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Ferns of the Wallowa Mountains, Oregon

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Oregon's Wallowa Mountains are one of the most scenic mountain ranges in the Pacific Northwest, with snow-capped peaks, dramatic river canyons, and classic glacial topography. Located in the northeastern corner of Oregon, the botanical diversity of the Wallowa flora is also well known, with its endemic and noteworthy species, as well



Fig. 1. Calcareous headwaters of Middle Fork Imnaha River, a remote basin where Cusick found green spleenwort (*Asplenium trichomanes-ramosum*). Photo by Peter Zika.

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as its significant Rocky Mountain floristic element. Some of the latter are disjunct species not known elsewhere in Oregon (Mason 1980). In addition, the Wallowa Mountains are a diversity hotspot in western North America for ferns and other vascular cryptogams (non-flowering plants including horsetails, clubmosses, spikemosses, and quillworts), of which botanists have documented 56 species, subspecies, or varieties (Mason 1980, Zika and Alverson 1996). (See list at end of article.) This total includes 42 taxa of ferns, as well as an additional 14 species of horsetails, clubmosses, spikemosses, and quillworts. In addition to describing this diversity, we will hypothesize the reasons for it, and tell the stories of botanists who have explored the Wallowas.

The Wallowa Mountains trend northwest to southeast, between the Baker and Wallowa valleys in Baker, Union, and Wallowa counties, Oregon. The range is approximately 50 miles long and 20 miles wide, and with elevations from 3000 to 9838 feet (at the summit of Sacajawea Peak). The topography was extensively glaciated during the Pleistocene, and Wallowa Lake is considered a classic example of a lake formed by the moraine of a valley glacier.

Geological Origins

According to geological researchers of plate tectonics, the Wallowa Mountains began as islands off the Pacific Coast. During the Permian era, some 260 million years ago, rocks that later became our inland mountains were part of an island arc in the Pacific Ocean called Wrangellia. The islands comprised volcanic, sedimentary (e.g., limestone), and metamorphic rocks. Drifting eastward, the islands eventually collided (in slow motion) with the North American Plate 115 to 145 million years ago. That subduction at the margin of the North American Plate created granitic batholiths (coarse-grained rock formations created by melting of the earth's crust and subsequent slow cooling 2 to 20 miles below the surface, Bishop 2003). The largest of these, the Wallowa batholith, forms the central high country of the Wallowa Mountains. During the middle of the Miocene period (about 15 million years ago), extensive floods of liquid basalt flowed out over the Northwest. Rearranged by tilting, folding, and uplifting, these basalt flows formed the western and northern topography of the Wallowa Mountains. The complex geology of sedimentary, metamorphic, granitic, and basaltic rocks contributes to a variety of substrates (e.g., acidic, basic, calcareous) for diverse habitats.

Fern Diversity: Climate and Substrates

Mountain ranges typically have relatively high numbers of ferns in their floras, for several reasons. Altitudinal zonation produces a variety of climatic zones within a small geographical area. Mountain ranges typically have higher annual precipitation than adjacent lowlands; water is a critical factor for fern reproduction. An abundance of rocky

substrates in mountainous areas also favors many fern species. Fern gametophytes face less competition during establishment in rock crevices or under rock overhangs than on soils where other vegetation thrives. The great variety of bedrock types in the Wallowa Mountains fosters a diversity of ferns. Basic (high pH) rocks tend to be uncommon in Pacific Northwest mountains; limestone, marble, and other calcareous rocks are particularly important to the subset of ferns known as “calciphiles.” More habitats are created by the presence of acidic rocks that form suitable habitat for species that avoid calcareous substrates: “calcifuges.”

Fern Collectors in the Wallowas

The Wallowa Mountains were a favorite haunt of William C. Cusick, who collected there from about 1878 through 1910 (Love 2007). Cusick collected at least 13 fern species from the Wallowas, and was the first to document a number of rare or disjunct species, including green spleenwort (*Asplenium trichomanes-ramosum*). Although other collectors passed through during the early to mid 20th century, Georgia Mason (1910-2007) of the University of Oregon was Cusick’s successor in thoroughly botanizing the region. Her 1975 flora (revised in 1980), “A Guide to the Plants of the Wallowa Mountains of Northeastern Oregon,” was the culmination of over a decade of fieldwork. She recorded thirty ferns and other vascular cryptogams in the first edition of the book, and added five species in the second edition. David Wagner, Director of the University of Oregon Herbarium from 1976 to 1993, started collecting there in the late 1970s and provided many of the revisions in the second edition of Mason’s book.

We began our fieldwork in the Wallowas in the 1980s: Zika as a botanist for the Oregon Natural Heritage Program, and Alverson by invitation to join Michigan botanists W.H. (Herb) and Florence Wagner (no relation to David Wagner) in their field studies of moonwort (*Botrychium*). The Wagners, studying moonworts throughout North America, chose the Wallowa Mountains as one of their key localities because of the high diversity of moonworts. They ultimately published three new species of moonworts with type localities in the Wallowas; details are given later in this article. We were fortunate to join Herb and Florence during a number of their field trips in the Wallowa Mountains, and every outing was a wonderful learning experience. At the same time, we kept our eyes open for additional ferns that had not previously been collected in the Wallowas, and published our results in a paper in the American Fern Journal (Zika and Alverson 1996). Our documentation of 56 taxa of ferns and other vascular cryptogams in the Wallowa Mountains amounts to over half the taxa of ferns, horsetails, clubmosses, spikemosses, and quillworts found in Oregon. The number of fern species makes this one of the most diverse fern localities in western North America.



Fig.2. Peter Zika with Drs. Herb and Florence Wagner, viewing Paradox moonwort (*Botrychium paradoxum*) at the first known locality for Oregon in August 1993. Since then it has been found in several other localities in the Blue and Ochoco Mountains. Photo by Ed Alverson.

Hunting for Rare Ferns



Fig. 3. Martin Bridge limestone, shown here with a dark volcanic intrusion near Cusick Mountain, supports calciphiles like *Cryptogramma stelleri*. Photo by Peter Zika.

Ferns reproduce by small, light spores, which have the ability to disperse long distances and form remote or disjunct colonies. As a result, ferns are often well represented on state rare plant lists. Several of Oregon's rare fern species were, until recently, known in Oregon only from historic records in the Willows. However, diligent field work by Peter Zika has confirmed that two of these are still extant members of the Oregon flora. One of these species, which is known from throughout its range to be restricted to moist, usually calcareous, rocky habitats, is Steller's rock brake (*Cryptogramma stelleri*). Frye (1934) first reported this fern from the Willows, but we could not locate a voucher specimen in any herbarium to confirm this sole record

of the species in Oregon. The mystery was solved in 1993 when Peter found a small population of Steller's rock brake on moist, north-facing limestone rocks in the Hurricane Creek drainage.

Similarly, green spleenwort (*Asplenium trichomanes-ramosum*, formerly *A. viride*) was known in Oregon from a single 1908 Willows Mountain collection by W.C. Cusick, but no one had been able to relocate the population. Cusick's enigmatic label read simply, "headwaters of the Imnaha, 9000 feet alt." In 1987, Peter Zika spent many days exploring the four upper forks of the Imnaha, which included six peaks, many ridges, and roughly 6 square miles of wilderness terrain above 9,000 feet, looking for the green spleenwort without success. Eventually Peter spotted a likely cirque, in fact, the only cirque with limestone cliffs shaded at mid-day. On those steep and cool north-facing exposures, at a slightly lower elevation than expected (7,550 ft.) were 47 clumps of the little evergreen spleenworts, clinging to the cliffs with other boreal species like *Salix vestita* and *Saxifraga oppositifolia*. They were a welcome sight, which lightened Peter's steps considerably on the two-day hike back out to the trailhead.



Fig. 4. One of the many trail-less peaks investigated in the high Willows while searching for Cusick's station of green spleenwort (*Asplenium trichomanes-ramosum*). Zika's tent is in foreground. Photo by Peter Zika.



Fig. 5. Martin Bridge limestone cliffs with the long-lost population of green spleenwort (*Asplenium trichomanes-ramosum*) at the headwaters of the Imhana River. Photo by Peter Zika.

Fern Families

Fern nomenclature has been in flux for the past several decades (Alverson 1993). Comparing the treatment of fern families in *Flora of the Pacific Northwest* (Hitchcock and Cronquist 1973) with *Flora of North America* (FNA) (1993), the most obvious difference has been the recognition in FNA of a large number of segregate families that were previously placed in a broadly circumscribed Polypodiaceae. These families include Aspleniaceae, Dennstaedtiaceae, Dryopteridaceae, Pteridaceae, and Woodsiaceae

Analysis of variation of mutations in DNA has greatly facilitated the circumscription of fern families in recent years. In 2006, Smith and others proposed a further refinement of family boundaries to create a new family (Woodsiaceae) composed of genera previously allied with *Dryopteris* and *Polystichum*.

Spleenwort Family (Aspleniaceae)

As mentioned above, the green spleenwort (*Asplenium trichomanes-ramosum*) is the sole representative of this family in the Wallowa Mountains. It is widely distributed around the northern hemisphere, but in western North America it is only known from widely scattered localities, mostly in the northern Rocky Mountains. It is often found on limestone but is not restricted to this rock type.

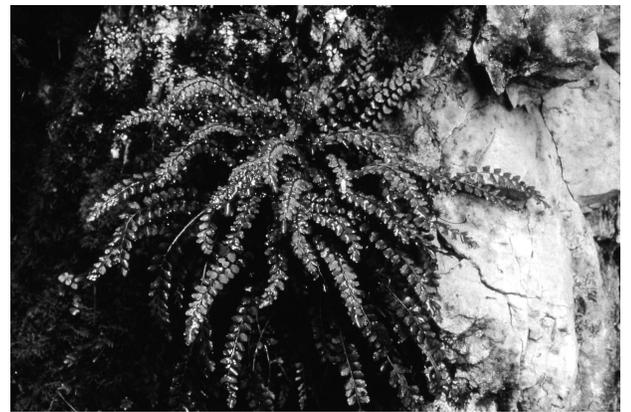


Fig. 6. *Asplenium trichomanes-ramosum* is known to occur in Oregon only in the Wallowa Mountains. Photo by Ed Alverson.

Polypody Family (Polypodiaceae)

In the Pacific Northwest, we have only one genus in the now narrowly circumscribed family Polypodiaceae: *Polypodium*. In the Wallawas, this genus is represented by one species, western polypody (*P. hesperium*), which is found on mossy rocks and cliffs at middle elevations, where its creeping rhizome can send roots down in to sheltered rock crevices.

Maidenhair Fern or Brake Family (Pteridaceae)

Western maidenhair (*Adiantum aleuticum*) is a widespread western fern that has been recently split from the eastern maidenhair fern (*Adiantum pedatum*). It prefers moderately moist forested or rocky sites; most of the records from the Wallawas are from shady mossy stream banks and similar moist habitats.

Although substrate preferences are important determinants of fern distribution in the Wallawas and elsewhere, they are not always absolute indicators. The small rock fern known as Indian's Dream (*Aspidotis densa*) is strongly associated with ultramafic rocks (e.g., serpentine and peridotite), but is not restricted to this habitat. In the Wallawas, where there is no serpentine, it occurs on granitic rocks. Several other rock ferns that grow on granitic substrates include lace fern (*Cheilanthes gracillima*) and American and Cascade parsley ferns (*Cryptogramma acrostichoides* and *C. cascadiensis*). Although Steller's rock brake (*Cryptogramma stelleri*) is a calciphile, *C. acrostichoides* and *C. cascadiensis* are calcifuges. Cascade parsley fern is not found in Mason's flora, or in *Flora of the Pacific Northwest*, because it was first described by Ed Alverson in 1989. It is a species primarily of the Cascade Mountains (the type locality is in the Cascades east of Seattle), but it also occurs in scattered sites in the northern Rocky Mountains. Sterile fronds are deciduous in Cascade parsley fern, compared to wintergreen fronds in American parsley fern. There are several microscopic differences, as well as strong genetic differences, seen in analysis of enzyme variation (Alverson 1989).

Cliff-brakes (*Pellaea*) are related to the lace fern and grow in similar dry, rocky habitats. These are generally small, densely tufted ferns with leathery, glaucous foliage and wiry leaf petioles. In the Wallowa Mountains, two cliff-brake species, Brewer's (*Pellaea breweri*) and Bridges' (*P. bridgesii*), grow in mid-elevation rocky habitats. Bridges'



Fig. 7. *Aspidotis densa*. Photo by Ed Alverson.



Fig. 8. *Pellaea breweri*. Photo by Ed Alverson.

cliff-brake has oval, undivided pinnae, differing from those of Brewer's cliff-brake that are mostly divided into two or three lobes. Brewer's cliff-brake is widely distributed in the Great Basin and Rocky Mountain regions, extending westward to scattered locations in eastern Oregon and Washington. Over its range, it grows on a variety of substrates, but prefers calcareous rocks, its primary substrate in the Wallawas. In contrast, Bridges' cliff-brake grows primarily argillite (a type of sedimentary rock) or occasionally granitic. Its distribution is centered in the Sierra Nevada Mountains of California, with disjunct populations in the Wallawas and nearby Idaho.

Wood Fern Family (Dryopteridaceae)

Wood ferns (*Dryopteris*) are typically large ferns of moist forest habitats. The two species found in the Wallowas are spreading wood fern (*Dryopteris expansa*) and male fern (*D. filix-mas*). Spreading wood fern is widespread in the Pacific Northwest, as well as elsewhere in northern latitudes in both the new and old world. In the Pacific Northwest it is most common in moist forests west of the Cascades. Male fern is also a widely distributed northern species, but in the Pacific Northwest is an uncommon fern of moist rocky mountainous terrain

Eight species of sword or holly fern (*Polystichum*) grow in Oregon, and six occur in the Wallowa Mountains. This is as great a concentration of *Polystichum* species as anywhere in North America. The western sword fern (*Polystichum munitum*) is a typical fern of mesic forest habitats west of the Cascades, but is also widespread (though less common) in forested habitats east of the Cascades, and is known from several localities in the Wallowas. In 1992 we found a small colony of Anderson's sword fern (*Polystichum andersonii*), another moisture loving sword fern that had not previously been reported from the Wallowas. The small colony we found was growing at about 5,250 ft. elevation under Engelmann spruce (*Picea engelmannii*) in a moist canyon bottom. This species has more finely dissected fronds than western sword fern and occurs primarily in British Columbia and southeastern Alaska. Anderson's sword fern also occurs in Washington, Idaho and Montana, but Oregon is the southern limit of its range.



Fig. 10. *Polystichum kruckebergii* is uncommon in rocky subalpine habitats throughout its range in the Pacific Northwest. Photo by Ed Alverson.



Fig. 9. Peter Zika proudly displaying a prize specimen, the first collection of *Polystichum andersonii* from the Wallowas. Photo by Ed Alverson.

Four species of *Polystichum* in the Wallowas are associated with rocky habitats, often on granitic substrates. Imbricate sword fern (*Polystichum imbricans*) is a once-pinnate species closely related to western sword fern, but grows in drier, more open habitats. Imbricate sword fern, rare east of the Cascades, is known from one collection in the Wallowas, where it grows on granitic rocks at 7,200 ft. elevation in the upper portion of the Eagle creek drainage in Baker County. The teeth along the leaf margins of mountain holly fern (*Polystichum lonchitis*), another once-pinnate fern, are spiny, resembling holly leaves. It is found only at higher elevations in mountainous regions, and is widespread around the northern hemisphere. Although elsewhere it is considered a calciphile, most of the documented sites in the Wallowas are on granitic rocks. Two additional related species, rock sword fern and Kruckeberg's holly fern (*P. scopulinum* and *P. kruckebergii*) grow in rocky subalpine habitats near Ice lake and China Cap Peak, respectively. Both species are small ferns with pinnae that are incised or pinnatifid. The pinnae of Kruckeberg's holly fern are shorter than those of rock sword fern, and have teeth along the margins that are spiny like those of mountain holly fern. Both species often occur on serpentine soils elsewhere in their range, but in the Wallowas occur on other rock types.

Bracken Fern Family (Dennstaedtiaceae)

Bracken (*Pteridium aquilinum* var. *pubescens*), the primary taxon found in the Pacific Northwest, is either one of the world's most widely distributed vascular plant species, or is a global complex of closely related species and varieties. In the Wallawas it occurs in forests and meadows, mostly at middle elevations, on granitic and possibly other substrates.

Cliff Fern Family (Woodsiaceae)

Genera in the Woodsiaceae are characterized by small to large, usually soft-textured fronds, including the lady ferns (*Athyrium*), oak ferns (*Gymnocarpium*), fragile ferns (*Cystopteris*), and cliff ferns (*Woodsia*). Our species of the latter two genera are often confused, being small, clumping, twice pinnate ferns with ovate-lanceolate frond outlines. Cliff ferns have firmer-textured, evergreen fronds, often grow in more exposed or xeric habitats, and have brown (rather than green or straw colored) stipe bases, as compared to fragile ferns. Both cliff fern species in Oregon (Laurentian cliff fern and Oregon cliff fern, *Woodsia scopulina* ssp. *laurentiana* and *W. oregana* ssp. *oregana* respectively), are found in the Wallawas, where they usually grow over basaltic rocks. Both species are widely distributed polyploid complexes with their different chromosome races recognized as subspecies.

If the number of specimens in the OSU herbarium is a measure, fragile fern (*Cystopteris fragilis*) may be the most common fern in the Wallowa Mountains. It typically occurs on rocky slopes or cliff crevices where water seeps out, at least early in the growing season.

Northwestern lady fern (*Athyrium filix-femina* ssp. *cyclosum*) is common and widespread in moist, shady locations. Some lady fern collections from the Wallawas have been determined as *Athyrium filix-femina* ssp. *californicum*, a subspecies with narrower fronds that is typically found in the Sierra Nevada mountains of California. A subalpine version (*A. alpestre*) grows in mountainous regions of the Pacific Northwest. The typical form of subalpine lady fern is found in Europe, and our plants are called var. *americanum*. Subalpine lady fern grows in concave microsites where snow drifts persist late into the summer; it has been reported from both granitic and basaltic substrates in the Wallowa Mountains.

Another fern on moderately moist sites is northwestern oak fern (*Gymnocarpium disjunctum*). This is a fern of moist, shady forest habitats, more commonly west of the Cascades, but occasionally in inland mountains as well. *Gymnocarpium disjunctum* is a diploid species that has been recognized as distinct species from the tetraploid common oak fern, *Gymnocarpium dryopteris*, which is not known to occur in Oregon.



Fig. 11. Mesic conifer forests in the canyon bottoms may support lush fern carpets of *Athyrium filix-femina* var. *cyclosum* and *Gymnocarpium disjunctum*. Photo by Ed Alverson.

Other Vascular Cryptogams

Horsetails (Equisetaceae), clubmosses (Lycopodiaceae), spikemosses (Selaginellaceae), and quillworts (Isoetaceae) are vascular cryptogams that traditionally have been categorized as “fern allies.” This term is now considered to be imprecise, because new evidence suggests that the clubmosses, spikemosses, and quillworts are only remotely related to the ferns, and in fact are a basal lineage that is sister to all of the other extant vascular plants. According to this view, however, the horsetails are fairly closely related to the true ferns (Smith *et al.* 2006).

Horsetails and Scouring Rushes

The Wallowa Mountains are home to four species of *Equisetum*. The common weedy field horsetail (*Equisetum arvense*) is widely distributed in moist habitats. Of the three species of scouring rushes, common, smooth and variegated (*Equisetum hyemale*, *E. laevigatum*, and *E. variegatum* ssp. *variegatum*), the first two are common and widespread in Oregon, but variegated scouring rush is rare. In Oregon, it seems to be associated with montane calcareous habitats, especially the silty floodplains of turbulent streams such as Hurricane Creek.

Clubmosses

Clubmosses (Lycopodiaceae) are mostly northern species that extend southward to Oregon. In the Wallowas there are two occasional species of clubmoss, stiff clubmoss (*Lycopodium annotinum*) and Alaska clubmoss (*Diphasiastrum sitchense*). In addition, Dave Wagner collected a fir clubmoss, *Huperzia occidentalis*, in the Lostine River drainage in 1992. The fir clubmosses were previously included in *Lycopodium* but differ from other lycopods in lacking horizontal stems (rhizomes), having sporangia borne in the axils of un-modified leaves, and by producing gemmae from which new plants can be produced vegetatively.

Alaska clubmoss is a species of rocky subalpine parkland, while stiff clubmoss and fir clubmoss are found in shady, moist conifer forests at middle elevations.

Quillworts

Four species of quillworts have been collected in the Wallowa Mountains: *Isoetes bolanderi*, *I. tenella*, *I. howellii*, and *I. occidentalis*. These primarily aquatic plants typically are rooted in the bottom of shallow lakes and ponds. In the Wallowas great numbers of *I. howellii* can be stranded by falling water levels in late summer or early autumn, forming a green turf. Quillworts look like little tufts of linear leaves and are distinguished, in large part, by the ornamentation of the megaspores.



Fig. 12. Although quillworts (*Isoetes*) are usually considered aquatic, they can be found on dry ground when stranded by dropping lake levels in the granitic zones of the Wallowas. Here, hundreds of *Isoetes* form a thin turf to the left of the large sedge clumps. Photo by Peter Zika.

Spikemosses

Spikemosses (*Selaginella*) are similar to clubmosses, but differ in being heterosporous, producing both relatively large megaspores along with smaller microspores (*Isoetes* are also heterosporous). Most North American *Selaginella* species are southern, and they are particularly diverse in the mountains of the American southwest and adjacent Mexico. Three species grow in the Wallowas. Wallace's spikemoss (*Selaginella wallacei*) is a lower elevation species; Alpine spikemoss (*S. watsonii*) and Rocky Mountain spikemoss (*S. scopulorum*) are primarily subalpine. All three grow in open rocky habitats, often on granitic rocks, where they form small moss-like mats. Distinguishing the different species is often difficult due to their compact growth, which obscures the critical leaf bases.

Grape Ferns, Moonworts, Rattlesnake Ferns, and Adder's-tongues

Finally, the most fascinating ferns in the Wallowas are the species of the Ophioglossaceae, including the grape ferns, rattlesnake ferns, and moonworts of the genus *Botrychium*, and the adder's-tongues of the genus *Ophioglossum*. These primitive ferns, along with the mostly subtropical whisk-ferns (*Psilotum*), form the basal lineage that is sister to all other extant ferns (Smith *et al.* 2006).

The northern adder's-tongue, *Ophioglossum pusillum*, has only recently been discovered in the Wallowas. It was collected in 2004 in the Eagle Creek drainage at an elevation of about 4800 feet, where it was growing in a moist meadow. This is an uncommon species in Oregon, known from only about 10 localities.

One of the reasons for high fern diversity in the Wallowa Mountains flora is the 15 species of grape ferns and moonworts. Thirteen of them are moonworts (subgenus *Botrychium*). This is possibly the greatest concentration of *Botrychium* species found anywhere in the world, including the type localities for three species described as recently as the 1980's and 1990's. A key aspect of the Wagners' research on *Botrychium* was the "genus community method" (Wagner and Wagner 1983) as a tool for comparative analysis to determine which morphological features have a genetic basis, as opposed to morphological variation resulting from differing environments. Because so many species of *Botrychium* occur together here, the Wallowas proved to be an important site for their research. In fact, 7 of the 15 species of *Botrychium* found in the Wallowas were described as new species by the Wagners.

Two of the species are widespread and common throughout a broad geographic range, leathery grape fern (*Botrychium multifidum*) and rattlesnake fern (*B. virginianum*). Three moonworts that are rare elsewhere, triangle moonwort (*Botrychium lanceolatum* ssp. *lanceolatum*), northwestern moonwort (*B. pinnatum*), and least moonwort (*B. simplex*), are relatively common and widespread in the Wallowas.

In 1986, the Wagners described two new species of moonworts from the Wallowa Mountains (Wagner and Wagner 1986). Upswept moonwort (*Botrychium ascendens*), with its type locality along Hurricane Creek, is related to common moonwort (*B. lunaria*), but has cuneate rather than lunate segments on the sterile fronds, orthophlores. Stalked moonwort (*Botrychium pedunculatum*), with its type locality in the Lostine drainage, is related to the northwestern moonwort (*Botrychium pinnatum*), but the stalk of its trophophore



Fig. 13. Herb and Florence Wagner in the Hurricane Creek canyon in 1983, while collecting the type specimen of *Botrychium ascendens*. Photo by Ed Alverson.



Fig. 14. The type locality for *Botrychium ascendens* is a montane meadow surrounded by groves of lodgepole pine and Engelmann spruce. Photo by Ed Alverson.



Fig. 15. Triangle moonwort (*Botrychium lanceolatum*), which is widely distributed in the northern parts of North America, is one of the more common moonworts in the Wallowas. Fig. 16. Upswept moonwort (*Botrychium ascendens*) was described by the Wagners in 1986, based upon type material from the Hurricane Creek drainage in the Wallowas. Fig. 17 Common moonwort (*Botrychium lunaria*) is the world's most widespread moonwort, occurring throughout the northern hemisphere, including the remote Azores and Commander Islands, as well as in scattered localities in the southern hemisphere. Photos by Ed Alverson.

is decidedly longer. Since their discovery in the Wallowas in the early 1980s, both *B. ascendens* and *B. pedunculatum* have been found in widely scattered locations across mountains of western North America, so they are not Wallowa endemics, but they are still rarities indeed.

The third moonwort with a type locality in the Wallowa Mountains was described in 1994, thus post-dates the publication of the Pteridophyte volume of *Flora of North America*. In 1992, while surveying for moonworts in the Lostine River Valley, we found a small population of a very distinctive moonwort with odd, linear shaped segments on the trophophore. We called it the "skinny" moonwort. Certain that we were the first to discover this new species of moonwort, we reported our find to Herb Wagner. He replied that, unknown to us, he knew all about this undescribed moonwort and had collected it in the Hurricane Creek valley in 1981. He had subsequently located herbarium specimens from scattered localities across northern North America, from California to Idaho, Colorado, and Quebec. Because the Wallowa Mountain population was especially vigorous and showed the distinctive characteristics of the species quite well, the Wagners accompanied us to the site in 1993 and collected the specimen they designated as the type (Wagner and Wagner 1994) of the new species, the slender moonwort, *Botrychium lineare*. A related species, the prairie moonwort (*Botrychium campestre*), is known primarily from the northern Great Plains, though a single disjunct population of *B. campestre* was found in the Hurricane Creek valley, which is 560 miles from the nearest site in Alberta (Zika and Alverson 1996).

Four other moonwort species found in the Wallowas are also relatively recently described or recently recognized taxa. They include the scalloped moonwort (*Botrychium crenulatum*) and Mingan moonwort (*Botrychium minganense*)



Fig. 18. Slender moonwort (*Botrychium lineare*) was described in 1996, based upon material collected at the type locality in the Lostine River drainage in the Wallowa Mountains. Fig. 19. Western moonwort (*Botrychium hesperium*) is a member of the Rocky Mountain floristic element that occurs in the Lostine River drainage in the Wallowas. Fig. 20. *Botrychium paradoxum*, a rare species of the Rocky Mountain region, is unusual because it produces sporangia on the portion of the plant that would normally be the sterile leaf blade. Photos by Ed Alverson.

(which form a group along with *B. lunaria* and *B. ascendens*); western goblin (*Botrychium montanum*), and western moonwort (*Botrychium hesperium*), which is most closely related to *B. pinnatum* and *B. pedunculatum*. All of these species typically occur in rocky meadows or open lodgepole pine woodland at middle elevations in the Wallowas.

By far the most unusual moonwort in the Wallowas is the paradox moonwort (*Botrychium paradoxum*). In this species trophophores have been entirely converted to a second fertile segment, with no sterile lamina to speak of. We observed one patch of *B. paradoxum* for several years and found that its morphology remained constant, showing it is not merely a mutant or odd growth form of another species (Zika and Alverson 1996). Our find of this species in the Lostine River drainage was the first locality where *Botrychium paradoxum* had been found in Oregon, but it has since been discovered in several other sites in the Blue and Ochoco Mountains, and also is known to occur in Utah, Montana, Saskatchewan, Alberta, and British Columbia (Ahrensleger and Lesica 1996). A recently described moonwort, *B. yaaxudakeit* (yah-KOO-dah-kit) described from the Yakutat, Alaska area (Stensvold et al. 2002), still needs verification in the Wallowas. This species is related to *B. lunaria*; a specimen exhibiting the chemical profile of this new species was included in a recent sample from Hurricane Creek, but field identification is needed before verifying that this taxon is a member of the Wallowas (and Oregon) flora. Clearly, the need continues for additional field investigations of moonworts in the Wallowas.

Over the years, we have puzzled over the question of why there are so many moonworts species in the Wallowa Mountains. For the most part, their habitats are not particularly unusual, but are typically montane meadows with a low growing grasses and forbs, usually with scattered trees nearby (particularly lodgepole pine and Engelmann

spruce). Invariably we find extensive colonies of wild strawberry (*Fragaria virginiana*) in these meadows, so we call them strawberry meadows. We suspect that the presence of calcareous substrates promotes moonwort species richness in these meadows. Where moonworts occur, the substrate is typically composed, at least in part, of alluvially transported calcareous boulders that originated on the limestone outcrops of the high ridges. The populations along the Lostine River occur in particularly complex habitats, where the substrate is a mix of alluvium and glacially transported rocks that originated from the range of bedrock types that occur in the upper Lostine drainage. Still, it appears that the presence of limestone and other calcareous materials appears to be correlated with moonwort species diversity. We have noted this pattern elsewhere, for example, in northeastern Washington, another moonwort hotspot in the Pacific Northwest, where calcareous bedrock is also widespread.



Fig. 21. The calcareous outcrops around and above Ice Lake support a number of unusual plants, including some *Botrychium* species. Photo by Peter Zika.

Overall, we hypothesize that a variety of factors that promote the high number of fern species that occur in the Wallowas. First, the topographic diversity, from relative low elevation valley bottoms to high peaks that are nearly 10,000 feet in height provides for a variety of vegetation and climatic zones. Second, the variety of bedrock types, significantly more varied than other mountain ranges in Oregon, promotes diversity of species that are associated with different rock types. Third, the Wallowas occur in a transition zone between two floristic regions, the Cascadian (or Vancouverian) and Rocky Mountain floristic provinces. Thus the flora of the Wallowas includes species typical of both provinces. We have enjoyed our years of exploring the Wallowas, and hope that this journey of discovery will continue to yield further surprises.

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Table 1. Ferns and Other Vascular Cryptogams of the Willowa Mountains, Oregon

Lycopodiaceae

<i>Huperzia occidentalis</i> (Clute) Kartesz & Gandhi	western firmoss
<i>Lycopodium annotinum</i> L.	stiff clubmoss
<i>Lycopodium sitchense</i> Rupr.	Alaska clubmoss

Selaginellaceae

<i>Selaginella scopulorum</i> Maxon	Rocky Mountain spikemoss
<i>Selaginella wallacei</i> Hieron	Wallace's spikemoss
<i>Selaginella watsonii</i> Underw.	alpine spikemoss

Isoetaceae

<i>Isoetes bolanderi</i> Engelm.	Bolanders quillwort
<i>Isoetes tenella</i> Leman ex Desv.	spiny-spore quillwort
<i>Isoetes howellii</i> Engelm.	Howell's quillwort
<i>Isoetes occidentalis</i> L.F. Hend.	western quillwort

Ophioglossaceae

<i>Botrychium ascendens</i> W.H. Wagner	upswept moonwort
<i>Botrychium campestre</i> W.H. Wagner	prairie moonwort
<i>Botrychium crenulatum</i> W.H. Wagner	scalloped moonwort
<i>Botrychium hesperium</i> (Maxon & Clausen) W.H. Wagner & Lellinger	western moonwort
<i>Botrychium lanceolatum</i> (S.G. Gmel.) Ångstr. ssp. <i>lanceolatum</i>	triangle moonwort
<i>Botrychium lineare</i> W.H. Wagner	slender moonwort
<i>Botrychium lunaria</i> (L.) Sw.	common moonwort
<i>Botrychium minganense</i> Vict.	Mingan moonwort
<i>Botrychium montanum</i> W.H. Wagner	western goblin
<i>Botrychium multifidum</i> (S.G. Gmel.) Trevis.	leathery grape fern
<i>Botrychium paradoxum</i> W.H. Wagner	paradox moonwort
<i>Botrychium pedunculatum</i> W.H. Wagner	stalked moonwort
<i>Botrychium pinnatum</i> St. John	northwestern moonwort

<i>Botrychium simplex</i> E. Hitchc.	least moonwort
<i>Botrychium virginianum</i> (L.) Sw.	rattlesnake fern
<i>Ophioglossum pusillum</i> Raf.	northern adder's-tongue
Equisetaceae	
<i>Equisetum arvense</i> L.	field horsetail
<i>Equisetum hyemale</i> L. var. <i>affine</i> (Engelm.) A.A. Eaton	common scouring rush
<i>Equisetum laevigatum</i> A. Br.	smooth scouring rush
<i>Equisetum variegatum</i> Schleich. var. <i>variegatum</i>	variegated scouring rush
Dennstaedtiaceae	
<i>Pteridium aquilinum</i> (L.) Kuhn var. <i>pubescens</i> Underw.	bracken
Pteridaceae	
<i>Adiantum aleuticum</i> (Rupr.) C.A. Paris	western maidenhair
<i>Aspidotis densa</i> (Brack.) Lellinger	Indian's dream
<i>Cheilanthes gracillima</i> D.C. Eat.	lace fern
<i>Cryptogramma acrostichoides</i> R. Br.	American parsley fern
<i>Cryptogramma cascadenis</i> E.R. Alverson	Cascade parsley fern
<i>Cryptogramma stelleri</i> (S.G. Gmel.) Prantl	Steller's rock brake
<i>Pellaea breweri</i> D.C. Eat.	Brewer's cliff brake
<i>Pellaea bridgesii</i> Hook.	Bridge's cliff brake
Aspleniaceae	
<i>Asplenium trichomanes-ramosum</i> L.	green spleenwort
Woodsiaceae	
<i>Athyrium alpestre</i> Butters var. <i>americanum</i> Butters	alpine lady fern
<i>Athyrium filix-femina</i> (L.) Mert. var. <i>cyclosorum</i> Rupr.	Northwestern lady fern
<i>Athyrium filix-femina</i> (L.) Roth. var. <i>californicum</i> Butters	Southwestern lady fern
<i>Cystopteris fragilis</i> (L.) Bernh.	fragile fern
<i>Gymnocarpium disjunctum</i> (Rupr.) Ching	western oak fern
<i>Woodsia oregana</i> D.C. Eaton ssp. <i>oregana</i>	Oregon cliff fern
<i>Woodsia scopulina</i> D.C. Eat. ssp. <i>laurentiana</i> Windham	Laurentian cliff fern
Dryopteridaceae	
<i>Dryopteris expansa</i> (C. Presl) Fraser-Jenkins & Jermy	spreading wood fern
<i>Dryopteris filix-mas</i> (L.) Schott	male fern
<i>Polystichum andersonii</i> Hopkins	Anderson's sword fern
<i>Polystichum imbricans</i> (D.C. Eaton) D.H. Wagner	imbricate sword fern
<i>Polystichum kruckebergii</i> W.H. Wagner	Kruckeberg's holly fern
<i>Polystichum lonchitis</i> (L.) Roth	mountain holly fern
<i>Polystichum munitum</i> (Kaulf.) C. Presl	western sword fern
<i>Polystichum scopulinum</i> (D.C. Eaton) Maxon	rock sword fern
Polypodiaceae	
<i>Polypodium hesperium</i> Maxon	western polypody



Fig. 22. The Wallowa Mountains rise above the pastoral Wallowa Valley. The mouth of the Hurricane Creek canyon is located in the center of the photo. Photo by Ed Alverson.