A NEW VARIETY OF *MONTIA PARVIFOLIA* (MONTIACEAE) IN THE HIGH IDAHO BATHOLITH OF CENTRAL IDAHO AND ADJACENT MONTANA

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ABSTRACT

Montia parvifolia (Moc. ex DC.) Greene var. **batholithica** Ertter & C.A.M. Prent. (Montiaceae) is described as a new variety from high elevations (2100–2800 m) in central Idaho and adjacent Montana, based on an overview of variation within the species using a combination of standard taxonomic analysis of herbarium specimens, morphometric analysis, fieldwork, and common garden studies. Taxonomic history of the species is summarized, morphology and life history are clarified, and variation elsewhere in the species is also briefly addressed.

RESUMEN

Se describe **Montia parvifolia** (Moc. ex DC.) Greene var. **batholithica** Ertter & C.A.M. Prent. (Montiaceae), nueva variedad de las altas elevaciones (2100–2800 m) en central Idaho y adyacente Montana, basados en la visión de conjunto de la variación intraespecífica, usando una combinación de análisis taxonómico standard de especímenes de herbario, análisis morfométrico, trabajo de campo, y estudios en jardín. Se resume la historia taxonómica de la especie, se clarifican la morfología y desarrollo, y se trata brevemente la variación de la especie.

INTRODUCTION

The current study focuses on a high-altitude variant of *Montia parvifolia* (Moc. ex DC.) Greene in the central Idaho batholith and adjacent Montana, which captured the attention of two of us (Ertter and Johnson) independently during our respective research on the flora of this area (Ertter & Moseley 1993; Johnson 2019). As discussed below, the combination of herbarium studies, field observations, morphometric analysis, and discontinuities in range and habitat support the taxonomic recognition of this variant. For convenience, we will initially refer to it as the High Idaho Batholith variant; except for a few populations in Montana, all others occur in the High Idaho Batholith Ecoregion as described in the EPA Level IV ecoregion map (McGrath et al. 2002).

As an initial step in our investigation, we needed to develop a better understanding of the morphology and life history of *Montia parvifolia* in general, in order to determine homologies between the highly reduced High Idaho Batholith variant and other populations of *M. parvifolia*. Holm (1905) and Swanson (1966) provide relatively detailed descriptions of the species' general morphology, but treatments in existing floras (e.g., Peck 1961; Hitchcock et al. 1964; Hultén 1968; Miller 2003b; Miller & Chambers 2012; Legler 2018) inconsistently characterize the species simply as a mat-forming, somewhat succulent perennial with branched caudices,

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stolons, and/or a short rhizome, tending to spread by slender rootstocks and/or stoloniferous branches, with the individual caudices or stems erect or ascending, bearing easily detached bulblets in the leaf axils. This non-standardized description does not readily accommodate the high-altitude variant, nor are all of the descriptive features evident on the majority of herbarium specimens of "typical" *M. parvifolia* (e.g., obvious rhizomes, stolons, or bulblets).

TAXONOMIC AND NOMENCLATURAL HISTORY

In the broad sense, *Montia parvifolia* is a relatively distinct species or species complex that has sometimes been given its own section or genus, *Naiocrene* (Torr. & A. Gray) Rydb. The species occurs along the west coast of North America from the islands of southwestern Alaska to central California, inland in montane settings to extreme southwestern Alberta, western Montana, central Idaho, and the Sierra Nevada of California. The majority of populations, which have provided core descriptive elements for the species, occur west of the Cascade Mountains crest. The species is also adventive in Scotland (Online Atlas of the British and Irish Flora, www.brc.ac.uk/plantatlas/plant/montia-parvifolia, accessed 4 December 2019).

Utah and Nevada are sometimes included in the species' range (Tidestrom 1925; Hitchcock et al. 1964; Welsh 1974; Miller 2003b), but without specific localities. In the absence of voucher specimens, more recent state and regional floras do not accept documented *M. parvifolia* anywhere in the Intermountain Region (Holmgren 1955; Welsh et al. 1987; Holmgren & Holmgren 2012). The mention of *M. parvifolia* in a bighorn sheep study plot in south-central Owyhee County, Idaho (Hanna 1978), is clearly meant to be the nomenclaturally similar *M. parviflora* (Douglas) Howell, currently in *Claytonia*.

Montia parvifolia was originally described as *Claytonia parvifolia* Moc. ex DC., with the type collected from Nootka Sound on Vancouver Island in southwestern Canada. Torrey and Gray (1838) placed the species in their *Claytonia* § *Naiocrene,* along with *C. linearis* Douglas, *C. dichotoma* Nutt. in Torr. & A. Gray, and *C. diffusa* Nutt. Rydberg (1906) recognized *Naiocrene* as a monotypic genus containing only *N. parvifolia* (Moc. ex DC.) Rydb., while treating the other three species as *Montiastrum* (A. Gray) Rydb. Heller (1908) accepted three additional species in his revision of *Naiocrene*: *N. filicaulis* (Douglas) A. Heller from coastal Oregon, *N. flagellaris* (Bong.) A. Heller from near Sitka, Alaska, and *N. obtusata* (A. Heller) A. Heller from north-central California. According to Heller, *N. parvifolia* itself was "probably an aggregate, as it is made to include plants which do not have the same appearance."

In his *Flora of California,* Jepson (1914) reduced *Montia filicaulis* and *M. obtusata* A. Heller to synonyms of *M. parvifolia,* without addressing *M. flagellaris* (Bong.) B.L. Rob. (which was outside the flora's boundaries). Rydberg (1932) recognized two species in his treatment of *Naiocrene* for *North American Flora*: the widespread *N. parvifolia* and coastal *N. flagellaris*, with Heller's other species submerged in the former. Most subsequent researchers followed Rydberg in recognizing these two taxa, either as separate species of *Naiocrene* (Nilsson 1967) or *Montia* (Peck 1941, 1961), subspecies of *M. parvifolia* (Ferris 1944) or *Claytonia parvifolia* (Hultén 1968), or varieties of *M. parvifolia* (Hitchcock et al. 1964, Welsh 1974) or *C. parvifolia* (Davis 1966). Neither Rydberg (1932) nor Peck (1941, 1961) nor Hultén (1968) addressed *Montia sweetseri* L.F. Hend., even though this species had been described prior to their treatments. Henderson (1930), Ferris (1944), Hitchcock et al. (1964), and Davis (1966) treated *M. sweetseri* as a synonym of *flagellaris*.

Hitchcock et al. (1964) justified the use of varietal rank on the grounds that, however striking the extremes, the differences were a matter of degree with evident intergradation. More recently, Chambers (1993), Miller (2003b), and Miller and Chambers (2012) have refrained from recognizing any infraspecific taxa for *Montia parvifolia* in their treatments of the genus for *The Jepson Manual* and *Flora of North America North of Mexico*. Miller (2003b, and pers. comm. to the first author) acknowledged the morphological distinctiveness of the form with larger flowers, leaves, and seeds (corresponding to var. *flagellaris* (Bong.) C.L. Hitchc. and *M. sweetseri*), but he discerned no geographic underpinning for this variation and decided that any formal infraspecific units were unwarranted pending a more in-depth study using modern methods.

Phylogenetic molecular analysis of tribe Montieae by O'Quinn and Hufford (2005) placed *Montia*

parvifolia within a monophyletic *Montia* sect. *Montia,* providing no support for the recognition of *Naiocrene* as a distinct genus. A single population from the core range of the species in western Oregon (*O'Quinn 241*, WS) was used to represent the species; to our knowledge, infraspecific variation has not yet been investigated using phylogenetic molecular analysis. Subsequent overview papers on the phylogeny of Montiaceae (e.g., Hershkovitz 2019) have accepted O'Quinn and Hufford's results.

Careful evaluation of reports of *Montia parvifolia* and proper curation of specimens in herbaria not only require searches under *Claytonia* and *Naiocrene*, but are further complicated by the nomenclatural similarity between *Montia parvifolia* and the distantly related small-flowered miner's-lettuce, *M. parviflora*. The latter species is currently treated as *Claytonia parviflora* Douglas ex Hook. (Miller 2003a), which is also the genus within which *M. parvifolia* was initially described. Collections of the two species are routinely mislabeled and misfiled under the wrong name, and the previously cited mention of *M. parvifolia* by Hanna (1978) is an example of how easily this confusion enters written reports. Evidently even the common names have been confused: "streambank springbeauty" is more appropriately used for *Montia parvifolia* (e.g., Peck 1941, 1961) but is applied to *Claytonia parviflora* by PLANTS (https://plants.usda.gov; accessed January 2020), ITIS (https://www.itis.gov/; accessed November 2020), and NatureServe (https://www.natureserve.org/; accessed January 2020); conversely, these databases use the misnomer "littleleaf miners-lettuce" for *M. parvifolia*.

MATERIALS AND METHODS

Morphology and Life History

Several intertwined approaches were used to develop a better understanding of the general morphology and life history of *Montia parvifolia*, so as to accommodate the extreme form expressed by the High Idaho Batholith variant.

Examination of herbarium material.—In addition to unmounted sets accumulated by Ertter and Johnson, approximately 260 herbarium specimens of *Montia parvifolia* were assembled from CIC, ID, MONTU, RM, SRP, UC/JEPS, and WTU. Loans were comprehensive for Idaho and Montana but only representative for other states and British Columbia, supplemented with separate examinations by Ertter of all specimens of *Montia parvifolia* in IDS, MO, UC/JEPS, and WIS.

Field work.—Limited fieldwork by Ertter in 2018 and 2019 allowed field observations and additional sampling of 10 populations in various parts of the species' range: Snowslide Lake in the Salmon River Mountains component of the High Idaho Batholith, the Clearwater River drainage of north-central Idaho, the Purcell and Selkirk mountains of extreme northern Idaho, the Klamath-Siskiyou mountains of Oregon, and near the type locality of *M. sweetseri* in coastal southwestern Oregon. Vouchers for the full range of intrapopulation variation, microhabitat descriptions, and photographs were obtained from each population visited. Although not used in the current study, samples in silica gel were also prepared from selected populations for possible use by future researchers.

Common garden.—Living material was collected from most of the populations visited by Ertter in 2018 and 2019; additional living material was obtained from the Wallowa Mountains by other collectors (Alexa DiNicola and Beth Corbin) in 2019. Plants were successfully cultivated by Ertter in Boise, Idaho, in pots that overwintered indoors. This allowed extended life history observations and on-going interpopulational comparisons under a common garden setting.

Standard Taxonomic Analysis

Morphological characterizations and measurements, primarily focusing on characters previously determined to be diagnostic within the species complex, were derived from the accumulated herbarium specimens and new collections. Ecogeographic data was also extracted from the same material, supplemented with label data and images obtained from the Consortium of Pacific Northwest Herbaria (http://www.pnwherbaria.org/index.php), the Consortium of California Herbaria (http://ucjeps.berkeley.edu/consortium/), the Intermountain Region Herbarium Network (intermountainbiota.org/portal/), and the Rocky Mountain Herbarium Database

(http://rmh.uwyo.edu/data/search.php). The results were then used as the basis for initial taxonomic hypotheses and selection of significant characters for morphometric analysis.

Morphometric Analysis

To provide a more rigorously statistical component to our study, a morphometric analysis was conducted by Kabins under the supervision of Prentice and Mansfield. From the herbarium specimens available, 80 (Table 1) were selected to represent morphological variation among populations throughout the range of the species. Eighteen were from the High Idaho Batholith (2130–2800 m in Idaho and Montana), 50 were from other populations throughout the Pacific Northwest, including coastal *M. sweetseri/flagellaris* forms, (5–2650 m in Alaska, British Columbia, California, Idaho, Montana, and Oregon), and 12 were intermediate in morphology, elevation, and geography (460–2200 m in Idaho, Montana, and Oregon). Thirteen useful characters (Table 2) were measured on each specimen, restricted to those that were both quantifiable and present on most specimens. Mann Whitney U tests were used to determine statistically significant differences among medians of the quantitative characters shown in Table 2 (SigmaPlot 13.0, Systat Software, Inc., San Jose, CA). Non-parametric tests were preferred to corresponding parametric tests because data were not normally distributed. All data for which a complete data set was available were analyzed using Principal Components Analysis (PCA–SigmaPlot 13.0).

RESULTS

Morphology and Life History

Combined examinations of herbarium specimens, living populations, and plants grown in a common garden setting provide the following overview of the general morphology and life history of *Montia parvifolia*, with a special focus on shoot architecture. This overview must be considered provisional, due to limited access to living populations *in situ*, the significant changes in morphology that can occur at different stages of a plant's life cycle (Figs. 1–4), and the uncertain response to indoor growing conditions. As a further complication, some features could not be reliably determined from herbarium vouchers. Not only do herbarium specimens represent a single stage in the life cycle, but the fleshy stems, leaves, and bulblets of *Montia parvifolia* proved to be exceptionally resistant to drying, in either plant presses or silica gel. Cells of healthy plants had to be killed, either mechanically or by freezing, before drying would take place even in a forced hot air drier. As one result, most bulblets detach in the process, making the presence or absence of bulblets difficult to establish on herbarium specimens.

Where available, we have adopted terminology that has been consistently used in current descriptions of *Montia parvifolia* and related species. In the absence of such, we have chosen to use a simplified neutral terminology, indicated below in ***bold italics,*** that allows an explicit description of the diagnostic features, in particular those dealing with shoot architecture, without assuming unconfirmed homologies. The detailed study of shoot morphology in *Claytonia sibirica* L. by O'Quinn and Hufford (2006) provides a possible alternate terminology in a complex that has many parallels with *M. parvifolia*.

Morphology.—Young plants of *Montia parvifolia* initially have a simple taproot from which a ***primary stem*** arises, bearing a number of alternate leaves. This stem can either remain compact with closely overlapping leaves, or it can become elongated and recumbent (Fig. 2, right-hand plant). If the latter, the distal portion of the primary stem eventually develops a rosette of ***basal leaves*** that may be differently shaped than the ***stem leaves*** produced earlier. The remainder of the primary stem may shrivel and die at this stage, with the result that flowering plants often occur as individual rosettes (Fig. 1) rather than as interconnected mats. In at least some populations, specialized ***overwintering leaves*** develop on the apex of the primary stem distal to the basal leaves. These are small, swollen, rounded, sessile or subsessile leaf-blades that form propagules during the dormancy period (Fig. 4).

Two forms of ***aerial stem*** can arise from the axils of the basal leaves, both of which characteristically develop bulblets in the axils of alternate leaves or bracts. The typical form (***flowering stem***) bears a raceme of one to several flowers distally (Fig. 1). The other form (***flagelliform stem***), which tends to be more elongate and

Table 1. Specimens of *Montia parvifolia* used for morphometric analysis shown in Tables 2 and Fig. 6. B – var. *batholithica*; C – Coastal; I – Intermediate; P - Typical *parvifolia*.

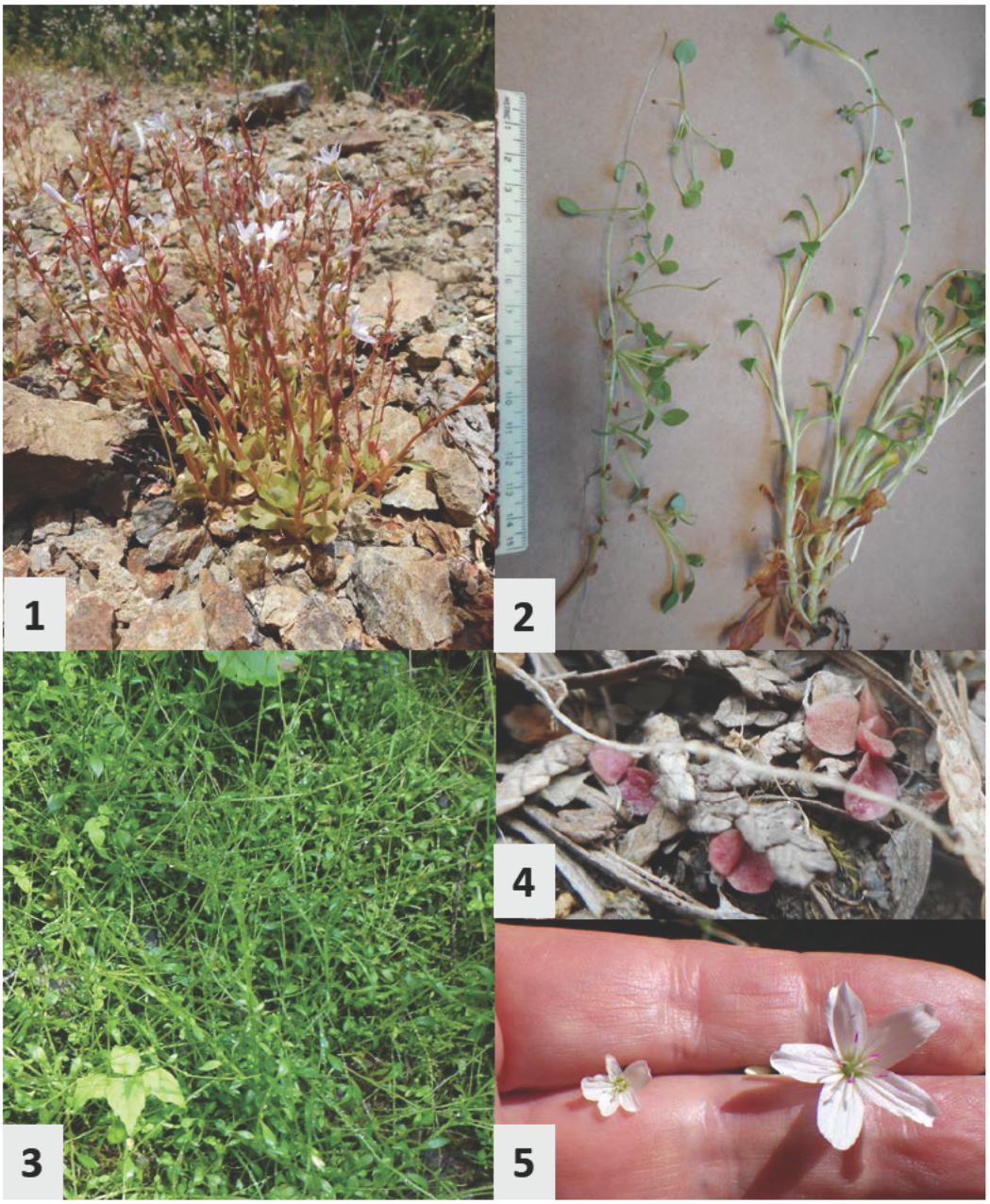
Form	State, County	Collector	Herbarium & Accession #	Elev (m)	Latitude	Longitude
B	ID, Lemhi	Atwood 14151 (1 of 2)	ID 107146	2680	47.43°	-116.36°
B	ID, Lemhi	Atwood 14151 (2 of 2)	ID 101911	2680	47.43°	-116.36°
B	ID, Lemhi	Atwood 14187	ID 101985	2800	45.12°	-114.61°
B	ID, Lemhi	Ertter 9455	CIC 045773	2680	45.13°	-114.59°
B	ID, Lemhi	Mancuso 349	ID 108278	2620	45.17°	-114.63°
B	ID, Valley	Ertter 22100	CIC 050938	2260	45.16°	-115.93°
B	ID, Valley	Ertter 7750	CIC 022107	2500	45.16°	-116.11°
B	ID, Valley	Ertter 7750	ID 101772	2500	45.16°	-116.11°
B	ID, Valley	Ertter 8714 (1 of 2)	CIC 022108	2500	45.09°	-115.97°
B	ID, Valley	Ertter 8714 (2 of 2)	ID 101770	2500	45.09°	-115.97°
B	ID, Valley	Handley 2832	UC 1981485	2150	45.00°	-115.95°
B	ID, Valley	Jones 6197	RM 166946	2130	44.92°	-116.09°
B	MT, Beaverhead	Lesica 4019	MONTU 104524	2800	46.67°	-114.25°
B	MT, Deerlodge	Lackschewitz 5704	MONTU 75215	2710	45.98°	-113.41°
B	MT, Missoula	Lackschewitz 1701	MONTU 63369	2530	46.67°	-114.24°
B	MT, Ravalli	Lackschewitz 1578	MONTU 63371	2640	45.84°	-114.48°
B	MT, Ravalli	Lackschewitz 1912	MONTU 63370	2350	46.50°	-114.39°
B	MT, Ravalli	Lackschewitz 523	MONTU 63367	2260	45.98°	-114.36°
C	AK (Baranof I.)	Heller s.n.	WTU 87311	10	56.29°	-134.66°
C	AK (Baranof I.)	Stensvold 6379	WTU 333150	10	56.58°	-134.86°
C	AK (Chichagof I.)	Walker 855	RM 85455	10	57.51°	-134.91°
C	AK (Kuiu I.)	Eyerdam 7582	ID 31493	5	56.72°	-134.36°
C	OR, Curry	Abrams & Benson 10647	RM 100547	610	42.68°	-124.42°
C	OR, Curry	Dennis 2827	WTU 256808	10	42.30°	-124.40°
C	OR, Curry	Denton 3693	WTU 262709	680	42.38°	-124.29°
C	OR, Curry	Thompson 12806	WTU 4497	30	42.38°	-124.42°
I	ID, Idaho	Bingham 573	ID 121063	1400	45.23°	-116.25°
I	ID, Idaho	Christ 12079	ID 19645	450	46.14°	-115.60°
I	ID, Idaho	Constance 1639	WTU 9632	550	46.15°	-115.98°
I	ID, Idaho	Thomas 3924	CIC 50926	1790	45.42°	-114.44°
I	ID, Idaho	Thomas 4382	CIC 50927	1400	45.58°	-114.52°
I	ID, Idaho	Thomas 86	CIC 50928	700	46.51°	-115.17°
I	ID, Shoshone	Moseley 2535	ID 110747	2400	47.41°	-115.76°
I	MT, Ravalli	Lackschewitz 152	MONTU 63368	1520	45.27°	-113.68°
I	OR, Grant	Smith & Ertter 6482	UC 1872536	2190	44.71°	-118.56°
I	OR, Union	Bafus 338	WTU 278655	1950	45.11°	-117.46°
I	OR, Wallowa	Maguire 27065	UC 738405	2200	45.22°	-117.09°
I	OR, Wallowa	Mason 8989	RM 453734	1980	45.26°	-117.39°
P	BC (Hope)	Calder & Savile 8371	RM 256394	980	49.24°	-121.26°
P	BC (Revelstoke)	Hitchcock & Martin 7562	WTU 68079	590	50.95°	-118.40°
P	BC (VI)	Rosendahl & Brand 8	RM 35238	180	48.55°	-124.42°
P	BC (VI)	Waldron 2024	RM 54395	180	48.25°	-123.25°
P	CA, Butte	Ahart 15718	JEPS 11617	230	39.81°	-121.72°
P	CA, El Dorado	Robbins 1817	UC 746854	2590	38.90°	-120.20°
P	CA, Humboldt	Vollmer & Beane 142	RM 228426	180	40.47°	-123.80°
P	CA, Mariposa	Jepson s.n.	JEPS 43290	1490	37.73°	-119.54°
P	CA, Mendocino	Wiggins 14125	RM 259123	400	39.75°	-123.52°
P	CA, Nevada	Heller 7142	RM 46325	2290	39.31°	-120.32°
P	CA, Tuolumne	Jepson 4576	JEPS 43280	2650	38.04°	-119.54°
P	ID, Bonner	Christ 12894	ID 58914	1520	48.20°	-116.12°
P	ID, Bonner	Christ 851	ID 11758	1520	48.37°	-116.16°
P	ID, Kootenai	Bjork 6277	ID 122130	1910	47.46°	-116.45°
P	MT (Glacier NP)	Jones s.n.	MONTU 2963	2290	48.62°	-113.76°
P	MT, Flathead	Hillman 150	MONTU 49927	2100	48.77°	-113.74°
P	MT, Glacier	Beaman & Stone 1605 (1 of 2)	RM 262127	2210	48.83°	-113.65°
P	MT, Glacier	Beaman & Stone 1605 (2 of 2)	MONTU 52769	2210	48.83°	-113.65°
P	MT, Glacier	Lesica 3489	MONTU 103140	2130	48.85°	-113.60°
P	MT, Lincoln	Cummins s.n.	MONTU 49523	1220	48.32°	-115.68°
P	MT, Lincoln	Harvey 5483	MONTU 48995	390	48.34°	-116.02°

Table 1. continued

Form	State, County	Collector	Herbarium & Accession #	Elev (m)	Latitude	Longitude
P	MT, Missoula	Kirkwood 1097	MONTU 15010	1160	46.87°	-113.99°
P	MT, Missoula	Kirkwood 1098	MONTU 15091	1220	46.86°	-113.99°
P	OR, Clatsop	Rossbach 371	WTU 96459	980	45.97°	-123.68°
P	OR, Douglas/Jackson	Mitchell 86	RM 453737	1220	42.99°	-122.54°
P	OR, Josephine	Semsrott 1688	WTU 349030	810	42.43°	-123.73°
P	OR, Josephine	Williams & Goff W&G-94	WTU 345570	1340	42.43°	-123.73°
P	OR, Lane	Franklin 363	RM 453740	460	44.20°	-122.26°
P	OR, Polk	Steward 6760	WTU 155547	210	44.33°	-123.46°
P	WA (Olympic NP)	Jones 3217	WTU 21846	90	48.04°	-122.76°
P	WA, Ferry	Olmstead 99-150	WTU 349637	1660	48.49°	-118.57°
P	WA, Grays Harbor	Jones 3953	WTU 23693	180	47.48°	-123.69°
P	WA, King	Deady 02-5	WTU 362692	500	47.38°	-121.69°
P	WA, Kittitas	Kruckeberg 5642	WTU 218243	1720	47.40°	-121.06°
P	WA, Lewis	Legler 13481	WTU 410374	90	46.62°	-123.10°
P	WA, San Juan	Brooking 05-36	WTU 381775	30	48.46°	-122.83°
P	WA, San Juan	Habegger EH1102	WTU 395108	20	48.53°	-122.97°
P	WA, Skagit	Hitchcock 3443	WTU 45405	10	48.44°	-122.61°
P	WA, Snohomish	Thompson 17422	WTU 171123	1070	47.98°	-121.39°
P	OR, Tillamook	Thompson 3080	WTU 23621	300	45.54	-123.69°
P	ID, Shoshone	Moseley 2690	ID 112868	1830	47.42	-116.02°
P	WA, King	Grant s.n.	WTU 43947	1220	47.75	-121.10°

Table 2. Mean ± standard deviations of characters from the three groups of populations analyzed; "Other populations" includes both Typical and Coastal specimens (See Table 1). Groups with the same letters are not significantly different. Groups with differing letters are significantly different ($p<0.05$).

Category Variables	High Idaho Batholith Mean ±SD significance	Intermediates Mean ±SD significance	Other Populations Mean ±SD significance
Maximum Flowering Stem Length (mm)	93.8 ±20.3 A	160 ±60.8 B	186 ±67.8 B
Minimum Flowering Stem Length (mm)	79.6 ±28.3 A	99.2 ±34.8 AB	114 ±57.6 B
Maximum Flagelliform Stem Length (mm)	91.5 ±25.5 A	158.7 ±79 B	178.1 ±92.6 B
Minimum Flagelliform Stem Length (mm)	50.4 ±21.8 A	57.5 ±23.1 A	96.5 ±57.1 B
Number of Flowering Stems per plant	.82 ±0.9 A	2.53 ±1.1 B	5.7 ±5.07 C
Number of Flagelliform Stems	2.5 ±1.3 A	2.92 ±3.0 AB	3.28 ±5.81 B
Total Number of Aerial Stems per plant	3.32 ±1.64 A	5.4 ±3.23 B	9.06 ±7.35 B
Petal Length (mm)	6.17 ±2.7 A	6.1 ±2.28 A	7.67 ±3.5 A
Leaf-blade Length (mm)	3.23 ±2.3 A	8.9 ±5.4 B	8.9 ±5.4 B
Distal Leaf-blade Width (mm)	1.43 ±1.2 A	2.7 ±2.3 AB	3.0 ±2.4 B
Proximal Leaf-blade Width (mm)	1.17 ±0.7 A	1.9 ±0.9 B	2.1 ±2.9 B
Ratio of Leaf-blade Length to Distal Leaf-blade Width	2.44 ±1.4 A	4.3 ±2.1 B	4.0 ±2.6 B
Ratio of Leaf-blade Length to Proximal Leaf-blade Width	2.87 ±1.9 A	5.1 ±2.3 B	5.7 ±3.3 B



Figs. 1–5. **1.** Representative plant from population of *Montia parvifolia* (typical form) in the Klamath-Siskiyou Mountains, with flowering stems mostly 1–2 dm long (*Ertter & DiNicola 23198*, Josephine Co., OR [SRP]). **2.** Variation in winter growth in indoor common garden conditions. Left-hand plant is robust flagelliform stem of intermediate morphotype from the Clearwater River drainage (*Ertter et al. 23292,* Idaho Co., ID [CIC]). Right-hand plant shows elongating primary stems of typical form from the Klamath-Siskiyou Mountains (*Ertter & DiNicola 23179,* Curry Co., OR [CIC]). **3.** Tangled flagelliform stems of *Montia parvifolia* growing in spray of waterfall in northern Idaho (*Ertter et al. 23373,* Boundary Co., ID [CIC]). **4.** Late-summer clusters of overwintering leaves (cluster less than 1 cm diam.) of *Montia parvifolia* (intermediate form) in the Clearwater River drainage (*Ertter et al. 23292,* Idaho Co., ID [CIC]). Dried "threads" in the center of the photo are the remnants of long-petiolate basal leaves. **5.** Variation in flower size in *Montia parvifolia* in common-garden setting. Left-hand flower is from intermediate form (*Ertter et al. 23292,* Idaho Co., ID [CIC]), right-hand flower is from coastal form (*Ertter & DiNicola 23185,* Curry Co., OR [CIC]).

slender, never develops flowers but instead can form plantlets at the nodes (Fig. 2, left-hand plant). Flagelliform stems, sometimes referred to as slender stolons, can become prostrate and tangled, especially in dense populations (Fig. 3). The ratio of flowering to flagelliform stems can differ significantly among populations and is probably influenced by growing conditions. All populations examined in the Klamath-Siskiyou mountains of southwestern Oregon and adjacent California had only flowering stems (Fig. 1), in contrast to populations from the immediate coast (i.e., near the type locality of *Montia sweetseri*) and central Idaho that usually had both flowering and flagelliform stems. Herbarium specimens from islands in southeast Alaska, the source of the type of *Claytonia flagellaris* Bong , appear to consist primarily of long, tangled, flagelliform stems. The extent to which this difference is genetic vs. environmentally influenced remains to be determined, but it at least indicates the capability and tendency of *M. parvifolia* to resort to vegetative reproduction in coastal and montane situations with shorter, cooler, or otherwise less favorable growing conditions.

Life history.—The relatively narrow scope of the current study did not allow field investigations of dormant populations throughout the range of *Montia parvifolia*, but it appears that this stage of life history is yet one more feature in need of more study. The species is routinely categorized as a perennial, but our observations confirm those of Swanson (1966) that the species can function as an annual in extreme environmental conditions. In at least one late-season population visited (*Ertter et al. 22974*, Seven Devils Mountains, Idaho Co., ID [CIC]), plants were completely shriveled by late September, with only seeds present as propagules. In another population (*Ertter et al. 23292,* Selway River, Idaho Co., ID [CIC]), plants had shriveled by late July, except for clusters of overwintering leaves that had formed on the proximal rudiment of the primary stem (Fig. 4). As discussed later, parent plants of the High Idaho Batholith variant probably do not survive the harsh winter conditions of the subalpine zone, relying primarily on detached rootless bulblets and overwintering leaf clusters as propagules. The extent that comparable life history strategies occur elsewhere in the species' range remains to be determined.

These field observations, in combination with examination of cultivated material and herbarium specimens, confirm that at least some populations of *Montia parvifolia* can function as annuals, with the parent plants shriveling at the end of the growing season. In addition to seeds and axillary bulblets, the unrooted clusters of overwintering leaves that form on the proximal rudiment of the primary stem after the remainder of the plant shrivels (Fig. 4) can serve as vegetative propagules during periods of dormancy. Growth resumes with the formation of adventitious roots, yearly incremental growth (which can be as short as 1 mm) of the primary stem, new basal leaves, and aerial stems. We refer to this life history as ***cryptically perennial or functionally annual.***

Standard Taxonomic Analysis

Interpopulation variation within *Montia parvifolia* was noted in the following characters, of which a subset (those more quantifiable and present on most specimens) were also used for morphometric analysis:

1) Length, width, and persistence of primary stem.
2) Size, shape, and number of basal leaves, ranging from oblanceolate blades with scarcely differentiated petioles (as in Fig. 1) to broadly obovate blades with well-defined petioles (as in Fig. 2, plant on left).
3) Ratio of flowering to flagelliform stems, as well as length of both types.
4) Pedicel length.
5) Number, size, and color of flowers (Fig. 5).

Presence and features of axillary bulblets might vary as well, but this was difficult to confirm from herbarium specimens alone, due to the tendency of bulblets to detach during the drying process.

Seed size has also been noted as taxonomically significant within *Montia parvifolia* (e.g., Hitchcock et al. 1964), and descriptions in Montiaceae routinely include seed texture and eliasomes. Unfortunately, mature fruit and seeds are present in only a small subset of collections for *M. parvifolia*, and none at all have yet been found for the High Idaho Batholith variant. This variant evidently relies more on vegetative than sexual reproduction, with flowers usually sparse or absent. Existing specimens lack any plants with mature fruit and seeds,

no flowers have yet developed on living collections, and challenging access precludes regular repeat visits to wild populations to catch plants in fruit before winter conditions make them completely inaccessible. As a result, descriptions of the fruit and seeds could not be prepared for the High Idaho Batholith variant, and seed size was not included in the morphometric analysis.

Based on the characters examined, most herbarium specimens of *Montia parvifolia* fall into three morphological extremes, summarized in Table 3, plus a fourth intermediate morphotype. The first extreme encompasses the majority of populations, from the core range in coastal mountains from British Columbia to central California, which share the following characters: relatively well-developed primary stems, numerous oblanceolate basal leaves with scarcely differentiated petioles, and flagelliform stems usually absent. Similar plants, though with flagelliform stems more often present, occur east through the Idaho Panhandle into Montana. We refer to all of these populations as typical *parvifolia* or the typical form.

The second morphological extreme, represented by some populations along the immediate coast (mostly in Oregon and the Alaska islands), differs in having more broadly ovate basal leaf-blades and the regular presence of flagelliform stems, which are often more numerous than flowering stems; flowers and seeds also tend to be larger than in typical *parvifolia* (at least in Oregon). This coastal extreme includes the types of var. *flagellaris* and *M. sweetseri*. These two extremes—typical and coastal—were analyzed together in the morphometric analysis (Tables 1 and 2, Fig. 6a,b).

Populations from the High Idaho Batholith of central Idaho and adjacent Montana, which are the focus of the present study, comprise the third morphological extreme. Plants are comparable to the coastal extreme in basal leaf shape and presence of flagelliform stems, but are significantly smaller in all features. This extreme is described below as var. *batholithica*.

In addition to these three extremes, a fourth morphotype is that of intermediates between the typical and the High Idaho Batholith morphological extremes. In this morphotype, maximum stem lengths and basal leaf shape are intermediate between the two extremes, flagelliform stems are common, and pedicels are among the longest occurring anywhere in the species. The intermediate morphotype is primarily represented by mid-elevation populations from the Clearwater River drainage in north-central Idaho and northwestern Montana, and provisionally including less distinct populations occurring in the mountains of northeastern Oregon and adjacent Washington. Individual collections from elsewhere in the species' range also have intermediate morphologies, but as sporadic occurrences rather than as an ecogeographic pattern.

Along with the morphological differences summarized in Table 3, variation in habit was manifested by plants overwintering indoors in common garden conditions. Plants representing the typical and coastal extremes produced growth spurts of the primary stem, which sometimes branched but usually did not form new plantlets until the tips could root (Fig. 2, right-hand plant). In contrast, primary stems of representatives of the intermediate morphotype remained more compact, instead producing exceptionally lush flagelliform stems arising from the axils of the basal leaves and forming new plantlets at each node (Fig. 2, left-hand plant). Living material of the High Idaho Batholith extreme has produced only flagelliform stems, significantly longer than any found in wild populations but overall retaining the smaller size that distinguishes this extreme from all other morphotypes.

Morphometric Analysis

With the exception of petal length, all characters evaluated among the 80 populations of *Montia parvifolia* identified in Table 1 differed between the populations from the High Idaho Batholith and those from elsewhere in the species' range (Table 2). Other populations from central Idaho, western Montana, and the Wallowa Mountains of northeastern Oregon, all representing the intermediate morphotype from elevations intermediate between the High Idaho Batholith populations and lower populations elsewhere in the species' range, differed from the High Idaho Batholith populations in eight of the 13 characters assessed. The number of flowering stems per plant and the minimum flagelliform stem length differed between these intermediate populations and the lower elevation populations from throughout the rest of the species' range (Table 2).

The first three axes explained 71% of the variation among the 13 characters analyzed by PCA (Fig 6). In

Table 3. Summary of key differences among extremes within *Montia parvifolia,* based on herbarium specimens and field studies. Some maximum sizes can be exceeded when plants are cultivated indoors.

	typical *parvifolia*	coastal extreme (*flagellaris/sweetseri*)	var. *batholithica*
primary stems	usually well-developed, 1–2(–3) mm thick	usually well-developed, ± 2(–4) mm thick	vestigial or absent, ± 1 mm thick
maximum aerial stem length	25(–35) cm	40 cm	15 cm
flagelliform stems	often absent, rarely more than flowering stems	usually present, sometimes more than flowering stems	usually at least as many as flowering stems
basal leaf-blade shape	elliptic (rarely broader), tapering gradually to petiole	broadly obovate-elliptic to rhombic, tapering abruptly to petiole	broadly obovate-elliptic, tapering abruptly to petiole
basal leaf-blade size	(8–)10–23(–30) × (2–)3–11 mm ([1.5–]2–4 times as long as wide)	8–24 × 7–22 mm (1–2 times as long as wide)	4–15 × 3–10(–12) mm (1–2 times as long as wide)
pedicel length	5–10(–15) mm	(5–)10–15(–20) mm	5–12 mm
petal length	7–12 mm	10–15 mm (or less in AK)	6–10 mm
petal color	white to pink or pale pinkish lavender	white or pink	white, sometimes pink-tinged
elevation	12–2650 m (only to 1900 m in Idaho)	0–680 m	2100–2800 m
distribution	coastal BC s to CA, inland to sw AB, w MT, n ID	islands of se AK s to coastal sw OR	High Idaho Batholith of central ID and adjacent MT

this analysis, the populations from the High Idaho Batholith were separate from populations from the rest of the range of the *M. parvifolia* whether the second or third PCA axis was ordinated against PCA axis 1.

TAXONOMIC TREATMENT

Our combined studies suggest that sufficient ecogeographically correlated morphological differences exist among populations of *Montia parvifolia* to warrant further systematic investigation, ideally a full-scale revision comparable to that of *Claytonia* by Miller and Chambers (2006) that also incorporated molecular phylogenetic analysis. However, the only variant we are formally recognizing at this time is the high-altitude extreme in the High Idaho Batholith of Idaho and adjacent Montana that provided the impetus for our study. This variant emerged as morphologically distinct in both the standard taxonomic and morphometric analyses, with a relatively well-defined ecogeographic range at at an isolated margin of the species' range. It is here described as a variety of *M. parvifolia*, using terminology as established in the Morphology and Life History section of Results. We use this rank because of the lack of sharp boundaries, especially in Montana, of primarily quantitative characters, and to coincide with the most common infraspecific rank used in the Pacific Northwest (e.g., Hitchcock et al. 1964).

Montia parvifolia (Moc. ex DC.) Greene var. **batholithica** Ertter & C.A.M. Prent., var. nov. (**Figs. 7–10**). Type: U.S.A. Idaho. Valley Co.: ca 1 mi NE of Pearl Lake at head of Pearl Creek, ca 14 air mi NNE of McCall, T20N R4E S9 NENE, 8000 ft, base of cirque cliffs on N face of south "Chain-of-Pearls" peak, 25 Jul 1989, *Ertter & Moseley 8714* (holotype: UC 1563790; isotypes: CIC, ID, NY, OSC).

Differing from other forms of *Montia parvifolia* in the combination of short stature (to 15 cm), vestigial primary stem, (0–)1–3(–5) basal leaves with broadly obovate-elliptic blades (1–2 times as long as wide), flagelliform stems usually equaling or exceeding flowering stems in number, pedicels no more than 12 mm long, petals no more than 10 mm long, and distribution above 2100 m elevation in the central High Idaho Batholith in Idaho and adjacent Montana.

Plants cryptically perennial or functionally annual, probably overwintering and propagating primarily by axillary bulblets and terminal clusters of overwintering leaves. **Primary stem** vestigial, unbranched, 1–5(–12) mm long, ± 1 mm thick, each year's growth usually dying over the winter. **Leaves:** basal leaves (0–)1–3(–5), forming a rosette at apex of primary stem, 1–5 cm long, petiole 0.5–3 cm long, blade green to reddish, broadly obovate-elliptic, 4–15 × 3–10(–12) mm (1–2 times as long as wide), tapering abruptly to petiole, apically

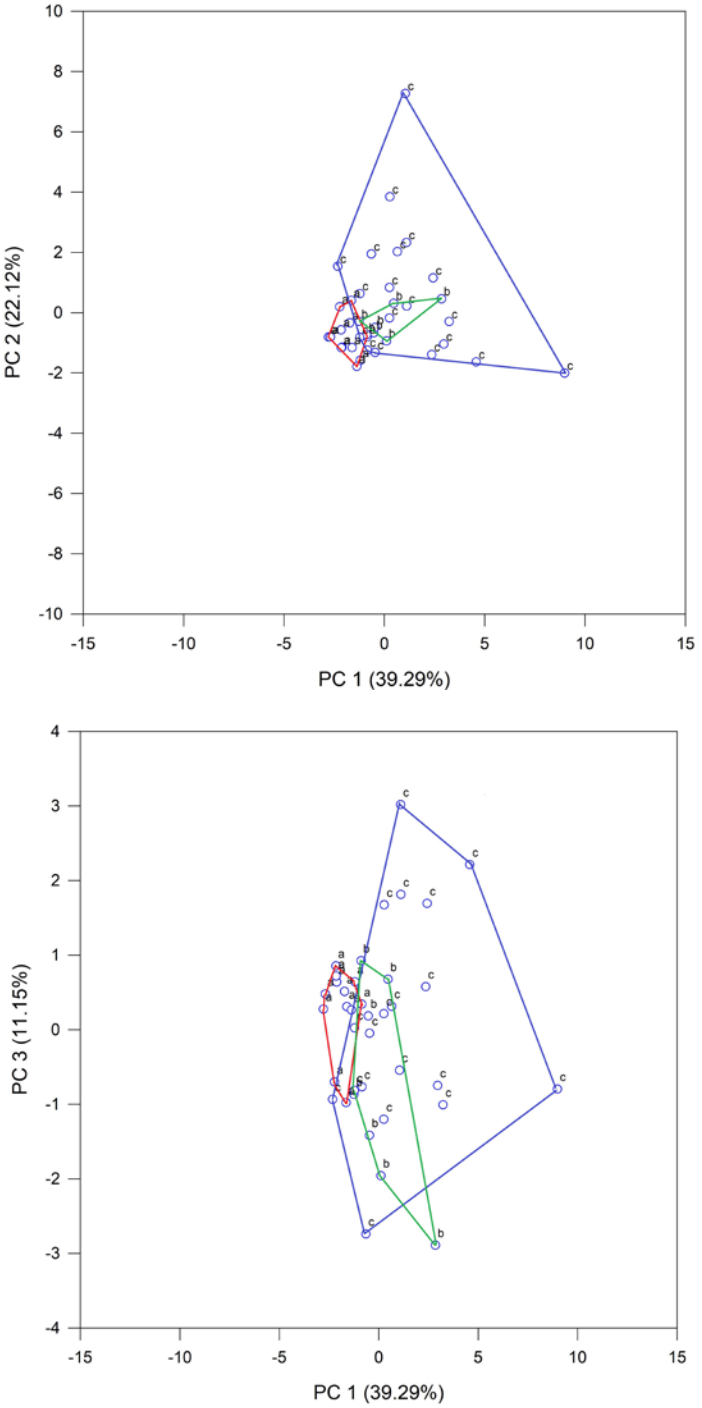
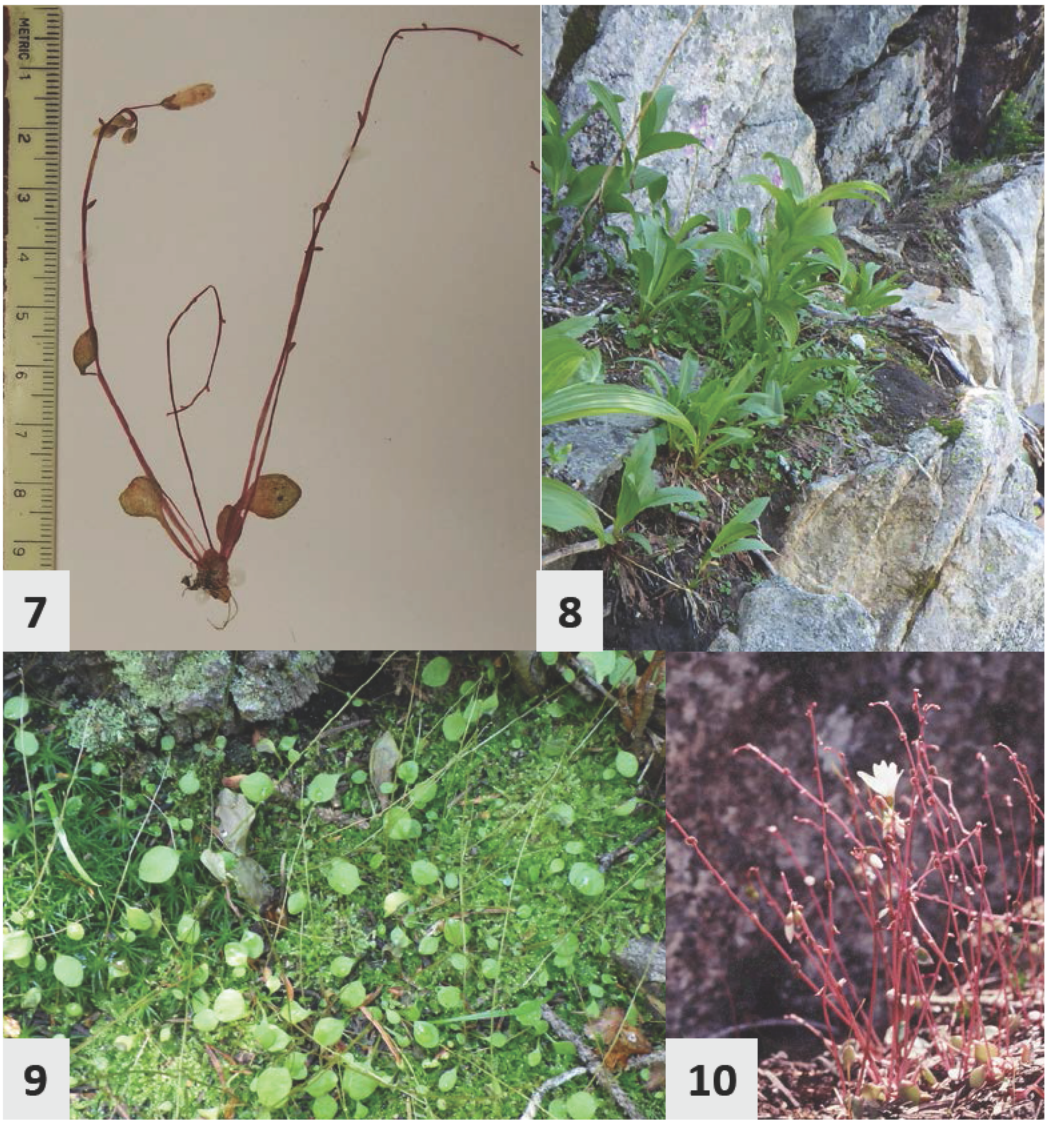


Fig. 6A & B. The PCA of 13 characters from a subset of 37 of the 80 populations shown in Table 1. Fig. 6A (top) shows coordinates of the first and second PCA axes. Fig. 6B (bottom) shows coordinates of the first and third PCA axes. Populations from the High Idaho Batholith and adjacent Montana are marked "a" (red group); populations from intermediate elevations/geographies are marked "b" (green group); populations from throughout the rest of the species' range, including both typical and coastal extremes, are marked "c" (blue group).



Figs. 7–10. **7.** Herbarium specimen of *Montia parvifolia* var. *batholithica,* showing petiolate basal leaves with obovate-elliptic blades, overwintering leaves already formed at apex of vestigial primary stem, and both flowering and flagelliform stems (*Mancuso 349* [ID] from Bighorn Crags, Lemhi Co., ID). **8.** Typical habitat of *Montia parvifolia* var. *batholithica* (Snowslide Lake cirque, Valley Co., ID). Plants grow in mossy mats in shallow soil on ledges of granitic cliffs. **9.** Colony of *Montia parvifolia* var. *batholithica* with intertwined flagelliform stems (*Ertter et al. 23455,* trail to Snowslide Lake, Valley Co., ID). **10.** Erect flagelliform and flowering stems of *Montia parvifolia* var. *batholithica* (*Ertter et al. 9455,* Bighorn Crags, Lemhi Co., ID)

obtuse; tight cluster of new overwintering propagule leaves forming distally to basal leaves (with some intermediates), swollen, ± ovoid to globose, 1–5 mm, sessile or short-petiolate. **Flagelliform stems** (0–)1–4 (usually ≥ flowering stems in number), (3–)5–15 cm long, ± ¼ mm thick, reddish, threadlike, unbranched, initially erect, often becoming prostrate, sometimes forming tangled mats; nodes 4–10, usually developing bulblets in at least some nodes, nodal bracts hyaline, ± 1 mm long. **Flowering stems** 0–2(–5), 6–10.5 cm long, reddish, sturdier than flagelliform stems (± ½ mm thick), terminating in a raceme of 1–5 flowers; nodes (proximal to

flowers) 1–4, proximal nodes sometimes with reduced leaves resembling those of basal rosette, nodes otherwise with bracts. **Pedicels** 5–12 mm long. **Flowers:** sepals 2–3 mm long; petals white, sometimes pink-tinged, 6–10 mm long (longest in Bighorn Crags); anthers pink or yellow. **Seeds** unknown.

Additional collections examined: **U.S.A. IDAHO: Idaho Co.:** N-S running ridge-top 1 airmi N of Bruin Mt, 1 airmi to the W and 20 airmi N of McCall, 17 Aug 2017, *Johnson & Mortimer 17-585* (ID). **Lemhi Co.** (all Bighorn Crags): above Skyhigh & Turquoise Lakes, T21N R16E S32, 2 Aug 1990, *Atwood 14187* (ID); cirque at head of Mirror Lake drainage, ca ¾ mi S of Mirror Lake, 8800 ft, 1 Aug 1990, *Atwood 14151* (ID); SE of Terrace Lakes, T21S R16E Sec 28 SW, 8800 ft, 31 Jul 1990, *Ertter et al. 9455* (CIC, ID, MO, NY, OSC, RM, UC, US, WTU); unnamed pond ca 0.6 mi SE of Ship Island Lake, 8600 ft, 31 Jul 1990, *Mancuso 349* (ID). **Valley Co.:** head of Fisher Creek 17 airmi due N of McCall, T21N R3E Sec 17 SWSW, 8200 ft, 20 July 1988, *Ertter & D'Alcamo 7750* (CIC, ID, OSC, UC); Snowslide Lake ca 10 airmi NE of McCall, 7300 ft, T19N R4E Sec 14 S of center, 21 Jul 1988, *Ertter, D'Alcamo, & Davidson 7780* (UC); NE-facing cirque slope SW of Pot Lake E of Box Lake, T19N R4E Sec 4 SWNE, 7800 ft, 27 Jul 1989, *Ertter, Moseley, & Davidson 8788* (UC); S side of Deep Lake ca 3 airmi SE of Secesh Summit on Warren Wagon Rd, 45.161°N, 115.933°W, 2266 m, 20 Jul 2014, *Ertter & DiNicola 22100* (CIC, UC, WTU); trail to Snowslide Lake, 44.9877°N, 115.9350°W, 2150 m, 14 Jul 2019, *Ertter et al. 23455* (CIC, WTU); Snowslide Lake Trail ca 9.5 airmi NE of McCall, T19N R4E Sec 10 SE, 3 Aug 1999, *Handley 2832* (USFS in RM, UC); Rain Peak, 6 airmi to the E and 12 airmi to the N of McCall, 8755 ft, 29 Jul 2016, *Johnson & Adams 16-191* (ID); unnamed peak 1.5 airmi NE of Log Mountain, 6 airmi to the S and 25 airmi E of McCall, 1 Aug 2017, *Johnson & Mortimer 17-230* (ID); Payette Lake, 7000 ft, 24 Jul 1899, *Jones 6197* (MO, RM). **MONTANA: Beaverhead Co.:** E-facing slope of Monument Peak ca 15 mi SW of Jackson, Beaverhead Mts, T6S R17W S33, 9200 ft, 28 Jul 1986, *Lesica 4019* (MONTU). **Deerlodge Co.:** ridge above Warren Lake, Anaconda-Pintlar Range, 8900 ft, 24 Aug 1974, *Lackschewitz 5704* (MONTU). **Missoula Co.:** N slope of Lolo Peak, Bitterroot Mts, 8300 ft, 6 Aug 1969, *Lackschewitz & Fageraas 1701* (MONTU). **Ravalli Co.:** above Kerlee Lake, Como Peaks Ridge, Bitterroot Mts, 7400 ft, 26 Jul 1968, *Lackschewitz & Fageraas 523* (MONTU); N slope of Watchtower Peak, Bitterroot Mts, 8650 ft, 27 Jul 1969, *Lackschewitz & Fageraas 1578* (MONTU); below S Ranger Peak, Bitterroot Mts, 7700 ft, 24 Aug 1969, *Lackschewitz & Fageraas 1912* (MONTU); Wyant Lake, Bitterroot Mts, 8300 ft, 21 Aug 1971, *Lackschewitz 3309* (MONTU).

Etymology and common name.—The varietal epithet refers to the Idaho Batholith. Batholith springbeauty is an appropriate common name.

Phenology.—Flowering July to August.

Life history.—The highly reduced size and subalpine habitat of var. *batholithica* have thus far prevented any field studies during periods of dormancy, but field studies during the growing season, cultivated material, and herbarium specimens suggest that each year's plants die at the end of the growing season, leaving a combination of detached axillary bulblets, seeds (if produced), and terminally produced overwintering leaves on a short rudiment of the primary stem as propagules. In cultivation, parent plants have generally died back by late summer without having flowered but after producing abundant axillary bulblets and terminal overwintering leaf clusters. In cool indoor conditions, abundant new plants start developing in early winter (probably the climatic equivalent of post-snowmelt conditions in their normal habitat), presumably primarily from inconspicuous axillary bulblets. No deeply buried overwintering structures have been noted in either natural or cultivated populations. Variety *batholithica* is evidently adapted to shallow moist soils and the long harsh winters of the High Idaho Batholith by relying primarily on detached unrooted vegetative propagules, from which small, delicate, shallow-rooted plants develop and die in a single short growing season, often without flowering.

Elevation.—From 2100 to 2800 m elevation.

Habitat.—Populations of *Montia parvifolia* var. *batholithica* are most commonly found on the north- or east-facing walls of cirques, generally scattered in moist mossy mats on shallow soil over ledges (Fig. 8), outcrops, boulders, and talus, or in moist crevices, often near streams or seepage. At least one population (*Ertter et al. 23455*) occurs on equivalent habitat along a rocky streamlet and the mossy floor of a spruce forest. Plants generally grow in moist shaded sites with shallow soil and limited competition (Figs. 8, 9), with the most common vascular plant associates being species of *Micranthes, Lewisia, Cystopteris, Dodecatheon, Ligusticum, Juncus,* and *Carex*. Flowering stems are most often formed on plants growing in partial sun (Fig. 10), while plants growing in full shade are more likely to have only flagelliform stems (Fig. 9).

The Idaho localities occur predominantly on granitic substrates of the Idaho Batholith, though at least one in the Bighorn Crags is recorded on quartzite (*Atwood 14187*). Most localities from the Bitterroot Mountains in Montana are also on Idaho Batholith granitics. Other populations in Montana occur on mountain ranges

consisting primarily of metamorphosed sediments of the Belt Series, possibly on granitic intrusions (P. Lesica, pers. comm. 2019) but with specific substrate mostly not indicated on the specimen label.

Distribution.—*Montia parvifolia* var. *batholithica* is known from three population clusters: western Salmon River Mountains in west central Idaho, Bighorn Crags in east central Idaho, and mountains in adjacent Montana. The first two population clusters are in the Idaho Batholith south of the main Salmon River. The majority of collections are from seven known localities in the western Salmon River Mountains, in Valley and Idaho counties, Idaho. Four more collections are known from the Bighorn Crags in Lemhi County, Idaho. Also included in our circumscription of var. *batholithica* are seven additional collections from the Bitterroot, Beaverhead, and Anaconda ranges of Montana.

At least in Idaho, var. *batholithica* is well separated from other forms of *Montia parvifolia*. It is the only representative of the species that occurs in central Idaho south of the main Salmon River Canyon (aka River of No Return), which bisects the central part of the state as a major biogeographic barrier. Elsewhere in Idaho, the species occurs primarily in the northern part of the state, except for isolated occurrences in the Seven Devils Mountains and Centennial Range (addressed in more detail elsewhere). North of the Salmon River Canyon, intermediate and typical forms of *M. parvifolia* can be found in a wide variety of habitats and substrates, mostly from 400 to 1300 m, with the highest known populations approaching 1900 m elevation. In contrast, var. *batholithica* is found only above 2100 m, and no other representatives of *M. parvifolia* overlap its distribution in Idaho, even at lower elevations.

The distinctiveness of var. *batholithica* in Montana is more problematic. Almost all populations from south of Missoula, specifically all populations above 2200 m in the Bitterroot, Beaverhead, and Anaconda ranges, are here included in var. *batholithica*. Unlike the situation in Idaho, however, this distributional range includes other forms of *Montia parvifolia* growing at lower elevations (i.e., below 1900 m) on both sides of the Bitterroot divide; i.e., in the Bitterroot River drainage in Montana and the Selway River drainage in Idaho. The Bass Creek drainage in Ravalli County is particularly intriguing, in that both var. *batholithica* and the intermediate morphotype of *M. parvifolia* have been collected at different elevations in the same drainage; whether these occur in a clinal series or as relatively discrete entities remains to be determined. The intermediate morphotype of *M. parvifolia* has also been collected at two other sites at the east base of the Bitterroot Range: Rock Creek (1310 m, *Lackschewitz 2679,* MONTU; 1160 m, *Stickney 816*, USFS in RM) and Trapper Creek (1860 m, *Cory 1526*, MONTU). The closest population of typical *parvifolia* occurs 25 miles from Bass Creek along Rattlesnake Creek northeast of Missoula, documented by several collections by Kirkwood in the 1920s. In this drainage, the typical form occurs to at least 1220 m in elevation, but the uppermost collection from Rattlesnake Falls, at 1370 m (*Kirkwood 2104*, MONTU), appears to be the intermediate morphotype with only flagelliform stems.

Conservation.—*Given the restricted habitat and relatively few known occurrences (eleven in Idaho, seven in Montana), the conservation status of *Montia parvifolia* var. *batholithica* needs to be evaluated. While there are probably additional populations of these inconspicuous plants to be discovered in remote localities, we can affirm that populations are seldom encountered, even by those of us keeping an eye out for them. Climate change is the most obvious threat, which could significantly reduce available habitat. Other possible threats include mining and recreation.

Biogeography.—*The distribution of *Montia parvifolia* var. *batholithica* primarily coincides with the High Idaho Batholith Ecoregion (HIBE), as described in the EPA Level IV ecoregion map (McGrath et al. 2002). This ecoregion is characterized by the dramatic carving of glaciers from the Pinedale events, 15,000–20,000 ybp (Richmond 1986). Cirques, tarns, moraines, arêtes, horns, and steep headwalls dominate much of the ecoregion, creating a blend of subalpine and alpine habitat. Despite the lack of known glacial extents, the HIBE roughly begins at the lower bounds of the Pinedale alpine glaciers, between 1800 to 2400 m elevation, and continues to peaks over 3000 m elevation (McGrath et al. 2002). The annual precipitation for the HIBE is greater than other nearby Level IV ecoregions and supports *Pinus albicaulis* Engelm., *Abies lasiocarpa* (Hook.) Nutt , *Pinus contorta* Douglas ex Loudon, *Tsuga mertensiana* (Bong.) Carrière, and *Larix lyallii* Parl. in open-canopied parklands or as scattered trees, often as krummholz, among glacial cirques and exposed sites.

Ertter and Moseley (1993) noted that the discontinuous high elevations of the western Salmon River Mountains, now encompassed by the HIBE, provided an example of island biogeography in a continental setting, with each peak harboring a different assemblage of subalpine species. This observation was subsequently pursued as a master's thesis by Johnson (2019), who conducted floristic surveys for 20 peaks of the HIBE and investigated patterns of α- and β-diversity using non-metric multidimensional scaling ordination and clustering approaches. Both Ertter and Johnson encountered var. *batholithica* several times during their respective fieldwork, setting the stage for the current collaborative paper.

Johnson's (2019) research covered only the western and southern portions of the HIBE, which included only the westernmost (western Salmon River Mountains) of the three population clusters of *Montia parvifolia* var. *batholithica*. Within his research area, Johnson found statistical evidence for three distinct floristic cluster groups of HIBE-restricted species, correlated with geography, temperature, precipitation, and topographic ruggedness. He furthermore found trends in species traits (i.e., growth habit, life strategy, dispersal mechanism, and habitat requirements) among the floristic cluster groups that correlated with trends in topographic heterogeneity. These trends were compatible with Graae et al.'s (2018) landscape ecology theoretical framework, which combined concepts from population and community ecology to address meta-community dynamics and landscape heterogeneity.

Montia parvifolia var. *batholithica* occurs primarily in the northernmost of Johnson's three floristic cluster groups (northwest and southwest of Payette Lake), with a single collection (*Johnson & Mortimer 17-230*) from near Log Mountains in the central floristic cluster group (southeast of McCall). Although var. *batholithica* is easy to overlook, the lack of collections from the southeastern floristic cluster group (i.e., Sawtooth and White Cloud mountains) probably is not simply an artifact of collector bias, given that this popular area is if anything more botanized than the other cluster groups. A more likely explanation for the apparent absence of var. *batholithica* from the southeastern part of the HIBE is the environmental variable trend of increasing alpine harshness; i.e , decreasing average annual temperature and increasingly glacially carved topographic ruggedness (Johnson 2019).

ADDITIONAL VARIATION IN *MONTIA PARVIFOLIA*

As previously emphasized, the focus of the current study has been on the taxonomic status of the High Idaho Batholith variant of *Montia parvifolia,* here described as var. *batholithica,* so that it can be addressed in regional conservation efforts. Although we confirm that the complex variation throughout the range of the species is ripe for analysis using modern methodologies, coupled with more extensive fieldwork and common garden studies, doing so is beyond our current scope or future plans. To aid possible future studies by others, we provide this synopsis of our observations on other variants within *M. parvifolia*.

Typical parvifolia.—We assign the majority of populations to the "typical *parvifolia*" form, using basal leaf shape as the primary diagnostic character (Fig. 1). The relatively abundant basal leaf-blades tend to be elliptic, tapering gradually to the petiole basally and acute to obtuse apically. This character is specific to basal leaves as defined in the Results section; stem leaves can resemble those of other variants. Given the narrow focus of our current study, it is quite possible that additional ecogeographically correlated variation exists within this broad circumscription, which includes the types of both *Montia filicaulis* and *M. obtusata*.

Our acceptance of this form as typical *parvifolia* follows established use and is compatible with the brief protologue and the numerous collections of this morphotype from Vancouver Island in British Columbia. However, a full-scale revision of the complex should confirm this application, perhaps with the designation of an epitype for clarification. An initial question is whether the type is the excellent colored drawing cited by de Candolle (accessible as Number 1955 of the Torner Collection of Sessé and Mociño Biological Illustrations, Hunt Institute of Botanical Documentation: https://huntbot.org/torner/illustration/1955), or whether there is a more appropriate extant collection by Sessé and Mociño that de Candolle had access to. The illustration could be a relatively broad-leaved representative of what has usually been considered the typical morphotype, but it cannot be unequivocally excluded from belonging to the same coastal morphotype discussed below that

includes the types of *Claytonia flagellaris* and *Montia sweetseri*. Resolving the status of the type does not affect our recognition of var. *batholithica*, so we defer this challenge to researchers who have more experience with variation in the species on Vancouver Island, especially around the type locality of Nootka Sound.

As here circumscribed, populations of typical *parvifolia* occur in diverse habitats and substrates in the western mountains of central British Columbia to as far south as the Santa Lucia Mountains of Monterey County, California. The variant extends across the mountains of northern California and south in the Sierra Nevada to Fresno County (*Quibell 35* [RSA]), reaching elevations of 2850 m (*Taylor 4309*, Alpine Co., CA [UCD]). In the Sierra Nevada, elevations and habitats are comparable to those of var. *batholithica*, but without the diagnostic morphology. Typical *parvifolia* also extends inland across the mountains of northern Washington, northern Idaho (Bonner, Boundary, and Kootenai counties), and southern British Columbia into northwestern Montana, including Glacier National Park. The species barely enters Alberta, where it is considered critically imperiled. A widely and curiously disjunct population of typical *parvifolia* (*Christ 12858*, ID, WS) from the Centennial Mountains in Clark County, eastern Idaho, should be included in any future study.

Swanson (1966) noted that *M. parvifolia* is the most xerophytic-adapted species in Montiaceae, with a very thick cuticle that separates on drying, and typical *parvifolia* appears to be more xerophytic than other variants. Swanson also proposed that the species' xerophytic adaptations "suggest that ample time was involved in the evolution of these distinctive features."

Intermediates.—The majority of populations assigned to the intermediate morphotype (Fig. 2 [left-hand plant]) form a band separating typical *parvifolia* from var. *batholithica* in north-central Idaho and Montana. The habit somewhat resembles an oversized var. *batholithica*, but pedicels are generally much longer and basal leaf shape and number are intermediate between var. *batholithica* and typical *parvifolia*. Populations occur primarily in rocky shaded sites along rivers, on diverse substrates, primarily metamorphic but also granitic, basaltic, and ultramafic. This is the only variant in the Clearwater River drainage of north-central Idaho, in Clearwater and Idaho counties; representatives of both the intermediate and typical morphotypes occur in the St. Joe Mountains of Kootenai and Shoshone counties. A small isolated population (*Bingham & Miller 573*, Idaho Co., ID [ID]; *Ertter et al. 22974*, same locality [CIC]) is known from the Seven Devils Mountains at the same general latitude as var. *batholithica*, but on a metamorphic substrate at only 1420 m elevation. Bingham (1987) noted that his collection was "intergradient between vars. *parvifolia* and *flagellaris*," and that the species was "scarce" in the Seven Devils Mountains.

Intermediate populations also occur in Montana, mostly north of the range of var. *batholithica* and/or at lower elevations. The transitional situation between intermediate morphotypes and typical *parvifolia* in and around Glacier National Park is unresolved. Most collections from the Wallowa and Blue mountains of northeastern Oregon and adjacent southeastern Washington are also provisionally placed in the intermediate category, though varying toward typical *parvifolia*.

Coastal variant.—The coastal variant of *Montia parvifolia* coincides with collections sometimes segregated with the epithets *flagellaris* or *sweetseri*, relying primarily on the relatively large, broadly obovate-elliptic basal leaves. In addition to leaf shape, the coastal variant tends to have larger flowers (Fig. 5) and a higher percentage of flagelliform stems than typical *parvifolia*. According to Nilsson (1967), *flagellaris* is tetraploid (2*n*=44), in contrast to diploid *parvifolia* (2*n*=22), with this difference also reflected in pollen size. It is unknown to what extent this ploidy difference is uniform throughout each form.

Populations of this variant are strictly coastal, from extreme southwestern Oregon to Chichagof Island in southeastern Alaska. The majority of collections are from Curry County, Oregon, and the islands of southeastern Alaska, with scattered other populations along the coast elsewhere in Oregon, Washington, and British Columbia. This distribution overlaps that of typical *parvifolia*, which also has coastal populations (including the type from Nootka on Vancouver Island). At least one collection from coastal British Columbia (Le Roy Bay at mouth of Smith Inlet, *McCabe 1814* [UC]) is morphologically comparable to var. *batholithica*; its taxonomic significance is uncertain.

Based on samples in our study, the question arises as to whether the coastal variant might actually consist

of two distinct units. The more widespread, which includes the type of *Montia sweetseri*, is best represented in southwestern Oregon, where it occurs on protected cliffs and outcrops. In contrast, populations from the islands of southeastern Alaska, including the type of *Claytonia flagellaris*, are more likely to occur on sandy beaches, gravelly lake shores, and stream beds. Alaska plants also differ in having longer (4 dm+), more tangled stems, with flowering stems often absent. The extent to which these differences are simply responses to different environments, and whether other features (e.g., flower size, seed size, chromosome number) also differ, remains to be determined by future researchers.

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