

Cryptogramma cascadensis, a New Parsley-Fern from Western North America

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The genus *Cryptogramma* R. Br. is widely distributed in the temperate and boreal regions of the northern hemisphere and South America. All but one of the 8–10 taxa recognized belong to section *Cryptogramma* Prantl, which comprises plants commonly known as “parsley-ferns.” Species belonging to this section, as exemplified by the Eurasian species *C. crispa* (L.) R. Br., are small, tufted ferns possessing dimorphic fronds, with erect fertile leaves bearing contracted, linear segments, and shorter, spreading, finely dissected sterile fronds. North American parsley-ferns currently known include the widespread *C. acrostichoides* R. Br., and *C. sitchensis* (Rupr.) T. Moore [*C. acrostichoides* var. *sitchensis* (Rupr.) C. Chr.], a taxon of Alaska and adjacent northwest Canada. The delicate calciphile *C. stelleri* (S. Gmelin) Prantl, the sole member of section *Homopteris* (Rupr.) C. Chr., is widespread in northern North America.

Biosystematic studies of *Cryptogramma* have been conducted with the aim of producing a modern taxonomic treatment of the genus as it occurs in North America. This work has led to the conclusion that in addition to the taxa currently known from North America, an additional undescribed species is worthy of recognition.

The purpose of this paper is to validly publish the name of this species in preparation for the treatment of *Cryptogramma* in *Flora of North America*, and to provide a discussion of the diagnostic features of the new taxon. Additional biosystematic data and an analysis of evolutionary patterns, currently in preparation, will be forthcoming.

***Cryptogramma cascadensis* Alverson, sp. nov.** (Fig. 1)—TYPE: U.S.A., Washington, King Co., 5 km NW of Snoqualmie Pass, above Source Lake along the old trail to Snow lake, on open southeast facing talus of an avalanche track below Chair Peak, T23N R11E S30, 1110 m, 6 Oct 1984, Alverson 876 (holotype OSC, isotypes MO, NY, ORE, UC, WS, WTU).

Ab *C. acrostichoides* R. Br. foliis textura tenuiore, deciduis, non in anno sequenti marcentibus, et ab *C. crispa* (L.) R. Br. foliis sterilibus raro quadripinnatis differt.

Small, clumped, finely dissected ferns with deciduous fronds. Rhizomes decumbent to erect, strongly multicapital, stout, 4–8 mm wide including old attached frond bases; densely clothed with broadly lanceolate to linear scales up to 6 × 2 mm; scales generally bicolorous. Fronds strongly tufted, the fertile erect, 5–25 cm long, the sterile spreading, 3–20 cm long; deciduous and usually not persisting into the following year, soft, glabrous. Stipes ca. 1 mm wide when dry, collapsing and strongly furrowed, green to stramineous, dark brown only at very base; stipe scales like those of the rhizome or more or less concolorous, becoming sparse above. Fronds deltate to ovate-lanceolate, 1/2 to equaling petiole, 2–3

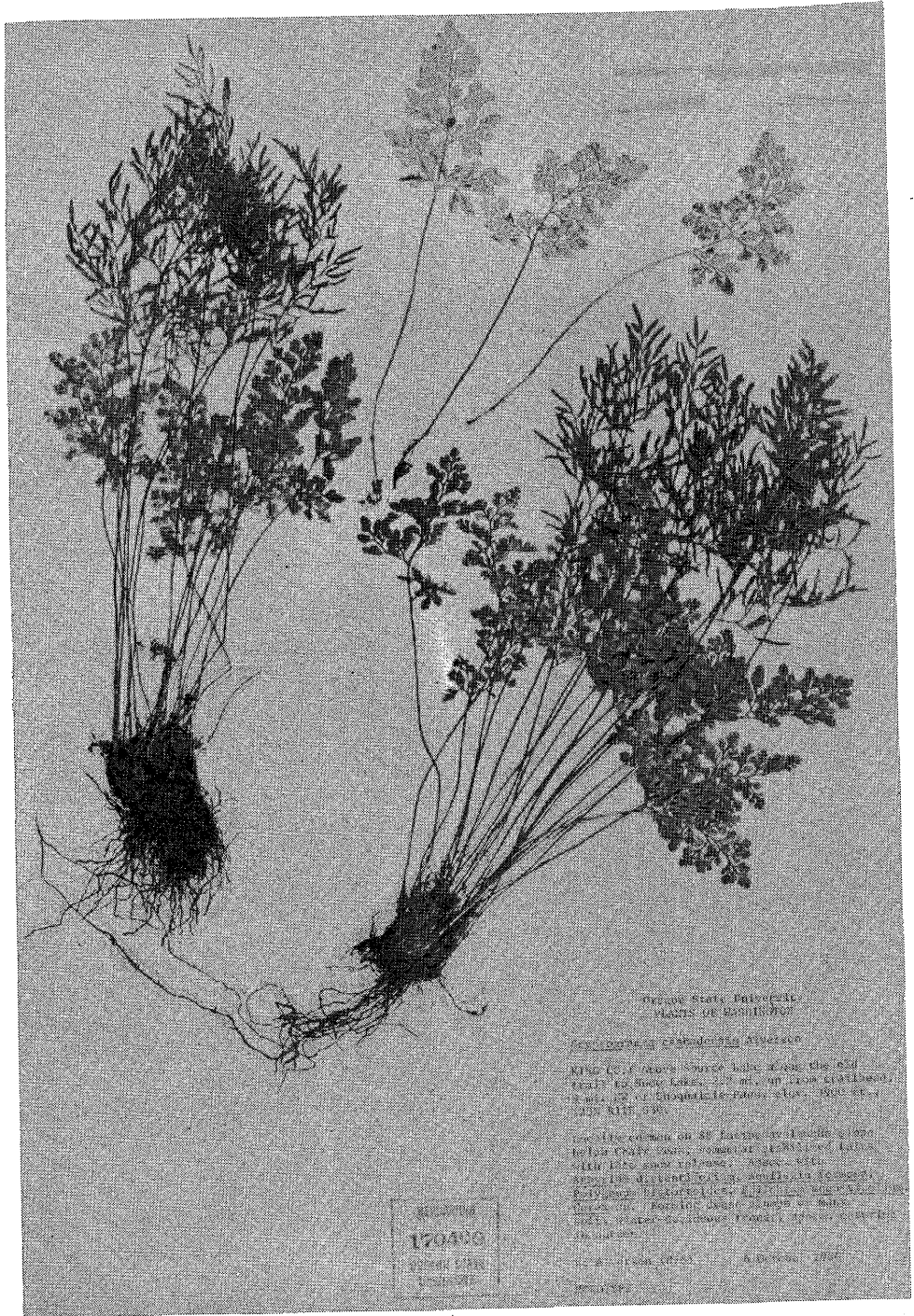


Fig. 1. Photograph of the holotype of *C. cascadensis*.

times pinnate, thin and translucent when dried. Segments of sterile fronds typically cuneate-based, oblong to flabellate, widest at a point $\frac{1}{2}$ to $\frac{2}{3}$ of the way above the base; the apical $\frac{1}{2}$ to $\frac{1}{3}$ regularly dentate, and often more deeply incised every 2nd–4th tooth; segments of fertile fronds ascending to erect, strongly differentiated from sterile fronds, linear, 3–12 \times 1–2 mm; veins free, branching once or twice, veins ending in elongate, clavate to linear, surficial hydathodes. Sori round to oblong, coalescing at maturity, fertile segments revolute, protecting sporangia, at maturity often becoming plane with drying and exposing the receptacular surface; spores tetrahedral, yellow, avg. 49.6 μm in diameter; receptacular paraphyses stalked, capitate, unicellular, often abundant, particularly along the margins of the fertile segments. $2n = 30 \text{ II}$.

Representative specimens: **CANADA. British Columbia.** Selkirk Range, 20 Aug 1885, Macoun s.n. (CAN, NY); Mt. Cheops, 7500 ft, 13 Aug 1904, Heacock 459 (COLO, GH, NY, RM, US); The Lions, 4600 ft, 27 Jul 1961, Peterson s.n. (UBC); Mt. Revelstoke N.P., between Millar Lake and Jade Lake, 7000 ft, 15 Aug 1969, Soper, Shchepanek & Szczawinski 12,491 (CAN, CAS, V); Mt. Lindeman, W of Chilliwack Lake, 14 Sep 1984, Ceska & Ogilvie 18,487 (V). **U.S.A. California.** Eldorado Co., Susie Lake, 7650 ft, 13 Aug 1909, McGregor 108 (CAS, NY, US); Fresno Co., Vidette Meadows, 25 Jul 1916, Campbell s.n. (CAS); Modoc Co., below Eagle Lake, Warner Mts., 7600 ft, 13 Aug 1918, Jepson 7961 (JEPS, MICH); Mono Co., Slate Cr. Basin, E of Mt. Conness, 11,000 ft, 9 Sep 1934, Clausen 993 (CAS, US); Nevada Co., 0.5 mi W of Basin Pk., 8200 ft, 6 Sep 1971, True 6997 (CAS); Plumas Co., Mt. Harkness, Lassen Volcanic N.P., 7400 ft, 23 Jul 1957, Gillett 887 (CAS, JEPS, MICH); Shasta Co., Mt. Lassen, timberline, 9 Aug 1931, Copeland 1424 (CAS, POM, UC); Siskiyou Co., above Horse Camp, Mt. Shasta, 8250 ft, 18 Aug 1938, Cooke 11,502 (CAS, GH, UC); Tehama Co., Brokeoff Mt. Trail, Lassen Volcanic N.P., 7000 ft, 13 Aug 1957, Gillett 1056 (CAS, JEPS, MICH); Tuolumne Co., W of Fairview Dome, Yosemite N.P., 22 Aug 1922, Hall 170 (UC). **Idaho.** Adams Co., Black Lake, Seven Devils Mts., 20 Jul 1931, Johnston s.n. (CAS); Blaine Co., divide between Alpine Creek and Twin Lakes, Sawtooth Primitive Area, 10,000 ft, 30 Jul 1944, Hitchcock & Muhlick 10,500 (NY, UC, UTC, WS, WTU); Bonner Co., Priest River Experimental Forest, 22 Jul 1943, Daubenmire 43,261 (NY, WS, WTU); Elmore Co., 1 mi S of Lower Spangle Lake, Sawtooth Primitive Area, 19 Jul 1944, Hitchcock & Muhlick 10,146 (CAN, CAS, GH, NY, RM, UC, US, UTC, WS, WTU); Idaho Co., Cool Water Mt., 11 Jul 1936, Gail s.n. (ID); Kootenai Co., without locality, 1891, J.B.L. 11, (UC); Shoshone Co., Freezeout Summit, 27 Jul 1958, Baker 15,415 (ID, NY, WTU); Valley Co., Brundage Mt., 7600–7800 ft, 5 Jul 1937, Pennell & Constance 20,749 (US). **Montana.** Missoula Co., Squaw Peak, 2375 m, 7 Jul 1964, Harvey & Pemble 7075 (MONTU); Ravalli Co., Mt. Jerusalem, 9000 ft, 11 Aug 1968, Lackschewitz & Fageraas 693 (MONTU). **Oregon.** Baker Co., W. base of Red Mtn., Wallowa Mts., 7500 ft, 5 Sep 1957, Head 1637 (NY, OSC); Clackamas Co., Breitenbush Lake area, 24 Aug 1962, Rodin 6926 (ARIZ); Deschutes Co., Hidden Lake, Paulina Mts., 8 Jul 1928, Detling 28 (ORE); Douglas Co., Old Bailey Mt., 7 Jul 1924, Applegate 4125 (CAS, WILLU); Hood River Co., near Eden Park, Mt. Hood, 6000 ft, 5 Jul 1926, English 174 (WS); Jackson Co., Mt. Pitt, 7000 ft, 27 Jul 1887, Colville & Applegate 233 (US); Jefferson Co., Three-Fingered Jack, 6500–7000 ft, 5 Sep 1976, Crosby 1073 (OSC); Klamath Co., Wizard Island, Crater Lake N.P., 21 Aug 1949, Baker 6363 (ID, NY, OSC, RSA, UC, WS, WTU); Lane Co., West Lava Camp, McKenzie Pass, 5200 ft, 22 Aug 1937, Ireland 1025 (ORE); Linn Co., Mt. Washington, 6000–7000 ft, 31 Aug 1976, Crosby 991 (OSC); Wallowa Co., Chimney Lake, Wallowa Mts., 21 Jul 1950, Kruckeberg 2367 (CAN, COLO, ID, NY, RSA, WS, WTU). **Washington.** Chelan Co., slopes of Mt. Stuart, 1520 m, 28 Aug 1893, Sandberg & Leiberg 1821 (NY); Ferry Co., Twin Lakes, 3500 ft, 5 Sep 1927, St. John 8874 (WS); King Co., Snow Lake trail, 3600 ft, 22 Sep 1986, Alverson 1036 (OSC); Kittitas Co., Stafford Creek drainage, 1.5 mi SE of Earl Peak, 5800 ft, 14 Aug 1981, Alverson 534 (ORE); Lewis Co., Reflection Lake, Mt. Ranier, 5000 ft, 23 Aug 1901, Flett 1923 (NY, WTU); Pierce Co., Glacier Basin, Mt. Ranier, 6700 ft, Aug 1925, Grant s.n. (CAS, WTU); Skamania Co., Mt. St. Helens, 4500 ft, 4 Aug 1925, St. John et al. 7453 (WS); Snohomish Co., Lake Serene, 2600 ft, 10 Jul 1983, Alverson 584 (ORE); Yakima Co., Wodan's Vale, Mt. Adams, 4 Oct 1902, Suksdorf 2793 (WS).

Morphological comparisons.—This new species has not previously been distinguished from *C. acrostichoides*. The two species are most clearly separated on the basis of habit, texture, and micromorphology, although they also differ more subtly in typical outline and segment shape of sterile fronds.

Evidence from common-garden trials demonstrates that the traits by which *C. cascadenis* and *C. acrostichoides* differ are intrinsic to each species, and not a product of differing environmental conditions. Numerous transplants of both taxa have been cultivated in a greenhouse for three years, and all of the diagnostic differences have been maintained.

The best diagnostic feature distinguishing the two taxa is that the sterile fronds of *C. cascadenis* are fully deciduous in the autumn, while those of *C. acrostichoides* are evergreen or nearly so. In natural habitats, the withered fronds of *C. cascadenis* quickly decay and detach from the rhizome, with little accumulation of dead foliage around the base of the plant. The fronds of *C. acrostichoides* are strongly marcescent, often resulting in the accumulation of a substantial quantity of dead foliage and organic matter at the base of the plant. Though diagnostic for *C. acrostichoides*, these old fronds are often removed by collectors in an effort to "tidy up" specimens, so this character may not always be evident on herbarium specimens.

Fronds of *C. cascadenis* are relatively thin and soft, and upon drying become more or less translucent. The sterile fronds of *C. acrostichoides* are thicker, with a coriaceous texture when mature. The characteristic color of *C. cascadenis* is grass green, while mature fronds of *C. acrostichoides* are a darker verdigris green. Furthermore, the abaxial surfaces of the sterile fronds of *C. acrostichoides* are lighter in color than the adaxial surfaces, in contrast to the uniformly colored surfaces of *C. cascadenis*. The stipes of *C. acrostichoides*, particularly those of the fertile leaves, are rigid and straw-like, even upon drying. Those of *C. cascadenis* are less firm, and upon drying, collapse inward, so that when dry the diameter of the stipes is about 1 mm, compared to the 2 mm diameter typical in *C. acrostichoides*.

Hydathodes occurring at vein endings on the adaxial surface of the fronds of *C. cascadenis* are elongate, clavate to linear, and are flush with the lamina surface. The hydathodes of *C. acrostichoides* are sunken below the lamina surface, due to the thicker, more coriaceous lamina. They are also shorter and wider, typically ovate to shortly clavate in outline, only occasionally approaching linear in outline.

Scattered along both surfaces of the fronds of *C. acrostichoides* are very small, appressed, unbranched cylindrical trichomes. These trichomes are most numerous in the sulca of the rachis and along the costae of the pinnae and pinnules. Such trichomes are essentially lacking in *C. cascadenis*, and their absence is a useful micromorphological character that distinguishes this species.

Fronn outlines and shapes of sterile segments are extremely variable in *Cryptogramma*, even on different fronds of a single plant, a factor that has caused considerable confusion in the past (Fernald, 1935). Both species are characterized by a distinctive "profile," but within-species variability is sufficiently great that these characters are not always diagnostic. Sterile laminae of *C. cascadenis*

are typically deltate in outline, while those of *C. acrostichoides* are often more ovate-lanceolate, but plants with more deltate laminae do occur. Shape of the ultimate segments varies in a similar manner; those of *C. cascadenis* are typically flabellate in outline, while those of *C. acrostichoides* tend to be oblong to ovate-lanceolate, but with considerable variation in each.

In favorable habitats, such as moist subalpine talus slopes, *C. cascadenis* is very strongly multicipital, growing into large patches bearing many hundreds of fronds. *Cryptogramma acrostichoides* is typically much less strongly multicipital, usually forming smaller, discreet clumps.

Evolutionary considerations.—The significance of these morphological distinctions is bolstered by biochemical data obtained from allozyme analysis. Nei's Genetic Identity statistics obtained from an electrophoretic study of 13 populations *C. acrostichoides* and *C. cascadenis* showed a high degree of genetic differentiation between the two species, with a mean genetic identity of 0.36 for interspecific population comparisons (Alverson & Windham, unpubl. data). This value is comparable to genetic identities of congeneric fern species obtained in previous electrophoretic studies (Haufler, 1987).

Cryptogramma cascadenis shares several morphological features with the European *C. crispa*, a tetraploid species with $2n = 60$ pairs of chromosomes (Manton, 1950), such as the thin-textured, deciduous sterile fronds and surficial hydathodes. However, *C. cascadenis*, like *C. acrostichoides*, is diploid with $2n = 30$ pairs of chromosomes (Fig. 2). *Cryptogramma crispa* also differs from *C.*

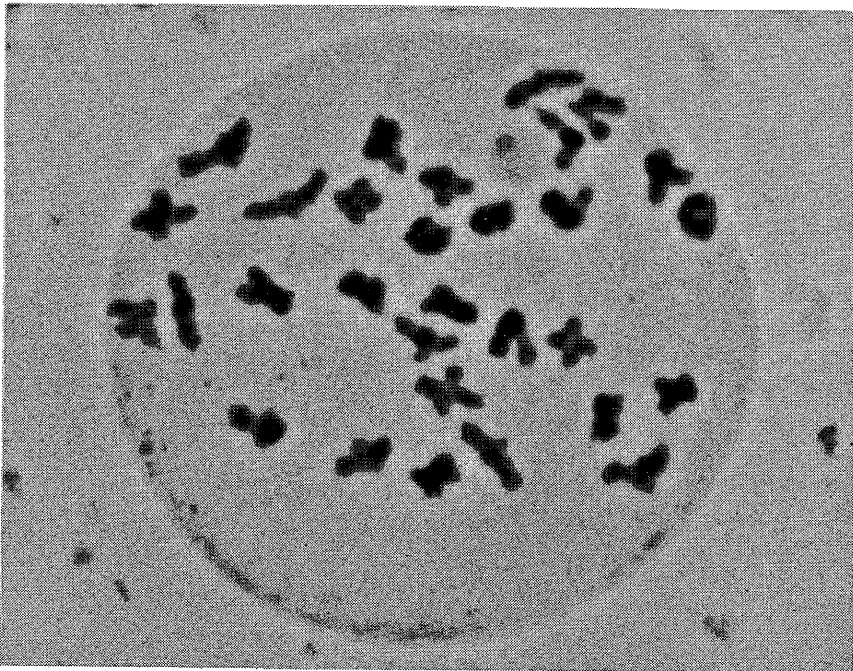


FIG. 2. Meiotic chromosomes of *C. cascadenis* (Alverson 1036, OSC).

cascadensis in several morphological characters, including sterile leaves typically larger and more finely dissected, with many more ultimate segments; firm, straw-like petioles; and concolorous rhizome scales. While the true evolutionary relationship between *C. cascadensis* and *C. crispa* has not been established, their morphological and cytological distinctness suggests that they are not conspecific. Other species of *Cryptogramma* sect. *Cryptogramma* from different geographic regions, such as *C. fumariifolia* (Phil.) Christ of South America, *C. raddeana* Fomin of northeast Asia, and *C. brunoniana* Hook. & Grev. of the Himalayas, all appear by virtue of their evergreen sterile fronds to be more closely allied to *C. acrostichoides* than to *C. cascadensis* or *C. crispa*.

Geographic distribution.—The epithet *cascadensis* refers to the Cascade mountain range, where this species is a typical inhabitant of rocky subalpine habitats. *Cryptogramma cascadensis* occurs along the entire length of the Cascades, from southern British Columbia, through Washington and Oregon, to the volcanic peaks of Mt. Shasta and Mt. Lassen (Fig. 3). The distribution of *C. cascadensis* extends southward in California along the high Sierra as far as Fresno County. A second center of distribution for this species is in the northern Rocky Mountains of Idaho, western Montana, southeast British Columbia, northeast Washington, and northeast Oregon. Here *C. cascadensis* is a representative of the coastal or Cascadian floristic element that is disjunct in the high rainfall regions of the northern Rockies (Daubenmire, 1975). *Cryptogramma cascadensis* typically grows on granitic and volcanic rocks; it occurs, for example, on nearly every volcano in the Cascade Range. Elevations range from as low as 1000 m in the Washington Cascades and as high as 3400 m in the Sierra Nevada. A complete listing of herbarium specimens annotated as *C. cascadensis*, including locality data, is available from the author upon request.

Cryptogramma cascadensis is not known with certainty from the Olympic Mountains of Washington, although suitable habitats must exist. Two herbarium sheets with *C. cascadensis* reputedly collected in the Olympic Mts. have been examined (without specific locality, Piper 1905, WTU; Elwha Basin, Leach & Leach s.n., ORE), but both are mixed sheets also containing plants of *C. acrostichoides*. In the absence of further corroborating evidence, these records are presumed to be in error.

Ecological considerations.—Morphology of *C. cascadensis*, particularly the deciduous habit and thin frond texture, suggest that this is a species most suited to mesophytic habitats in regions with deep winter snow accumulations. In contrast, *C. acrostichoides* is a relatively xerophytic species, with thick evergreen fronds that withstand significant moisture stress, and in addition can photosynthesize in autumn, winter, and early spring (if not covered by snow).

This assessment is supported by field observations. At the type locality in Washington near Snoqualmie Pass, where both species are present, colonies of *C. cascadensis* are generally found in habitats that are released from the snowpack later in the season, either because of concave microtopography, or because of heavy snow accumulation due to winter avalanches. In the subalpine of the Sierra Nevada, at the outlet of Heather Lake, Eldorado Co., California, *C. cascadensis* grows in its typical habitat, a cool, north-facing talus slope. At the

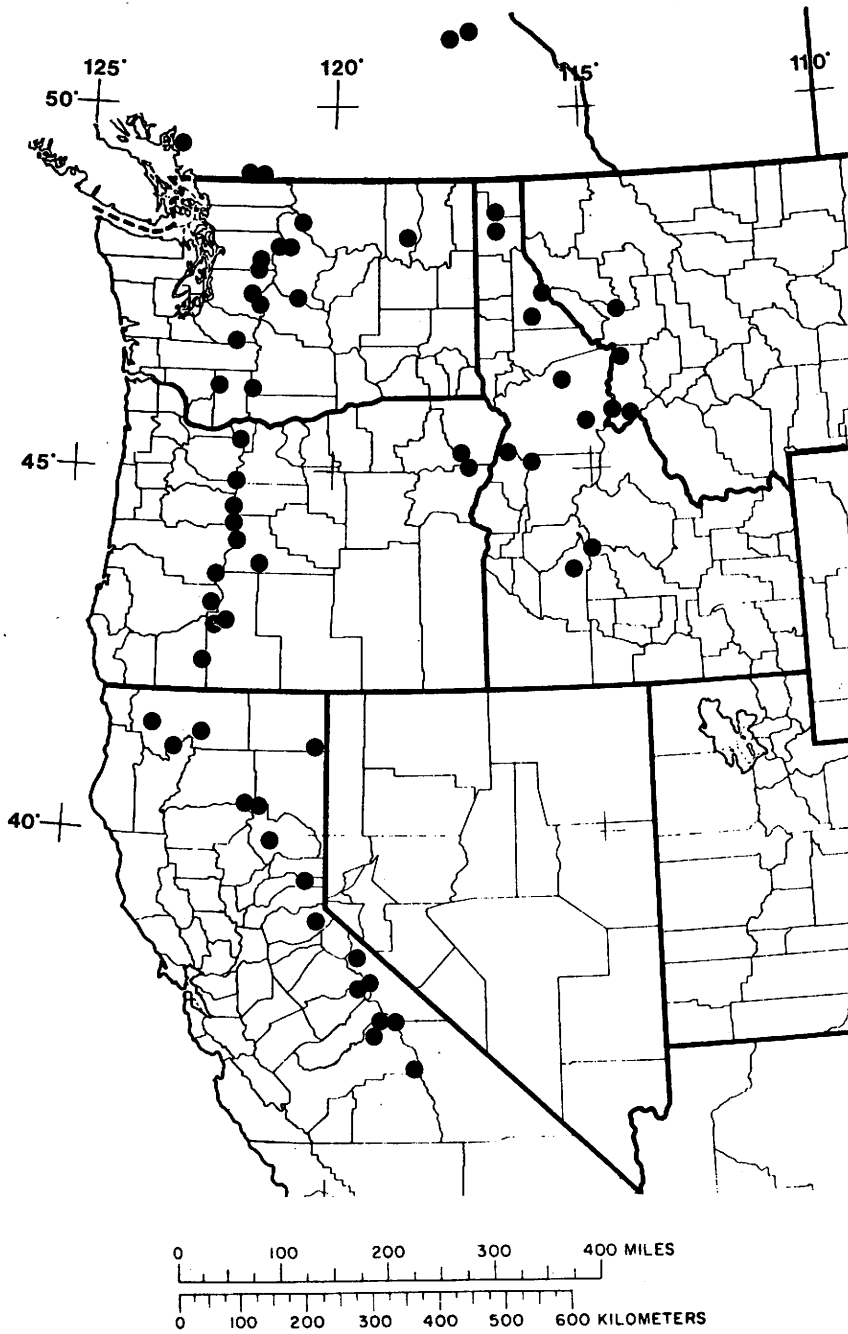


FIG. 3. Geographic distribution of *C. cascadensis*. Each dot represents one or more herbarium collections.

same locality, *C. acrostichoides* is abundant on the opposing south-facing slope, where in late August of 1987 the plants were completely withered by drought.

Like many cheilanthoid ferns, *C. acrostichoides* regularly survives periods of drought with dehydrated, curled, and brittle fronds that readily rehydrate and resume normal functioning when moisture becomes available. *Cryptogramma cascadenis* apparently does not possess this drought tolerance mechanism, and must avoid moisture stress by occupying mesic microsites, such as Heather Lake. When cultivated plants of *C. cascadenis* were left unwatered, their fronds at first wilted, then withered and died, and did not come back to life when watered again. In the texture and color of its foliage, *C. cascadenis* is remarkably similar to *Athyrium alpestre* ssp. *americanum*, a common associate in moist subalpine habitats, a convergence attributable to selection for similar ecological conditions.

The consistent correlation of a suite of subtle but distinct morphological features with characteristic ecological requirements and a coherent geographical range provides ample evidence that an additional distinct member of the *Cryptogramma crisa* complex, *Cryptogramma cascadenis*, is present in western North America.

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LITERATURE CITED

- DAUBENMIRE, R. 1975. Floristic plant geography of eastern Washington and northern Idaho. *J. Biogeogr.* 2:1-18.
- FERNALD, M. L. 1935. Critical plants of the upper Great Lakes region of Ontario and Michigan. *Cryptogramma crisa* and *C. acrostichoides*. *Rhodora* 37:238-247.
- HAUFLER, C. H. 1987. Electrophoresis is modifying our concepts of evolution in homosporous pteridophytes. *Amer. J. Bot.* 74:953-966.
- MANTON, I. 1950. *Problems of Cytology and Evolution in the Pteridophyta*. Cambridge: University Press.