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Authors: Heron, Keegan, Windham, Michael D., Farrar, Donald R., and Pryer, Kathleen M.

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Looking Back on 130 Years of Fern and Lycophyte Research in Glacier National Park, Montana: A Modern Taxonomic Account

Keegan Heron[1]
Department of Biology, Duke University, Durham, NC 27708, USA
heron.keegan@gmail.com

Michael D. Windham[1]*
Department of Biology, Duke University, Durham, NC 27708, USA
michael.windham@duke.edu

Donald R. Farrar
Department of Ecology, Evolution and Organismal Biology, Iowa State University, Ames, IA 50011, USA
dfarrar@iastate.edu

Kathleen M. Pryer
Department of Biology, Duke University, Durham, NC 27708, USA
pryer@duke.edu

Abstract.—Glacier National Park encompasses over one million acres in the mountains of northwestern Montana, along the United States–Canada border. Our survey of online databases indicates that the earliest extant fern and lycophyte collections from this area were taken by Robert S. Williams in 1892. In the summer of 1919, Paul C. Standley, a botanist with the United States National Museum, conducted a survey of the flora of the newly created Park and recorded 39 species of ferns and lycophytes. In 2002, a revised flora for the Park by Peter Lesica increased this number to 61. Here we summarize 130 years of collections-based research on the ferns and lycophytes of Glacier National Park, documenting how our understanding of the flora has changed through time. In the summer of 2019, the lead author conducted a field survey to relocate as many ferns and lycophytes as possible within park boundaries. In parallel, we scoured herbarium online portals and databases for high-resolution digitized specimen images to confirm or refute historical vouchers of ferns and lycophytes collected from the Park. In a few cases, specimen loans were requested from herbaria to confirm our determinations. The results from our combined field and online herbarium studies are presented here. Of the 61 taxa recognized by Lesica in 2002, we were able to confirm all but seven. In sum, we recognize here a total of 71 fern and lycophyte taxa for the Park. Most previously unreported taxa belong to *Botrychium,* a genus that has seen a flurry of recent taxonomic work by co-author Farrar and collaborators. These new data are presented here together with updated nomenclature and discussion to provide a current taxonomic account of the fourteen fern and lycophyte families known to occur in Glacier National Park. We anticipate this study will provide a useful foundation for further investigations in the Park.

Key Words.—ferns, herbarium online portal databases, lycophytes, Paul C. Standley, Peter Lesica

[1] Equal contributions
*Author for correspondence: michael.windham@duke.edu

***This research is dedicated to the following indigenous American peoples: Blackfeet (Niitsitapi or Siksikaitsitapi), Kootenai (K̓upawiȼq̓nuk or Ksanka), Pend d'Oreille (Ql̓ispé or Kalispel), and Salish (Séliš), caretakers of this land before it was designated Glacier National Park in 1910*.**

Located in northwestern Montana, Glacier National Park (often referred to herein simply as the "Park") comprises over one million acres of towering mountains, heavily forested valleys, alpine meadows, raging meltwater streams, and the iconic glaciers (or what is left of them) that are its namesake (Hall and Fagre, 2003; Lesica, 2002; Fig. 1A). The Park straddles the Continental Divide, sharing a border with Canada to the north, as well as with the Blackfeet Nation (one of the largest indigenous American communities) to the east, and the Flathead National Forest to the west. In 1932, Waterton Lakes National Park in Alberta, Canada was combined with Glacier National Park to form the world's first International Peace Park, a United Nations Education, Scientific and Cultural Organization (UNESCO) World Heritage site (Thomas and Mow, 2016).

In the summer of 1919, nine years after Glacier National Park was established, Paul C. Standley, a botanist employed by the United States National Museum (Smithsonian Institution), conducted a survey of the flora of the newly created Park. Among the over 900 specimens he collected that year, Standley (1920, 1921) catalogued 39 species of ferns and lycophytes, two more than had been previously recorded for the entire state of Montana (Fitzpatrick, 1904). In 2002, when Peter Lesica published his comprehensive *Flora of Glacier National Park*, *Montana* the number of ferns and lycophytes reported for the Park had risen to 61.

In the summer of 2019, a century after Standley's survey of the Park's flora, and while employed as a botanical technician by Glacier National Park, the lead author set out to relocate as many of the reported ferns and lycophytes as possible. In parallel, the authors also scoured recent publications and several regional herbarium online portals (*e.g.*, The Consortium of Pacific Northwest Herbaria [https://www.pnwherbaria.org/]) for new Park records, to confirm or refute (to the best of our ability) the identification of historical records of digitized ferns and lycophytes collected in the Park. Here, we present the results of our combined field and online herbarium studies, together with revised nomenclature, to provide an update on the fern and lycophyte flora of Glacier National Park. We anticipate that this study will be a useful foundation for future systematic and ecological investigations in the Park.

Materials and Methods

Study Area.—Glacier National Park is located in the northwestern corner of Montana along the spine of the Rocky Mountains (Fig. 1A, B). It encompasses over 1 million acres (4,000 km^2), over 130 named lakes, more than 1,000 different species of vascular plants (Lesica, 2002), hundreds of species of animals, and six mountain tops exceeding 3000 m. It is estimated that there

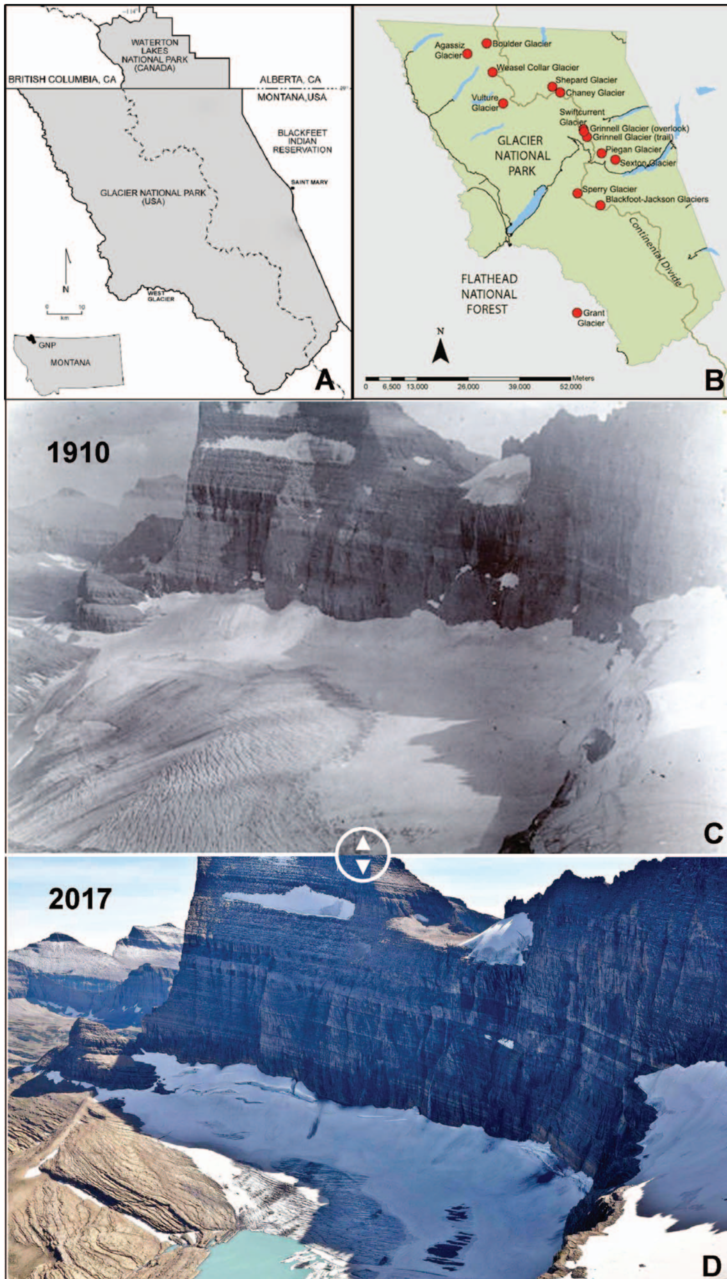

Fig. 1. Glacier National Park, Montana. A. Map of Glacier National Park and surrounding areas, modified from Resler and Tomback (2008); B. Red dots represent glaciers throughout the Park that have been re-photographed by USGS since 1997; C. Grinnell Glacier, 1910, photo by Morton Elrod, K. Ross Toole Archives, University of Montana; D. Grinnell Glacier, 2012, photo by Dan Fagre, USGS. Map in B, and photos in C and D from the USGS Repeat Photography Project http://nmrsc.usgs.gov/repeatphoto.

were roughly 150 glaciers present in the mid-nineteenth century (Fagre and Martin-Mikle, 2018) and most of these were still present in 1910 when the Park was established. Fagre *et al.* (2017) showed that in 2005, only 32 glaciers larger than 0.1 km^2 remained, including 26 that are named (several shown in Fig. 1B). Since 1997, scientists have been documenting glacial decline via the Repeat Photography Project (United States Geological Service, 2020) by comparing photographs and data recorded from the Park since 1850. For example, pairing historic images with contemporary photos (Fig. 1 C, D) are effective visuals for documenting how climate change has contributed to the dynamic landscape changes so evident today in Glacier National Park.

The Park's location situates it between two climatic zones, the Northern maritime and the Northern continental (Finklin, 1986), and its plant community composition and distribution patterns are largely related to geology and climate (Lesica, 2002). Weather patterns in the park are heavily influenced by Pacific storms coming from the west and cold arctic air arising from the north. These wind currents, known locally as chinook winds, can be exceptionally strong on the east side of the park, as air makes its way unencumbered from the crest of the mountains to the Great Plains. These wind patterns cause a pronounced difference in the vegetative communities between the two sides of the Park (Lesica, 2002).

Field Methods.—In 2019, in an attempt to survey Glacier National Park for contemporary fern records, the lead author followed the same approaches outlined in Standley (1920) by "visiting all portions of the Park normally seen by tourists." Although infrastructure within the Park has changed considerably over the last 100 years, many of the tourist attractions more easily accessible in the early 20^{th} century remain the same today. All locations specifically described by Standley (1920) were visited. Additional sources that were used to locate ferns in the Park included *Flora of Glacier National Park, Montana* (Lesica, 2002), the herbarium collection located at Glacier National Park headquarters, and the Park staff who generously shared their accumulated knowledge of fern locations. Ferns and lycophytes were actively searched for anywhere from 25 to 35 hours per week from May 15 to August 15 in the summer of 2019. A significant part of this was spent travelling to various parts of the Park, both by car and by foot, and locations where species had historically been found were prioritized. Upon locating a target species, its GPS coordinates, aspect, and habitat were noted, and photographs were taken (where available, photographs were posted to iNaturalist (2021) and are listed in Table 1 according to their unique iNaturalist ID number).

Online methods.—Our research utilized available online resources to search through several Herbarium Consortium Online Portals for recent and historical fern and lycophyte specimens collected from Glacier National Park that were available as high-resolution images and could be examined for identification accuracy (see Table 1). These included: The SEINet North American Plant Portal Network (https://swbiodiversity.org/); The Consortium of Pacific Northwest Herbaria (https://www.pnwherbaria.org/); The Smithsonian Department of Botany Collections (https://collections.nmnh.si.edu/search/

botany/); and The Pteridophyte Collections Consortium (https://pteridoportal.org/portal/index.php).

Results

The results of our combined field and online herbarium studies are presented in Tables 1 and 2. Table 1 lists the 71 fern and lycophyte taxa that we confirm here to have been verified by voucher records for Glacier National Park. It includes data for fourteen families and links the nomenclature used by Standley (1920) and Lesica (2002) with the taxon name we accept here to reflect current taxonomy (mostly following PPG 1, 2016, unless otherwise noted). Table 1 also identifies: those taxa (33) that were relocated by the lead author in the field in 2019; the timespan for which we have confirmed historical collections of each taxon based on metadata available in online herbarium databases; and a representative voucher specimen for each taxon.

Of our 71 confirmed taxa, the majority belong to the eusporangiate ferns (32 in Equisetaceae and Ophioglossaceae) and lycophytes (14 in Isoëtaceae, Lycopodiaceae, and Selaginellaceae). Leptosporangiate ferns are represented by 25 taxa, and only one of these (a hybrid) is newly reported here for the Park. The most species-rich genera in the Park are *Botrychium* and *Equisetum*, with 19 and 10 taxa, respectively. These are also the two genera that are most difficult for the non-specialist to find and/or identify accurately.

Table 2 lists the seven fern and lycophyte taxa included by Lesica (2002) that we were unable to verify for Glacier National Park, plus two other records that exist only as annotations on herbarium specimens. In a couple of cases, although we did see a few vouchers (not listed) purporting to represent a reported taxon, we determined them to be inconclusive and in need of further study.

Discussion

The number of fern and lycophyte taxa confirmed for Glacier National Park has increased from 0 to 71 in the last 130 years, with slightly more than half of these collected by Standley (1920). Field studies over the last century have added about 30 more taxa. These more recent discoveries have been driven by a variety of factors. Foremost among these is improved access to the wilderness that still comprises 95% of the Park. A combination of >100 miles of roads and >700 miles of maintained trails now provide a gateway to much more of the Park than was accessible to early collectors like R. S. Williams and P. C. Standley. The prodigious accumulation of knowledge on local ferns and lycophytes documented here also represents the cumulative efforts of scores of botanists, with many of their collections now becoming widely accessible through online portals. In the past decade, the digitization of herbaria has become a global enterprise with millions of high-resolution specimen images and their associated metadata now being easily accessible in online public databases (Page *et al.*, 2015; Soltis, 2017). Our access to these images (see

TABLE 1. Lycophyte and fern taxa **confirmed** for Glacier National Park in this study. Classes, subclasses, and families are organized phylogenetically following the classification in PPG 1 (2016). For information on the rarity status of any of these taxa, consult NatureServe (2021).

Classification	Taxon name adopted in this study	Taxon name in Standley (1920)	Taxon name in Lesica (2002)	[1]Time span of records	[2]Observed in 2019	Representative voucher specimen
Lycopodiopsida (lycophytes)						
Lycopodiaceae	*Dendrolycopodium dendroideum* (Michx.) A. Haines	*Lycopodium obscurum*	*Lycopodium dendroideum*	1892-1999	ID89723481	Standley 18859 (US)
	Diphasiastrum alpinum (L.) Holub	*Lycopodium alpinum*	*Diphasiastrum alpinum*	1919-2009	—	Standley 17957 (US)
	D. complanatum (L.) Holub	*Lycopodium complanatum*	*Diphasiastrum complanatum*	1892-2006	ID89716171	Standley 18575 (US)
	Huperzia continentalis Testo, A. Haines & A.V. Gilman	—	*Huperzia haleakalae*	1917-2019	—	Barkley 1735 (WTU)
	H. continentalis × *H. occidentalis*	*Lycopodium selago*	—	1895-1935	—	Maguire 453 (GH)
	H. occidentalis (Clute) Kartesz & Gandhi	—	*Huperzia occidentalis*	1932-1976	—	Maguire 454 (GH)
	H. selago (L.) Bernh. ex Shrank. & Mart.	—	—	1921-2013	—	Jack 2324 (GH)
	Lycopodium annotinum L.	*Lycopodium annotinum*	*Lycopodium annotinum*	1892-1994	ID89739094	Standley 16045 (US)
	L. lagopus (Laest. ex C. Hartm.) G. Zinserl. ex Kuzen.	*Lycopodium clavatum monostachyon*	*Lycopodium lagopus*	1919-1985	—	Standley 18523 (US)
Isoëtaceae	*Isoëtes bolanderi* Engelm.	—	*Isoëtes bolanderi*	1994	—	Damm & Christian s.n. (Glacier National Park Herbarium 23682[3])
Selaginellaceae	*Selaginella densa* Rydb. var. *densa*	*Selaginella densa p.p.*	—	1919	—	Standley 15318 (US)
	S. densa Rydb. var. *scopulorum* (Maxon) R.M. Tryon	*Selaginella densa p.p.*	*Selaginella scopulorum*	1901-1996	ID89738047	Standley 15732 (US, holotype)

Table 1. Continued.

Classification	Taxon name adopted in this study	Taxon name in Standley (1920)	Taxon name in Lesica (2002)	[1]Time span of records	[2]Observed in 2019	Representative voucher specimen
	S. densa Rydb. var. *standleyi* (Maxon) R.M. Tryon	*Selaginella densa p.p.*	*Selaginella standleyi*	1917-1949	—	Standley 17228 (US, holotype)
	S. wallacei Hieron.	*Selaginella wallacei*	*Selaginella wallacei*	1917-1993	ID89738495	Standley 17164 (US)
Polypodiopsida (ferns) Equisetidae						
Equisetaceae	*Equisetum arvense* L.	*Equisetum arvense*	*Equisetum arvense*	1910-2011	√	Standley 16727 (US)
	E. fluviatile L.	*Equisetum fluviatile*	*Equisetum fluviatile*	1910-1971	√	Standley 16027 (US)
	E. hyemale L. subsp. *affine* (Engelm.) Calder & Roy L. Taylor	*Equisetum hyemale*	*Equisetum hyemale*	1901-1966	√	Standley 16519 (US)
	E. laevigatum A. Braun	*Equisetum kansanum*	*Equisetum laevigatum*	1903-1996	ID89995871	Standley 16623 (US)
	E. pratense Ehrh.	—	*Equisetum pratense*	1934-1980	—	Maguire & Piranian 5425 (UTC)
	E. scirpoides Michx.	—	*Equisetum scirpoides*	1978-1980	—	Benham 408 (SAT)
	E. sylvaticum L.	*Equisetum sylvaticum*	*Equisetum sylvaticum*	1910-1998	√	Standley 15246 (US)
	E. variegatum Schleich. ex F. Weber & D. Mohr subsp. *variegatum*	*Equisetum variegatum p.p.*	*Equisetum variegatum* subsp. *variegatum*	1910-1993	√	Standley 16743 (US)
	E. × *ferrissii* Clute *(hyemale* × *laevigatum*)	*Equisetum praealtum; E. variegatum p.p.*	—	1919-2012	—	Standley 17614 (US)
	E. × *trachyodon* A. Braun *(hyemale* × *variegatum*)	*Equisetum variegatum p.p.*	—	1919-1933	—	Standley 18660 (US)
Polypodiopsida (ferns) Ophioglossidae						
Ophioglossaceae	*Botrychium ascendens* W.H. Wagner	—	—	2005	—	Farrar AS050623 (ISC)
	B. campestre W.H. Wagner & Farrar var. *campestre*	—	—	2005	—	Farrar CACA050623 (ISC)

Table 1. Continued.

Classification	Taxon name adopted in this study	Taxon name in Standley (1920)	Taxon name in Lesica (2002)	[1]Time span of records	[2]Observed in 2019	Representative voucher specimen
	B. campestre W.H. Wagner & Farrar var. *lineare* (W.H. Wagner) Farrar	—	—	2005	—	Farrar CALI050623 (ISC)
	B. "*campestre* × *tunux* (4x)"	—	—	2005	—	Farrar CAxTU050623 (ISC)
	B. crenulatum W.H. Wagner	—	—	2005	—	Farrar CR050623 (ISC)
	B. furculatum S.J. Popovich & Farrar (previously known informally as *B. adnatum* ined.)	—	—	1996-2005	—	Farrar FL050621 (ISC); Wagner FL980625 (ISC)
	B. gallicomontanum Farrar & Johnson-Groh	—	—	2005	—	Farrar GA050621 (ISC)
	B. hesperium (Maxon & R.T. Clausen) W.H. Wagner & Lellinger	—	*Botrychium hesperium*	1987-1999	—	Ahlensberger & Lesica 4422 (US)
	B. lanceolatum (S.G. Gmel.) Ångstr.	—	*Botrychium lanceolatum* subsp. *lanceolatum*	1976-1994	—	Wagner & Wagner 78511 (MICH)
	B. michiganense W.H. Wagner ex A.V. Gilman, Farrar & Zika	—	—	2005	—	Farrar MC050621 (ISC)
	B. minganense Vict.	—	*Botrychium minganense*	1919-2015	—	Wagner & Wagner 78523 (MICH)
	B. montanum W.H. Wagner	—	*Botrychium montanum*	1954-1978	—	Wagner & Wagner 78532 (MICH, paratype)
	B. paradoxum W.H. Wagner	—	*Botrychium paradoxum*	1978-1998	—	Wagner 78547 (MICH, paratype)

TABLE 1. Continued.

Classification	Taxon name adopted in this study	Taxon name in Standley (1920)	Taxon name in Lesica (2002)	[1]Time span of records	[2]Observed in 2019	Representative voucher specimen
	B. pinnatum H. St. John	—	*Botrychium pinnatum*	1976-1996	—	Lesica 6377 (MONTU)
	B. simplex E. Hitchc. var. *simplex*	—	*Botrychium simplex*	2001	—	Farrar SISI050621 (ISC)
	B. spathulatum W.H. Wagner	—	—	2005	—	Farrar SP050623 (ISC)
	B. tunux Stensvold & Farrar	*Botrychium lunaria p.p.*	*Botrychium lunaria p.p.*	2005	—	Farrar TU050623 (ISC)
	B. × *watertonense* W.H. Wagner	—	—	1998	—	Wagner WA980625 (ISC)
	B. yaaxudakeit Stensvold & Farrar	*Botrychium lunaria p.p.*	*Botrychium lunaria p.p.*	2001-2005	—	Farrar YA050622 (ISC)
	Botrypus virginianus (L.) Michx.	*Botrychium virginianum europaeum*	*Botrychium virginianum*	1901-1994	ID89736207	Standley 16945 (US)
	Ophioglossum pusillum Raf.	—	*Ophioglossum pusillum*	1993	—	Lesica & Bacon 6264 (MONTU)
	Sceptridium multifidum (S.G. Gmel.) Nishida ex Tagawa	*Botrychium silaifolium*	*Botrychium multifidum*	1901-1993	ID89724241	Standley 18585 (US)
Polypodiopsida (ferns) Polypodiidae						
Aspleniaceae	*Asplenium viride* Huds.	*Asplenium viride*	*Asplenium trichomanes-ramosum*	1901-2000	ID89737114	Standley 15368 (US)
Athyriaceae	*Athyrium distentifolium* Tausch ex Opiz subsp. *americanum* (Butters) Hultén	*Athyrium americanum*	*Athyrium alpestre* var. *americanum*	1895-1976	ID89736903	Standley 16841 (US)

TABLE 1. Continued.

Classification	Taxon name adopted in this study	Taxon name in Standley (1920)	Taxon name in Lesica (2002)	[1]Time span of records	[2]Observed in 2019	Representative voucher specimen
	A. filix-femina (L.) Roth subsp. *cyclosorum* (Rupr.) C. Chr.	*Athyrium filix-femina*	*Athyrium filix-femina* var. *cyclosorum*	1892-1969	ID89735691	Standley 15372 (US)
Cystopteridaceae	*Cystopteris fragilis* (L.) Bernh. subsp. *fragilis*	*Filix fragilis*	*Cystopteris fragilis*	1901-1976	ID89735958	Standley 16808 (US)
	C. montana (Lam.) Bernh. ex Desv.	—	*Cystopteris montana*	1932	—	Rugg s.n. (US; WTU)
	Gymnocarpium disjunctum (Rupr.) Ching	*Dryopteris linnaeana*	*Gymnocarpium disjunctum*	1901-1967	ID89737996	Standley 15650 (US)
	G. dryopteris (L.) Newm.	—	*Gymnocarpium dryopteris*	1921-1932	—	Maguire 424 (GH)
	G. × *brittonianum* (Sarvela) Pryer & Haufler *(dryopteris* × *disjunctum*)	—	—	1901-1935	—	Vreeland 969 (CAN; US)
Dennstaedtiaceae	*Pteridium aquilinum* (L.) Kuhn subsp. *pubescens* (Underw.) J.A. Thomson, Mickel & Mehlt.	*Pteridium aquilinum pubescens*	*Pteridium aquilinum*	1903-1960	ID91645636	Yuncker & Yuncker 7006 (DUKE)
Dryopteridaceae	*Dryopteris carthusiana* (Vill.) H.P. Fuchs	*Dryopteris dilatata p.p.*	*Dryopteris carthusiana*	1919-1999	ID89996468	Standley 18514 (US)
	D. cristata (L.) A. Gray	*Dryopteris cristata*	*Dryopteris cristata*	1901-2000	—	Standley 18527 (US)
	D. expansa (C. Presl) Fraser-Jenk. & Jermy	*Dryopteris dilatata p.p*	*Dryopteris expansa*	1901-1983	ID89717305	Standley 16488 (US)
	D. filix-mas (L.) Schott	*Dryopteris filix-mas*	*Dryopteris filix-mas*	1895-1996	ID89739486	Standley 15362 (US)
	Polystichum andersonii Hopkins	*Polystichum andersonii*	*Polystichum andersonii*	1919-1980	—	Standley 17443 (US)
	P. lonchitis (L.) Roth	*Polystichum lonchitis*	*Polystichum lonchitis*	1892-1983	ID89716066	Standley 15210 (US)

TABLE 1. Continued.

Classification	Taxon name adopted in this study	Taxon name in Standley (1920)	Taxon name in Lesica (2002)	[1]Time span of records	[2]Observed in 2019	Representative voucher specimen
	P. munitum (Kaulf.) C. Presl	—	*Polystichum munitum*	1994	ID89737788	Spribille s.n. (Glacier National Park Herbarium 21798)
Polypodiaceae	*Polypodium hesperium* Maxon	*Polypodium hesperium*	*Polypodium hesperium*	1900-1994	ID90499912	Standley 16685 (US)
Pteridaceae	*Adiantum aleuticum* (Rupr.) C.A. Paris	*Adiantum pedatum aleuticum*	*Adiantum aleuticum*	1892-1971	ID89737364	Standley 16817 (US)
	Aspidotis densa (Brack.) Lellinger	*Cheilanthes siliquosa*	*Aspidotis densa*	1895-1993	ID90501100	Standley 15576 (US)
	Cryptogramma acrostichoides R. Br.	*Cryptogramma acrostichoides*	*Cryptogramma acrostichoides*	1895-1978	ID89737581	Standley 17990 (US)
	C. stelleri (S.G. Gmel.) Prantl	*Cryptogramma stelleri*	*Cryptogramma stelleri*	1895-2009	ID89737009	Standley 17143 (US)
	Myriopteris gracillima (D.C. Eaton) Grusz & Windham	*Cheilanthes gracillima*	*Cheilanthes gracillima*	1895-1995	ID89736698	Standley 15558 (US)
Thelypteridaceae	*Phegopteris connectilis* (Michx.) Watt	—	*Phegopteris connectilis*	1909-1988	ID89737196	Jones s.n. (WIS)
Woodsiaceae	*Woodsia scopulina* D.C. Eaton subsp. *scopulina*	*Woodsia scopulina*	*Woodsia scopulina*	1901-1998	√	Standley 15191 (US)
	W. oregana D.C. Eaton	*Woodsia oregana*	*Woodsia oregana* subsp. *oregana*	1934-1954	√	Maguire 16372 (UTC)

[1] whenever the date 1892 is listed in this column, this refers to the earliest collection of the taxon known from the Park; these were made by R. S. Williams
[2] whenever possible, photographs of observations made in the field in 2019 were posted to iNaturalist (2021) and are listed here according to their unique ID number (*e.g.*, iNaturalist observation ID 87907372 can be found by visiting <inaturalist.org/observations/87907372>).
[3] verified and annotated by D.M. Brunton in 2004 (pers. comm.)
√ = specimen observed in field in 2019, but without photographic documentation in iNaturalist
— = not applicable

TABLE 2. Lycophyte and fern taxa, either from Lesica (2002) or other sources, for Glacier National Park **not confirmed** in this study. Classes, subclasses, and families are organized phylogenetically following the classification in PPG 1 (2016).

Classification	Taxon name	Information Source(s)
Lycopodiopsida (lycophytes)		
Isoëtaceae	*Isoëtes echinospora* Durieu	Listed in Lesica (2002) based on Maguire's (1939) report of his collection from Trout Lake [*Maguire & Piranian 5429*; GH, UTC] of *I. braunii* Durieu (=synonym of *I. echinospora*). However, GH and UTC specimens annotated as "probably *I. bolanderi*" and "*I. occidentalis*", respectively, by Shackleford (1997).
	I. howellii Engelm.	[*Pierce s.n.* (Glacier National Park Herbarium 23260)]. Herbarium sheet annotated as "*I. howellii* (probably)" by D.M. Brunton in 2004 (pers. comm.).
	I. occidentalis L.F. Henderson	[*Maguire & Piranian 5429*; GH, UTC]. Herbarium sheet at UTC annotated as "*I. occidentalis*" by Shackleford (1997), which is in conflict with his annotation "probably *I. bolanderi*" for the same collection deposited at GH.
Lycopodiaceae	*Diphasiastrum sitchense* (Rupr.) Holub	Lesica (2002). No vouchers confirmed; see Discussion
	Huperzia miyoshiana (Makino) Ching	Lesica (2002). No vouchers confirmed; see Discussion
	Lycopodium clavatum L.	Lesica (2002). No vouchers confirmed; see Discussion
Polypodiopsida (ferns) Equisetidae		
Equisetaceae	*Equisetum* × *litorale* Kühlew. ex Rupr. (*arvense* × *fluviatile*)	Lesica (2002). No vouchers confirmed; see Discussion
	E. palustre L.	Lesica (2002). No vouchers confirmed; see Discussion
Polypodiopsida (ferns) Ophioglossidae		
Ophioglossaceae	*Botrychium angustisegmentum* (Pease & A.H. Moore) R.T. Clausen	Lesica (2002). No vouchers confirmed; see Discussion

Methods) was crucial, both for identifying species with clear macromorphological differences and locating specimens of cryptic taxa that could be obtained on loan. Another factor driving the increase in species numbers in the Park, especially in the years since publication of Lesica's (2002) flora, is the recognition of taxa new to science. Intensified systematic and phylogenetic research using molecular tools developed in the late 1900s and early 2000s has led to the recognition of several new species, particularly within *Botrychium*.

Among ferns and lycophytes, the leptosporangiate ferns are usually more visible and straightforward to identify than the eusporangiate ferns (Equisetaceae and Ophioglossaceae), or the lycophytes (Isoëtaceae, Lycopodiaceae, and Selaginellaceae). Of the 25 leptosporangiate ferns that we confirm here for the Park (Table 1), 20 were relocated by the lead author in the summer of 2019. Three of the "missing" taxa—*Cystopteris montana*, *Dryopteris cristata*, *Polystichum andersonii*—are quite distinctive morphologically, and the failure to relocate these species is a direct reflection of their rarity. The other two leptosporangiate ferns confirmed for the Park but not relocated in 2019 are *Gymnocarpium dryopteris* and *G.* × *brittonianum*—in addition to being rare in the region, both are difficult to distinguish in the field from the much more common *G. disjunctum* (Pryer and Haufler, 1993).

Our success rate in the field survey was much lower with lycophytes and eusporangiate ferns, which often require specialized knowledge of microscopic and cryptic characters for accurate identification. The lead author was able to relocate just under a third of these (13 out of 46) in his 2019 field survey. In this case, most of the taxa not found in our survey belong to the genus *Botrychium* in the Ophioglossaceae (Table 1). Their ephemeral nature, largely subterranean life cycle, diminutive size, and simple morphology make these plants particularly difficult to find and identify in the field. A proclivity for the production of allopolyploid taxa, derived through hybridization and therefore morphologically intermediate between their diploid parents, further compounds this problem (Dauphin *et al.*, 2018; Farrar *et al.,* 2017).

To supplement the information summarized in Tables 1 and 2, we provide further discussion below on each of the fourteen fern and lycophyte families known to occur in the Park. The families are organized phylogenetically following the classification in PPG 1 (2016).

Lycopodiaceae.—This is the third most diverse family in the fern and lycophyte flora of Glacier National Park (Table 1). We confirm the occurrence of eight species and one interspecific hybrid distributed among four genera: *Dendrolycopodium, Diphasiastrum, Huperzia,* and *Lycopodium s.s.* By contrast, Standley (1920) listed six taxa (all included in *Lycopodium s.l.*) and Lesica (2002) reported ten species assigned to three genera. The generic taxonomy of the Lycopodiaceae has changed radically in recent years in light of a growing body of molecular data (see Øllgaard, 2012, 2015; PPG 1, 2016). Although it has become common practice to place the Park species herein called *Lycopodium annotinum* in the segregate genus *Spinulum* A. Haines, molecular phylogenetic analyses by Field *et al.* (2016) indicate that this species is sister to *Lycopodium s.s.*, and we favor maintaining these two small clades as a single genus with a shared chromosome base number of $x = 34$.

Three lycopods, *Dendrolycopodium dendroideum*, *Diphasiastrum complanatum*, and *Lycopodium annotinum* are among the earliest documented collections from the area, all taken in 1892 by R. S. Williams, one of the earliest field naturalist explorers in Montana (Steere, 1945). These are common in the

Park, and all three were observed during our 2019 resurvey (Table 1). Standley (1920) reported three additional taxa in the genus *Lycopodium*: *L. alpinum, L. clavatum monostachyon,* and *L. selago*. The first of these, now known as *Diphasiastrum alpinum*, is relatively common and well documented by a series of collections between 1919 and 2009 (Table 1). The taxon Standley (1920) referred to as *L. clavatum monostachyon* is now treated as a distinct species, *Lycopodium lagopus* (Wagner and Beitel, 1993); this taxon appears to be rare though documented by several collections between 1919 and 1985. With regard to *Lycopodium selago*, this name has been broadly applied in the past to a diversity of species now included in the genus *Huperzia* (see Bjork, 2020 and references therein). Specimens originally identified as *L. selago* by Standley (1920) have mostly malformed spores and appear to represent a hybrid between *Huperzia continentalis* and *H. occidentalis* (see Testo, Haines, and Gilman, 2016). Nevertheless, *Huperzia selago* sensu Testo, Haines, and Gilman (2016) has been collected in the Park (Table 1), where it appears to be very rare and confined to fen habitats.

Lesica (2002) recorded several additional taxa of Lycopodiaceae from the Park that are not on our list of accepted names (Table 1). Following the taxonomy of Wagner and Beitel (1993), Lesica (2002) reported *Huperzia haleakalae* from the Park. Testo, Haines, and Gilman (2016) restricted this name to populations endemic to Hawai'i and renamed the continental North American taxon *H. continentalis*; they specifically cite a collection from the Park (*Barkley 1735,* WTU) as a representative specimen (Table 1). Three other Lycopodiaceae taxa reported for the Park by Lesica (2002) appear on our unconfirmed list (Table 2). To date, we have seen no specimens attributable to *Diphasiastrum sitchense*; all collections identified as such appear to represent the closely similar species *D. alpinum*. Although there are a few herbarium collections from Montana that have been identified as *Huperzia miyoshiana*, none of them are morphologically identical to confirmed collections from the wet forests of the Pacific Northwest. Overall, these Montana collections more closely resemble *H. occidentalis*, a name that has been applied to most of them in the past and that we adopt here (Table 1). None of the major resources used to distinguish North American *Huperzia* species (*e.g.*, Gilman and Testo, 2015; Testo, Haines, and Gilman, 2016; Wagner and Beitel, 1993) attribute *H. miyoshiana* to Montana. Finally, we have seen no specimens of *Lycopodium clavatum s.s.* gathered within Park boundaries (Table 2); local collections belonging to the *L. clavatum* species complex produce a single strobilus per peduncle, indicating that they represent the segregate taxon *L. lagopus* (called *L. clavatum monostachyon* by Standley in 1920; see Table 1).

Isoëtaceae.—This family includes a single extant genus with more than 200 species (PPG 1, 2016). Although seemingly suitable aquatic habitats are common in the Park, Standley (1920) did not encounter *Isoëtes* during his fieldwork. Lesica (2002) reported both *I. bolanderi* and *I. echinospora* to be locally common, but most local *Isoëtes* collections lack the megaspores needed to unequivocally distinguish these species. The lead author investigated several promising habitats during his 2019 field survey but failed to relocate any plants of *Isoëtes*. The Glacier National Park herbarium, which is not digitized or available online, does have a single fertile specimen of *Isoëtes bolanderi* collected in 1994 (Table 1) whose identification was verified by Daniel Brunton in 2004 (pers. comm.). Three populations of *I. bolanderi* are known in nearby Canada, all from a small area in Waterton Lakes National Park in southern Alberta (Achuff *et al.*, 2011; Brunton *et al.*, 2020). One of these is within a few hundred meters of the US border.

Another *Isoëtes* collection we examined was *Maguire & Piranian 5429* from Trout Lake. Originally identified as *I. braunii* Durieu (=*I. echinospora*) by Maguire (1939), it is represented by two sterile sheets deposited at GH and UTC. Although likely conspecific, these were annotated as "probably *I. bolanderi*" and "*I. occidentalis*", respectively, by Shackleford (1997), as part of an unpublished PhD dissertation from Miami University. The latter taxon is thus included in our list of unconfirmed reports (Table 2), along with *I. echinospora*, which occurs in and around nearby Flathead Lake, but apparently has not been documented from the Park. Finally, a specimen in the Glacier National Park Herbarium, collected by J. R. Pierce in 1999, was annotated as "*I. howellii* (probably)" by Daniel Brunton in 2004 (pers. comm.; Table 2). A recent paper by Brunton *et al.* (2020) suggests that *I. howellii* may be a low-elevation subspecies of *I. bolanderi*. Clearly, the taxonomy of *Isoëtes* in Glacier National Park is in need of further study.

Selaginellaceae.—As commonly circumscribed (*e.g.*, PPG 1, 2016), this family includes a single extant genus encompassing more than 700 species, most of which occupy tropical and subtropical habitats. For Glacier National Park, we confirm the occurrence of two species (*Selaginella densa* and *S. wallacei*), the same two reported in 1920 by Standley (Table 1). Shortly after Standley's botanical survey of the Park (and based largely on his collections), Maxon (1920, 1921) split *S. densa* into three taxa (*densa, scopulorum,* and *standleyi*) that he treated as species. However, as pointed out by Tryon (1955), these taxa are completely intergradient in the central and southern Rocky Mountains. Therefore, we follow Tryon's taxonomic treatment, recognizing these three entities as varieties, all of which occur within the boundaries of Glacier National Park. Lesica (2002) reported three species of *Selaginella* from the Park (*S. scopulorum, S. standleyi*, and *S. wallacei*), apparently overlooking the fact that the largely High Plains taxon *S. densa s.s.* (our var. *densa*) had been collected by Standley in 1919 within the eastern border of the Park (Table 1). This area was not revisited during the 2019 field survey and the search for var. *standleyi* was ultimately unsuccessful (no documented vouchers since 1949; Table 1). However, the two more common taxa with more extensive collection histories (*S. densa* var. *scopulorum* and *S. wallacei*) were both observed in 2019.

Equisetaceae.—This ancient family comprises a single extant genus (*Equisetum*) with about 15 surviving species (Christenhusz *et al.*, 2019; Des Marais *et al.*, 2003; PPG 1, 2016). Glacier National Park is a major center of diversity for the group, with eight fertile species and two sterile hybrids on our list of confirmed taxa (Table 1). These taxa represent two deeply divergent subgenera (*Equisetum* and *Hippochaete*) that are occasionally treated as genera (Farwell, 1916; Milde, 1865). Four of the fertile species belong to subg. *Equisetum* (Christenhusz *et al.*, 2019; Hauke, 1978); three of these (*E. arvense, E. fluviatile*, and *E. sylvaticum*) were relocated during the 2019 field season, with *E. arvense* clearly being the most common fern in the Park. The fourth member of subg. *Equisetum* confirmed for the Park (*Equisetum pratense*) was not encountered by Standley (1920), but several herbarium specimens obtained on loan for our project support Lesica's (2002) report.

The remainder of the *Equisetum* species confirmed for the Park (four fertile species and two sterile hybrids) belong to subg. *Hippochaete* (Christenhusz *et al.*, 2019; Hauke, 1963). *Equisetum hyemale* subsp. *affine*, *E. laevigatum,* and *E. variegatum* subsp. *variegatum* are all common in appropriate habitats and were relocated by the lead author in 2019 (Table 1); the presence of *E. scirpoides,* a rarer taxon not reported by Standley (1920), was confirmed from herbarium specimens we obtained on loan. Much of the nomenclatural confusion apparent in this group relates to the presence of two sterile, interspecific hybrids: *E.* × *ferrissii* (*E. hyemale* × *E. laevigatum*) and *E.* × *trachyodon* (*E. hyemale* × *E. variegatum*). Lesica (2002) did not mention these hybrids, and Standley (1920) did not recognize them as such although he collected both. The collection Standley published as "*E. praealtum*" is *E.* × *ferrissii*, as is one of the specimens he identified as *E. variegatum*. Standley also collected *E.* × *trachyodon*, but attributed the specimen to *E. variegatum,* one of this hybrid's parental taxa.

The fern that has possibly expanded its already large range the most in the last 100 years is *Equisetum arvense*. Standley (1920) noted that it was "common, and often abundant, at all elevations except the highest . . . it seems to thrive particularly well on railroad embankments, and a thick stand of the plants is often seen growing from dry gravel and cinders". With the proliferation of vehicular traffic since Standley's writing, there are now miles of new roads throughout the Park, where, lined up in the ditches on either side, grow carpets of *E. arvense*. Found in all vegetation zones (Lesica, 2002), almost everywhere the soil has been disturbed—be it along a creek or in the headquarters gravel parking lot in West Glacier—one can expect to find shoots of *E. arvense* ready to colonize another territory.

Two taxa of subg. *Equisetum* (*E. palustre* and *E.* × *litorale*) appear on our unconfirmed list (Table 2). Online images of specimens from the Park attributed to *E. palustre* do not represent a single taxon, and we are unable to resolve the situation without more detailed analyses of microscopic features. Regarding *E.* × *litorale,* specimens identified as such by Standley (1920) were later annotated by R. L. Hauke as *E. arvense*, in conjunction with his monograph on *Equisetum* subg. *Equisetum* (Hauke, 1978). Collections attributed to *E.* × *litorale* by Lesica (2002) have partially malformed spores suggesting that they may be hybrids between different species of subg. *Equisetum*. However, these plants are not a good match for *bona fide* specimens of *E. arvense* × *E. fluviatile* (the hypothesized parentage of *E.* × *litorale*; Hauke, 1978). Given the diversity of potential parents in the Park (and the possibility that the spore abortion is due to environmental factors rather than hybridization), we cannot unequivocally assign these specimens to *E.* × *litorale*.

Ophioglossaceae.—As circumscribed by PPG 1 (2016), this family comprises four subfamilies, two of which are present in Glacier National Park. The Ophioglossoideae are represented in the Park by a single species, *Ophioglossum pusillum*, which is apparently confined to fen habitats and is quite rare, having been collected just once in 1993 (Table 1). By contrast, the Botrychioideae, is the most diverse fern lineage in the Park, including 19 species and two hybrids (Table 1). Standley (1920) recognized just three species belonging to Botrychioideae among his collections from Glacier National Park: *Botrychium lunaria, B. silaifolium*, and *B. virginianum*. The clear morphological differences among these three taxa were acknowledged in past classifications by their assignment to different subgenera (Clausen, 1938; Wagner and Wagner, 1993), and recent molecular phylogenetic analyses reveal that these groups are deeply divergent (Zhang *et al.*, 2020). As a result, it has become common practice in the two decades since publication of the *Flora of Glacier National Park, Montana* (Lesica, 2002) to place these species in different genera (see PPG 1, 2016). Collections identified as *Botrychium silaifolium* by Standley (1920) and *B. multifidum* by Lesica (2002) are herein called *Sceptridium multifidum*, and the specimens previously assigned to *Botrychium virginianum* are treated as *Botrypus virginianus*. Both are relatively common in the Park, with a long history of documentation extending from 1901 to the 2019 field studies of the lead author (Table 1).

Plants of the genus *Botrychium s.s.* make up the most diverse group of ferns within Glacier National Park, with seventeen species and two hybrids recognized (Table 1). Members of *Botrychium* are morphologically quite simple, comprised of a single underground stem and roots, and a single leaf produced above ground in a given year. The leaf is branched into two segments, a skeletonized sporophore producing spores, and a once or twice pinnate blade called the trophophore. Because this basic structure is common to all *Botrychium*, they are extremely difficult to distinguish by morphology alone and have often been called "cryptic" species (Dauphin *et al.*, 2017). Their relatively small size and frequent occurrence within dense native perennial herbaceous vegetation makes them difficult to find.

Recognition of the true diversity within *Botrychium* has been relatively recent. In his 1938 monograph of the genus (then recognized as subgenus *Eubotrychium*), Clausen listed just six species worldwide, with only *B. lunaria* reported for Glacier National Park. A few additional taxa were described over the next half-century, but the recognition of new species accelerated greatly when cytological studies revealed that roughly half of *Botrychium* taxa were allopolyploids. These new data, plus more critical morphological examination, led W. H. and F. S. Wagner to describe 16 new species from North America between 1956 and 2002 (*e.g.*, Wagner and Grant, 2002; Wagner and Lord, 1956). Subsequently, the documentation of genetic markers unique to individual taxa further substantiated identities of previously described diploids, and also revealed the diploid parents of allopolyploids (Gilman, Farrar, and Zika, 2015; Zika and Farrar, 2009). The advancement of these new techniques allowed Farrar and coworkers to distinguish even more morphologically cryptic species, especially within what was previously considered a single, worldwide species, *B. lunaria*. Stensvold and Farrar (2016) now recognize five diploid and one allotetraploid taxa within the *B. lunaria* complex (Dauphin *et al.*, 2017, 2018). Although *B. lunaria* was listed by both Standley (1920) and Lesica (2002) as being present in the Park (Table 1), its revised circumscription now excludes it. Continuing investigations of *Botrychium* now estimate the total number of taxa in the genus to be close to 40.

Glacier National Park has played a prominent role in the discovery of new *Botrychium* taxa and understanding their evolutionary origins. *Botrychium lineare*, now considered a variety of *B. campestre* (Table 1; Farrar and Gilman, 2017), was initially thought to be extremely rare and placed on the federal candidate endangered species list—until hundreds of plants were discovered in the Park (Barton and Crispin, 2004; Farrar and Gilman, 2017). *Botrychium* × *watertonense*, still known only from Glacier and the adjoining Waterton Lakes National Park in Canada, is the only known allopolyploid species that combines genomes from four different diploid species (Wagner *et al.*, 1984). Furthermore, analysis of plastid DNA shows *B.* × *watertonense* to have originated independently in these two known sites (Dauphin *et al.*, 2017). The rare taxon, *B. gallicomontanum*, basically an "eastern US" species, was surprisingly found in western prairies of the park (Popovich and Farrar, 2020). Also in the same prairies, was an enigmatic species found by Peter Lesica in 1996 and informally named *B.* "*adnatum*" by W. H. Wagner in 1998. The mystery of no additional discoveries of "*adnatum*" was not resolved until 2005, when it was found to be genetically identical to a Rocky Mountain taxon considered by W. H. Wagner to be a western form of *B. pallidum*. But although containing a genome of *B. pallidum* (and thus its similar morphology), "*adnatum*" and "*western pallidum*" plants proved to be an allotetraploid taxon with parentage by *B. pallidum* and an undescribed new diploid species. This widespread allopolyploid, now known from southern Canada to New Mexico, was named *B. furculatum* by Popovich & Farrar in 2020 (Table 1).

Are additional *Botrychium* yet to be discovered in Glacier National Park? With its wide range of habitats, from mountain meadows to native prairies, both favored by *Botrychium*, the answer is most likely yes! *Botrychium neolunaria*, the common North American species of the *B. lunaria* complex, is curiously absent from the Park. Farrar and colleagues collected 44 plants from six different sites in the Park, all with a morphology similar to *B. neolunaria,* however, genetic analyses proved them all to be an allotetraploid, *B. yaaxudakeit,* derived from hybridization between *B. neolunaria* and a North American form of *B. lunaria*. *Botrychium yaaxudakeit* is common from Alaska to southwestern Canada and disjunct to Oregon and California. *Botrychium neolunaria* can be distinguished from *B. yaaxudakeit* by its thinner, lightergreen leaflets and significantly smaller spores (37μ vs. 45μ), and we anticipate that it will one day be found in the Park.

Of current interest is the newly discovered diploid species *B. farrarii* ined., one of the parents of *B. furculatum* discussed above. *Botrychium* "*farrarii*" is currently known only from the Big Horn Mountains of northern Wyoming. The westernmost occurrence of the other diploid parent of *B. furculatum*, *B. pallidum*, is in the Bearlodge Mts. in northeastern Wyoming. For allopolyploid hybridization to have occurred between these two species they must have cohabited the same site at some time. Because allotetraploids *B. furculatum* and *B. gallicomontanum* occur in the prairies of western Glacier National Park (Table 1), and both share *B. pallidum* as a parent, it is intriguing to ask whether *B. pallidum* might still be found in these prairies. Might *B.* "*farrarii*" be there as well? In any case, Glacier National Park seems to have been an evolutionary hotbed for the generation of allopolyploids, which comprise 61% (11 of 19) of the *Botrychium* species in the Park.

Pteridaceae.—In Glacier National Park, this family is represented by five species currently assigned to four genera (Table 1). All are relatively common, and each has a long history of documentation extending from the late 1800's to their observation during our 2019 field survey (Table 1). The taxonomy of the two *Cryptogramma* species has remained unchanged since they were first reported for the Park (see Metzgar *et al.*, 2013), and the separation of the western North American populations of the *Adiantum pedatum* complex at varietal (Standley, 1920) or species level (*Adiantum aleuticum* in Huiet *et al.*, 2018; Lesica, 2002; Paris, 1991) also has stood the test of time. The most significant changes in the nomenclature of local Pteridaceae arise from the incremental exclusion of the genus *Cheilanthes* from the floristic inventory. The species referred to as *Cheilanthes siliquosa* by Standley (1920) was recognized as *Aspidotis densa* by Lellinger (1968) and Lesica (2002). Subsequent molecular phylogenetic analyses supported this move, indicating that this taxon is deeply divergent from *Cheilanthes s.s.* and sister to the genus *Gaga* (Li, Pryer, and Windham, 2012). In fact, a series of such studies over the past decade (Eiserhardt *et al.*, 2011; Grusz *et al.*, 2014; Ponce and Scataglini, 2018) has shown that none of the North American species attributed to *Cheilanthes* are appropriately placed in this genus. As typified by *C. micropteris* Sw., *Cheilanthes s.s.* comprises a clade of about 30 species found almost exclusively in the Southern Hemisphere. It is deeply diverged from the clade that includes the Glacier National Park species formerly known as *C. gracillima* and, as such, the latter has been transferred to the genus *Myriopteris* (along with ca. 45 closely related North American taxa; see Grusz and Windham, 2013).

Dennsteadtiaceae.—A single species belonging to this family is known from Glacier National Park—the very widespread *Pteridium aquilinum*—which was frequently encountered west of the Continental Divide in our 2019 field survey (Table 1). Collections from the area have been identified as either var. *pubescens* Underw. or, less frequently, var. *latiusculum* Desv. We have examined all specimens attributed to the latter and find that none of them match the current circumscription of this taxon. Therefore, we assign all specimens of *Pteridium* from the Park to *P. aquilinum* subsp. *pubescens* following the taxonomy of Thomson, Mickel, and Mehltreter (2008).

Cystopteridaceae.— This family has a complex nomenclatural history; in the past two decades it has been placed in synonymy under either Dryopteridaceae (*e.g.*, Lesica, 2002) or Woodsiaceae (Smith *et al.*, 2006). Its recognition as a distinct family with ca. 40 species is strongly supported by recent molecular phylogenetic studies (PPG 1, 2016; Rothfels *et al.*, 2012; Rothfels, Windham, and Pryer, 2013). The family is represented in the Park by two species of *Cystopteris* and two species and an interspecific hybrid belonging to *Gymnocarpium* (Table 1). The two *Cystopteris* taxa are at opposite ends of the spectrum in terms of abundance; *C. fragilis* subsp. *fragilis* is one of the most common ferns in the area (and the world) whereas *C. montana* is an arctic-alpine specialist collected from the Park just once, in 1932 (Table 1). *Cystopteris fragilis* subsp. *fragilis* is morphologically and cytologically diverse in Glacier, comprising tetraploid and hexaploid populations that hybridize to form heterotic but sterile pentaploids (Windham, pers. obs.). This situation is remarkably similar to that reported from comparable latitudes in Eurasia (Hanušová *et al.*, 2019).

The three *Gymnocarpium* taxa occurring in Glacier National Park also differ greatly in abundance. Most collections from the area (>90%) represent the Pacific Northwest diploid species *G. disjunctum*. The circumboreal allotetraploid *G. dryopteris*, which originated through hybridization between *G. disjunctum* and the rare eastern North American species *G. appalachianum* (Pryer and Haufler, 1993; Rothfels *et al.*, 2014), has rarely been collected in the Park. In fact, this species appears to be even rarer than its sterile triploid backcross with *G. disjunctum* (= *G.* × *brittonianum*), whose previously unreported presence was confirmed based on several herbarium specimens obtained on loan. Although the spores of *G.* × *brittonianum* are largely malformed, many plants produce a few unreduced spores that may allow the hybrid to establish new sporophytes via apomixis (Pryer and Haufler, 1993).

Aspleniaceae.—This family is represented in the Park by a single species (Table 1) belonging to the cosmopolitan *Asplenium trichomanes* L. clade (Xu *et al.*, 2020). For two centuries, this circumboreal taxon was known as *Asplenium viride*, the name used by Standley (1920). A competing name (*A. trichomanes-ramosum* L.) emerged from taxonomic obscurity in the late 20th century and was adopted by both the *Flora of North America* (Wagner, Moran, and Werth, 1993) and the *Flora of Glacier National Park, Montana* (Lesica, 2002). However, *Asplenium trichomanes-ramosum* is now considered invalid (nom. inval., see ICBN Art. 56 and ICBN Appendix V (nom. utique rejic.) under *Asplenium ramosum*, Vienna Code, McNeill *et al.*, 2006) and we here return to the legitimate name *A. viride*, which has been conserved over all other names. This species, first documented for the area in 1901, is relatively common and was observed in several places during our 2019 field season.

Thelypteridaceae.—This family is represented in Glacier National Park by a single taxon, *Phegopteris connectilis* (Table 1). The first collections of this species in the Park were apparently made by Marcus Jones in 1909. However, perhaps due to a combination of rarity and difficult access, it was not encountered by Standley (1920). Most collections come from the vicinity of Sperry Glacier (Lesica, 2002), whose remote location (8.7 trail miles from the nearest road) discourages all but the most intrepid botanists. Despite these challenges, the lead author was successful in relocating this distinctive species in 2019 (Table 1). *Phegopteris* and its close relatives (the phegopteroid lineage) diverged early in the evolutionary history of the Thelypteridaceae, and the generic boundaries in this group are relatively stable and widely accepted compared to those in the rest of the family (Almeida *et al.*, 2016).

Phegopteris connectilis is unique among the Park's ferns in being an apomictic triploid that produces mostly unreduced spores, which germinate to form triploid gametophytes that, in turn, give rise to new sporophytes without fertilization (Patel, Fawcett, and Gilman, 2019). This trait is most commonly found in species that occupy drought-prone habitats (Grusz *et al.*, 2021), and it is very unusual to see it so well developed in a mesic species like *P. connectilis*. Unreduced spores have been observed in two other ferns occurring in the Park: *Gymnocarpium* × *brittonianum* (= diploid *G. disjunctum* × tetraploid *G. dryopteris*; Pryer and Haufler, 1993) and *Huperzia continentalis* × *occidentalis* (Testo, Haines, and Gilman, 2016). These two hybrids regularly form discrete populations in the absence of one or both parents, suggesting they may be experiencing incipient apomixis. The origin of triploid *Phegopteris connectilis* has not been ascertained, but hybridity has not been ruled out (Patel, Fawcett, and Gilman, 2019). Thus, hybrid origins (and possibly triploidy) may be driving the evolution of apomixis in all three of these mesic lineages.

Woodsiaceae.—As defined by PPG 1 (2016), this family includes two species found in Glacier National Park; both of which were relocated by the lead author in 2019 (Table 1). The circumscription of Woodsiaceae has changed substantially since its resurrection by Smith *et al.* (2006); with the removal of Athyriaceae, Cystopteridaceae, and several small, mostly tropical families (Rothfels *et al.*, 2012), Woodsiaceae now comprises a monophyletic group of about 40 species. Despite the low number of extant taxa, some of the internal clades are deeply divergent and, as a result, the generic taxonomy of the family has become a point of contention. Where PPG 1 (2016) accepts a single genus of Woodsiaceae, Lu *et al.* (2019) recognizes three (including a hybrid nothogenus), and Shmakov (2015) proposes seven.

Depending on the generic scheme adopted, the species of Glacier National Park belong to either *Woodsia* (PPG 1, 2016), *Physematium* (Lu *et al.*, 2019), or *Woodsiopsis* (Shmakov, 2015). Recent molecular phylogenetic analyses with broad sampling of Woodsiaceae (Larsson, 2014; Lu *et al.*, 2019) indicate that *Woodsiopsis* and *Physematium sensu* Shmakov (2015) are non-monophyletic, and adoption of this scheme would require the placement of the two Glacier National Park species in separate genera. Because hybridization occurs between the deepest branches in the Woodsiaceae phylogeny, the recognition of two or more genera also requires the naming of hybrid nothogenera (Lu *et* *al*., 2019). Here we follow the single genus classification of Woodsiaceae (PPG 1, 2016), assigning both local taxa to the genus *Woodsia*. One of these (*W. scopulina* subsp. *scopulina*) is cytologically diverse in the Park, including both diploid and tetraploid populations distinguished primarily by spore size (Windham, pers. obs.). The exclusively diploid taxon from the Park previously identified as *W. oregana* subsp. *oregana* by Lesica (2002) is herein referred to simply as *W. oregana*. Molecular phylogenetic analyses by Larsson (2014) have shown that tetraploid plants formerly classified as subsp. *cathcartiana* (Windham 1993a, 1993b) are allopolyploids deserving of species rank.

Athyriaceae.—This family has a complex nomenclatural history; in the past two decades it has been placed in synonymy under either Dryopteridaceae (*e.g.*, Lesica, 2002) or Woodsiaceae (Smith *et al*., 2006). Its recognition as a distinct family with ca. 650 species (PPG 1, 2016) is strongly supported by recent molecular phylogenetic studies (Rothfels *et al*., 2012). The family is represented in the Park by two circumboreal species—*Athyrium distentifolium* and *A. filix-femina*—first collected in the 1890's and easily relocated during our 2019 field survey (Table 1). The Glacier National Park taxon here called *A. distentifolium* subsp. *americanum* has also been treated as a variety of *A. alpestre* (Lesica, 2002) or a distinct species (Standley, 1920); it differs from the typical European taxon in lacking even a vestigial indusium. In recent molecular phylogenetic analyses of Athyriaceae (Wei *et al*., 2018), *A. alpestre* was well supported as sister to the small segregate genus *Cornopteris* Nakai; this branch was, in turn, sister to *Athyrium s.s.* (typified by the other Glacier species, *A. filix-femina*). To establish monophyly in this portion of the phylogenetic tree, Wei *et al*. (2018) advocated placing *A. alpestre* in the monospecific genus *Pseudathyrium* Newman. Alternatively, *A. alpestre* can be maintained in *Athyrium* (as *A. distentifolium*) if *Cornopteris* is also included. Because *A. distentifolium* hybridizes with the type species of *Athyrium* (Schneller, 1989), we follow PPG 1 (2016), which includes this species in *Athyrium s.l*. It should also be noted that *A. filix-femina* is highly variable across its range, and local populations belong to the Pacific Northwest segregate known as var. or subsp. *cyclosorum*.

Dryopteridaceae.—In the narrow sense adopted by PPG 1 (2016), this family is represented in the Park by seven species, four belonging to the genus *Dryopteris* and three to *Polystichum* (Table 1). Standley (1920) also reported four species of *Dryopteris* from Glacier National Park, and the names of two of these remain unchanged. The taxon that Standley (1920) called *D. linnaeana* has since been removed from the genus and, more recently, the family as well (Rothfels *et al*., 2012). This name is a synonym of *Gymnocarpium dryopteris*, though the specimens collected and examined by Standley belong to the closely related species *G. disjunctum* (see discussion of Cystopteridaceae).

The collections identified by Standley (1920) as *Dryopteris dilatata* (Hoffm.) A. Gray were subsequently shown to represent two species, a diploid (*D. expansa*) and a circumboreal allotetraploid (*D. carthusiana*). The latter is thought to be a hybrid between two species (*D. intermedia* and the still hypothetical *D. semicristata*) not known to occur in western North America

(Sessa, Zimmer, and Givnish, 2012). Although the distinctions between *D. carthusiana* and *D. expansa* are subtle, they do not appear to hybridize in nature (Montgomery and Wagner, 1993). Three of the four species of *Dryopteris* confirmed for the Park (Table 1) are relatively abundant and were easily relocated in 2019 (Table 1). *Dryopteris cristata*, on the other hand, has only been collected in the vicinity of John's Lake in the McDonald Valley. Three separate trips to this small fen by the lead author in 2019 failed to relocate this species; the last collection from the Park dates to 2000 (Table 1).

Standley (1920) reported two species of *Polystichum* (*P. andersonii* and *P. lonchitis*) for Glacier National Park, and Lesica (2002) added *P. munitum* to the list (Table 1). The three taxa do not appear to be closely related based on molecular phylogenetic analyses (Driscoll and Barrington, 2007; Le Péchon *et al.*, 2016). *Polystichum lonchitis* is relatively common in the Park and was observed at several locations by the lead author in 2019. *Polystichum andersonii* was not relocated during the 2019 field season, but herbarium specimens seen online confirm its presence in the Park. Although all online images of *P. munitum* herbarium specimens from the area proved to be misidentified collections of *P. lonchitis*, there is a confirmed voucher for *P. munitum* in the Glacier National Park Herbarium collected by Spribille in 1994, and it was also observed in 2019 (Table 1).

Polypodiaceae.—In the narrow sense adopted by PPG 1 (2016), this family is represented in Glacier National Park by a single species, *Polypodium hesperium*. First collected in the Park in 1900, the nomenclature of this taxon has remained largely unchallenged for more than a century. Although uncommon, the species is easily distinguished from other members of the local fern flora and was relocated during our 2019 survey (Table 1). *Polypodium hesperium* is a tetraploid that arose through hybridization between two Pacific Northwest diploids (*P. amorphum* Suksd. and *P. glycyrrhiza* D.C. Eaton) and then spread south (to Chihuahua, Mexico) and east (to Glacier National Park) exploiting new habitats seemingly unavailable to its parental species (Sigel, Windham, and Pryer, 2014).

Conclusions

What has changed in Glacier National Park in the past 130 years? Visitation has steadily increased, from 19,000 tourists in 1919 to more than 3 million in 2019 (National Park Service, 2020). Facilitating this growth has been the construction of roads, campgrounds, and parking lots, allowing people access to previously remote wilderness areas. Well established hiking trails (>700 miles) now crisscross the Park. Less noticeable but just as impactful are recent climatic changes and their effects on the glaciers that are the hallmark of the area. Since 1900, average air temperatures in the Park have increased by 1.33 degrees Celsius (Pederson *et al.*, 2010), and the number and size of glaciers has drastically declined. Shifting climate patterns are known to affect plant distributions and population sizes, especially for those on the edge of their ranges (Lesica *et al.*, 2018). This suggests that as glaciers continue to shrink, the diminished snowmelt may impact fern and lycophyte diversity. Despite these alterations to the landscape, 95% of the Park remains a protected wilderness that has seen relatively limited human-mediated impacts (Lesica, 2002). This is reflected in the current inventory of ferns and lycophytes for the Park. Nine taxa attributed to the Park by various sources in the last 130 years (*e.g.*, Lesica, 2002, herbarium specimen annotations) remain unconfirmed (Table 2). Most of these belong to taxonomically difficult groups that require observation of cryptic characters for positive identification. Even with these deletions (some of which may be reversed by further studies), the 71 ferns and lycophytes confirmed here for Glacier National Park represent a substantial increase over the 61 reported by Lesica (2002). This is due, in large part, to intensified systematic and phylogenetic research focused on certain groups (most notably the genus *Botrychium*). Climatic changes over the next century will certainly contribute in unknown ways to the evolving dynamics of ferns and lycophytes within the Park over the coming years. However, from the perspective of the fern and lycophyte flora, it is clear that the stewardship and management of Glacier National Park by the National Park Service over the last 110 years has been exemplary, and that this region still merits its early nickname "The Crown of the Continent".

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