (Manton 1947). In the Pacific Northwest, Frank Lang demonstrated that the widespread western species P. hesperium Maxon was in fact an allotetraploid that originated via hybridization between the common licorice fern, P. glycyrrhiza D.C. Eaton, and a second diploid species, now known as P. amorphum Suksdorf, that occurs at higher elevations in the Cascades and coast ranges (Lang 1971). Polypodium glycyrrhiza is the common low-elevation species west of the Cascades, and grows on tree trunks, rocks, or soil banks. When growing on rocks, it is usually rooted in mats of moss on the tops of boulders or ledges, but not in crevices. Polypodium amor-

Another allopolyploid complex in the genus Polypodium relevant to the Oregon flora involves P. glycyrrhiza and a California species, P. californicum Kauff. These two diploid species have hybridized to form an allotetraploid species recently named P. calirhiza Whitmore and Smith, which extends north-

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In an interesting twist, Wagner found that the diploid species was first described as Neophrodium expansum in the 1840s by Presi, based upon a specimen collected on Vancouver Island in the 1790s. So even though our diploid species was only recently recognized as a distinct taxon based upon modern techniques, it was first collected and described over 150 years ago! Our common wood fern of moist forests is now known as D. expansa (Presi) Frasier-Jenkins and Jermy (Frasier-Jenkins and Jermy 1977).
Western North American representatives of the sword or holly fern genus, *Polystichum*, have been a subject of intensive study for over 30 years. Many of our species, including *P. californicum*, *P. knuckebergii*, and *P. scopulinum*, are known to be allotetraploid species representing various combinations of diploid species present in the region (W. Wagner 1973). David Wagner (1979) concluded that the sword fern of dry, rocky habitats, *P. imbricans* (D. Eaton) D. Wagner, is a distinct species from the common sword fern *P. munitum*, and not a variety. Because *P. munitum* has been implicated as one of the diploid parents in several allopolyploid species, this brought up the question of whether *P. munitum* or *P. imbricans* was involved. Contrary to what might have been expected, isoenzyme and DNA investigations have indicated that it was *P. imbricans*, and not the more common *P. munitum*, that was one of the two diploid parents of both *P. californicum* and *P. scopulinum* (Soltis et al. 1991).

Another taxonomic conclusion that came out of Wagner's research was that our serpentine endemic is not *P. mohrioides* (Bory) Presl, a species that occurs in the southern hemisphere, but is a separate species that should be called *P. lemmonii* (D. Wagner 1979).

Newly Described Oregon Fern Species

In my graduate research, I studied the parsley-fern genus, *Cryptogramma*. I concluded that our common North American species is properly called *C. acrostichoides* R. Br., and it is clearly distinct from the European parsley fern, *C. crispa*. In addition, I described a second diploid species from western North America, *C. cascadensis* Alverson (Alverson 1989). This new species is found in the Cascade, Sierra Nevada, and northern Rocky Mountains, where it tends to occur at higher elevations or in more mesic habitats than *C. acrostichoides*. Cryptogramma cascadensis is distinguished by a set of subtle morphological characters. For example, the pinnules tend to be cuneate rather than ovate, the fronds are deciduous in the fall rather than green through the winter, and the frond color is a lighter shade of green. Isoenzyme analysis provided evidence of substantial genetic differences between the two species.

The moonworts of *Botrychium* subgenus *Botrychium* are among the rarest and most fascinating ferns. These plants are seldom collected and are poorly represented in herbaria. In addition, they often occur in mixed populations, so it is not uncommon for specimens on a single herbarium sheet to represent more than one taxon (Wagner and Wagner 1983). As a result, past taxonomic treatments have been rather superficial, and have not recognized a number of interesting and distinctive morphological types. Over the past several decades, this group has been the subject of intensive field and lab research, particularly by W.H. (Herb) Wagner, his wife Florence, and their students and colleagues. This research has resulted in the description of many new species, some of which were first discovered in Oregon. Among these are *B. ascendens* Wagner, related to the widespread species *B. lunaria* (L.) Swartz, but a more delicate plant with fewer pairs of pinnae (Wagner and Wagner 1981). *Botrychium montanum* Wagner is a small, inconspicuous species in cedar swamps and other shady forests (Wagner and Wagner 1981), and probably survives in such shaded habitats through a beneficial relationship with a mycorrhizal fungus. *Botrychium crassirhizum* Wagner, also related to *B. lunaria*, has narrower pinnae that are angled upward (Wagner and Wagner 1986). *Botrychium pedunculosum* Wagner is related to *B. pinnatum* St. John (see below) but has a pedunculate sterile segment and a gray-green color (Wagner and Wagner 1986). The type localities for the latter two species are from the Wallowa Mountains in northeastern Oregon.

In addition to describing new species, the Wagners have re-interpreted the names of some other fairly well-known taxa. For example, they believe that *B. boreale* Mildes only occurs in Europe, and *B. pinnatum* is the appropriate name for the related species in western North America. *Botrychium lunaria* var. onondagenese (Underw.) House properly refers only to a shade form of *B. lunaria*. Most plants that key to this in Flora of the Pacific Northwest are actually *B. minganense* Victorin, another species in the *B. lunaria* group (Wagner and Lord 1956). While much new information has been obtained on Oregon botrychiums, it is clear that a great deal of work remains to be done.

A group related to *Botrychium* is the adders-tongue genus, *Ophioglossum*. Our species has in the past been called *O. vulgatum*, a species found in Europe but not North America. Based upon a number of morphological features including leaf shape, color, texture, and spore size, Wagner has concluded that the plants found in the Pacific Northwest belong to a species called the northern adders-tongue, *O. pusillum* Raf.
Botrychium paradoxum

(Wagner 1971). This taxon is found across the northern portions of North America. Another segregate of O. vulgatum is found in the eastern and southeastern U.S.

Of all the name changes recently proposed for Oregon ferns and fern allies, only a few of the new names are mandated by the regulatory framework of plant taxonomy. Following the latest taxonomic advice available at the time, Hitchcock and Cronquist (1973) used the name Athyrium distentifolium for the mountain lady fern, rather than the traditional name, A. alpestre. Lellinger (1981) has concluded that A. alpestre is the oldest applicable name after all, and that our plants are properly called A. alpestre (Hoppe) de Claireville ssp. americanum (Butters) Lellinger. The green spleenwort, formerly known as Asplenium viride Huds., is properly referred to an older name, A. trichomanes-ramosum L. Earlier authorities rejected the latter name because of confusion with A. trichomanes L., which is a different species also found in Oregon. Lellinger (1981) pointed out that the hyphenated form is not a valid basis for rejecting a name, as there are examples of other well-known ferns that have hyphenated specific epithets. Aspleniun trichomanes-ramosum is one of the rarest ferns in Oregon, known only from a single colony at timberline in the Wallowa Mountains (Zika 1988).

Why is it important to learn these new names? Names are crucial to our ability to learn, describe, and communicate knowledge and experiences, and thus improve our ability to observe, distinguish, and comprehend. Are all these changes really justified? To those who are not regular readers of the scientific literature, the number of changes described in this article may seem excessive. It is only natural to be skeptical when new, unpronounceable epithets replace familiar and time-honored names. I would hope that nomenclatural changes based on new information regarding evolutionary relationships would be supported by evidence that makes a compelling case for change. It would be overly cavalier to do otherwise. If supporting evidence is sufficiently strong, there is no place for taxonomic sentimentality. Science and natural history are all about discovery, and those who prefer tradition over progress may be missing the most interesting part of the program.

### Table 1. “New” names for northwest pteridophytes due to revised generic or species concepts and/or clarification of species concepts where the old name refers to a taxon not found in Oregon. In some cases these are actually newly-described species names, but others are names that had been described earlier but were not recognized by Hitchcock and Cronquist.

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