

Rhodora

JOURNAL OF THE
NEW ENGLAND BOTANICAL CLUB

Vol. 93

April 1991

No. 874

RHODORA, Vol. 93, No. 874, pp. 105–122, 1991

ADIANTUM VIRIDIMONTANUM, A NEW MAIDENHAIR FERN IN EASTERN NORTH AMERICA

CATHY A. PARIS

ABSTRACT

Recent systematic work on the *Adiantum pedatum* L. complex has demonstrated that the serpentine maidenhair fern in eastern North America, to which the name *A. pedatum* L. var. *aleuticum* Rupr. has traditionally been applied, is a disjunct member of the western North American lineage, a lineage divergent at the species level from the typical maidenhairs of the eastern woodlands. Also present in eastern North America is a previously unrecognized tetraploid species, the allopolyploid derivative of a sterile hybrid between the serpentine and the typical maidenhair ferns. Here a description of the new species is provided and a new combination is proposed for the western North American maidenhairs, including the disjunct serpentine populations in eastern North America. Although phenotypic plasticity, the existence of the previously unrecognized allotetraploid, and the presence of backcross hybrids have obscured species boundaries, the three species in North America are morphologically distinct and can be reliably separated using non-technical characters.

Key Words: *Adiantum*, maidenhair ferns, serpentine vegetation, Vermont

The *Adiantum pedatum* complex, the northernmost element of a genus widespread in the Old and New World tropics, is widely distributed in temperate regions of North America, eastern Asia, and the Himalayas. In eastern North America, two taxa have traditionally been recognized, *A. pedatum* L. *sensu stricto* and a smaller maidenhair of serpentine substrates, first reported by Fernald from the Shickshock Mountains of Québec (Fernald, 1905). Fernald referred this new maidenhair to *A. pedatum* L. var. *aleuticum* Rupr., the common maidenhair of wet rocks and ravines from California and Idaho north to Alaska. The occurrence of *A. pedatum* var. *aleuticum* and other western cordilleran species on the Gaspé Peninsula later figured in Fernald's argument that large areas of the Gulf of St. Lawrence region remained unglaciated

during the Pleistocene (Fernald, 1925; Paris, 1989). *Adiantum pedatum* var. *aleuticum* was subsequently located on numerous serpentine outcrops throughout southeastern Canada and New England (Jolley, 1922; Rugg, 1922; Mousley, 1923; Gawler, 1983; Zika and Dann, 1985).

Cody (1983) re-evaluated the relationship of the eastern serpentine maidenhair to those of the western mountains and concluded that Fernald was mistaken. After having examined more than 400 sheets of *Adiantum pedatum* from various habitats on both sides of the continent, Cody concluded that non-serpentine populations in western North America were even more distinct from the serpentine maidenhair than they were from the typical variety. He thus removed the serpentine maidenhair from *A. pedatum* var. *aleuticum* and described a new taxon, *A. pedatum* L. ssp. *calderi* Cody, comprising the maidenhairs on serpentine and sometimes dolomitic substrates in northeastern North America, Washington, and California. A chromosome count of $n = 29$ was provided for the new taxon, the same as for ssp. *pedatum* and ssp. *aleuticum* (Cody, 1983).

The relationship of the serpentine and the typical maidenhairs was recently clarified in a systematic study of the *Adiantum pedatum* complex in eastern North America (Paris and Windham, 1988). Results of an electrophoretic survey of two serpentine and six woodland (i.e., typical) populations showed that the two taxa are well differentiated genetically: the mean genetic identity value of .49 obtained for between-taxon population comparisons is typical in the ferns of congeneric species, not subspecies or varieties (Haufler, 1987). The low genetic identity of the two maidenhairs indicated that they are probably not related as progenitor and derivative. On the basis of preliminary isozyme evidence, Paris and Windham (1988) proposed that the eastern serpentine maidenhair was most closely allied to those of the western mountains, the relationship originally suggested by Fernald. Another important result of the study was the detection of a third species in eastern North America, an allotetraploid derived from a sterile hybrid between the serpentine and typical maidenhairs. The new species is so far known only from a few serpentine outcrops in north-central Vermont. Evidence for the allopolyploid origin of the new species has been presented elsewhere (Paris and Windham, 1988).

Ongoing isozyme and chloroplast DNA studies of the *Adiantum pedatum* complex worldwide indicate that maidenhairs in North

America represent two discrete lineages: *A. pedatum sensu stricto*, the typical maidenhair of eastern woodlands; and a western lineage, to which Ruprecht (1845) gave the name var. *aleuticum*. Results of these molecular studies confirm that the maidenhair on serpentine in eastern North America is a disjunct member of the western lineage (Paris and Stein, 1989; Paris, unpubl. data).

The new information on evolutionary relationships within the *Adiantum pedatum* complex demonstrates that taxonomic revision of the group is in order. The purpose of the present contribution is to provide a description of the new tetraploid species, to make a new combination at the species level for the western North American lineage in the *A. pedatum* complex, and to supply a key to the three species in North America.

LEAF ARCHITECTURE IN *ADIANTUM PEDATUM* S.L.

Fundamental to an accurate and comprehensible description of taxa in the *Adiantum pedatum* complex is a correct understanding of leaf architecture in the group. The *A. pedatum* leaf has traditionally been misinterpreted as pedately divided, with arching pinnae borne on the upper side of a dichotomizing rachis. This description is unlikely, however, in that dichotomizing axes are otherwise unknown in the Polypodiaceae *sensu lato*. Apparently the developmental program in this group of ferns is dedicated to the production of a pinnate leaf. Although Slosson (1906) provided a largely accurate explanation of *A. pedatum* leaf architecture, and Wagner (1952, 1956) subsequently improved upon it, these works have not yet influenced the way maidenhair leaves are described in the literature. The observations of Slosson and Wagner are summarized here as a basis for an accurate description of the maidenhair leaf in this and subsequent contributions.

Adiantum pedatum shows a heteroblastic series from simply pinnate leaves to leaves with the basal pinnae progressively elaborated. Leaf complexity is increased in successively older plants by increasing enlargement and dissection of the basal basisopic segments of the first and second basal pinnae, a pattern that is reiterated in higher order divisions of the basal pinnae (Slosson, 1906, *see* p. 42, plate 3, figs. 9 & 10). Because it is always the basal basisopic segment that is elaborated, without proliferation of the corresponding acroscopic segment, each order of dissection features paired segments with the basal acroscopic member simple and the basal basisopic member compound. This pattern pro-

duces a leaf in which isolated simple segments (the acroscopic members of segment pairs) alternate with pinnate axes along what appears to be the acroscopic side of an arching dichotomous rachis (Figure 1). Spatial constraints on the pattern of reiterated basal basiscopic development produce the familiar fan-shaped leaf blade. The major fork in the blade axis is produced by the departure of the much enlarged first basal pinna from the rachis, and so does not represent a true dichotomy (Wagner, 1952). The second basal pinna, though similarly enlarged, does not form a conspicuous fork.

Leaf architecture in *Adiantum pedatum* follows from a simple modification of the standard pattern of leaf development in the higher ferns; thus it is both appropriate and advisable to use standard terminology (Tryon, 1960) to describe the maidenhair leaf. The rachis of the maidenhair leaf is a continuation of the petiole axis, as it is in most ferns, but it has been displaced laterally by the greatly enlarged first basal pinna (Figure 1). Located to the other side of the rachis is the main axis of the second basal pinna. The next "branches" outward from these two are the proliferated basal basiscopic segments of the basal pinnae, and so forth. The term *pseudopedate* is suggested for the modified-pinnate type of leaf architecture found in *A. pedatum* and a few of its congeners (e.g., *A. aleuticum*, *A. hispidulum*, *A. oatesii*, *A. patens*), in preference to *pedate*, which describes a palmate leaf design.

NEW SPECIES

***Adiantum viridimontanum* Paris sp. nov. (Figure 2)**

Ab *Adianto pedato* L. et *A. aleutico* (Rupr.) Paris indusio falso longiore saepe plus quam 3.5 mm, sporis grandioribus circa 51.3 μm in diametro differt; illo segmentis ultimis triangularibus acutis, chartaceis, marginibus basiscopicis obliquis; hoc petiolulis longioribus.

Medium-sized terrestrial fern. Rhizomes slender, 2.0–3.5 mm diam., short-creeping, branching occasionally; rhizome scales concolorous bronzy-fulvous, lustrous, lanceolate, attenuate, with an ephemeral, filiform, \pm tortuous apex, entire, conform, loosely appressed. Leaves deciduous, 30–75 (–90) cm long, arching to stiffly erect, often densely clustered, anadromous (in some leaves, the higher order divisions catadromous); petioles castaneous to

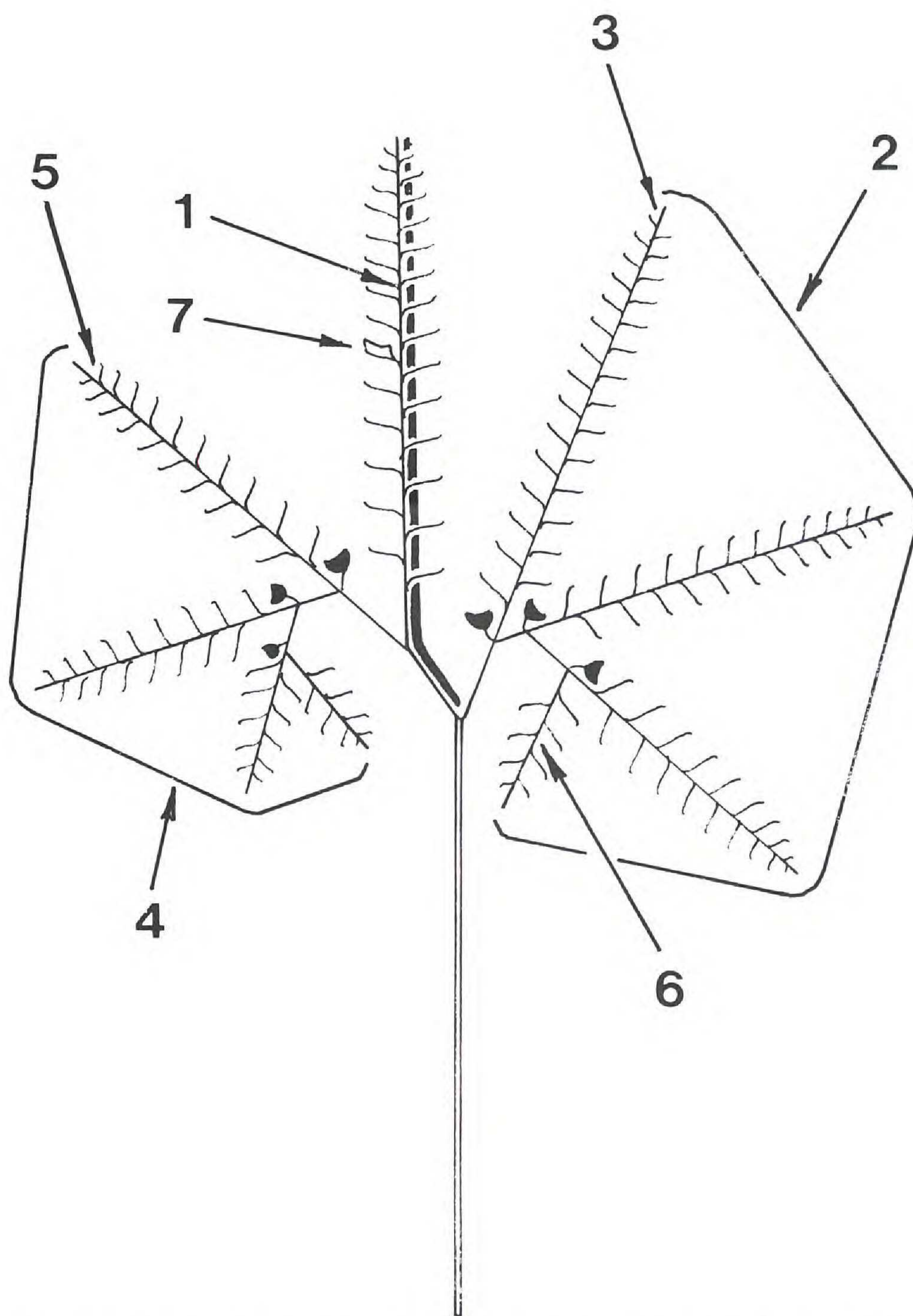


Figure 1. Schematic representation of the pseudopedate leaf of *Adiantum pedatum* and several of its congeners, including *A. aleuticum* and *A. viridimontanum*. 1 = rachis (shaded); 2 = first basal pinna; 3 = axis of first basal pinna; 4 = second basal pinna; 5 = axis of second basal pinna; 6 = highest-order axis; 7 = medial ultimate segment. Shaded segments are the simple acroscopic members of segment pairs, which alternate with pinnate axes along what appears to be the acroscopic side of an arching dichotomous rachis.



Figure 2. Holotype of *Adiantum viridimontanum* (Belvidere Mountain, Eden, Vermont, 28 August, 1985, *Paris 856* (vT)).

atropurpureous, lustrous, 2.0–3.0 mm diam., with a single, gutter-shaped vascular bundle, petiole scales similar to the rhizome scales but more or less spreading, tortuous, fugacious except at petiole base; blades flabellate in shade to funnel-shaped in full sun (flattened in pressed specimens), pseudopetate, 10–35 × 10–

35 (–45) cm, basal pinnae (2–) 3–7-pinnate and much enlarged basiscopically, blade 1-pinnate above, the apical part of the blade narrowly oblong to lanceolate, scarcely exceeding the basal pinnae; rachis castaneous to atropurpureous, lustrous, straight, displaced somewhat by the first basal pinna, 1–2 mm diam., glabrous. Ultimate segments long-triangular, 9.5–22.5 × (3.8–) 4.2–7.5 mm, ca. 2.5 times as long as broad; borne in the plane of the blade in shade, often twisted out of the plane of the blade in full sun; the acroscopic margin lobed, the lobes separated by narrow (usually less than 1.0 mm) incisions; the basiscopic margin oblique; the apex acute, usually entire; firm-herbaceous to chartaceous; glabrous; stalks short, (0.4–) 0.6–1.5 (–1.9) mm, the dark color commonly passing into the segment base; fertile segments with marginal lobes recurved to form conspicuous false indusia, these transversely oblong, mostly 2–5 (–10) × 0.6–1.4 mm, dark brown at maturity, with scarious margins. Sori more or less round, subterminal on veins that end in the false indusium, borne on the abaxial surface of the false indusium. Spores tetrahedral-globose, yellow, mostly 45–58 μm diam. (mean = 51.4 μm diam.), perispore smooth. Gametophytes superficial, cordate, glabrous. $n = 58$ (Paris and Windham, 1988).

Sporulating summer-fall. Restricted to serpentine sites, where it occurs in rock clefts, on talus slopes, and in well-developed serpentine soils. 245–800 m. North-central Vermont.

TYPE: U.S.A. Vermont. Lamoille Co., Eden: Belvidere Mountain, exposed SE-facing talus slope at the pit of the old asbestos mine, 800 m, 28 August, 1985, *Paris 856* (HOLOTYPE: VT; ISOTYPES: GH, US).

ADDITIONAL SPECIMENS EXAMINED: U.S.A. Vermont: Lamoille Co.: **Eden:** Belvidere Mountain, exposed SE-facing talus slope at the old asbestos mine, 800 m, *Paris 341* (NY); dry embankment, road to the old asbestos mine, in rocky but well-developed soil, 770 m, *Paris 337* (VT); road to the old asbestos mine, in well-developed soil, in shade, 750 m, *Paris 208* (VT); *Mrs. Jolley, s.n.* in July 1922 (GH); Orleans Co.: **Lowell:** dunite roadcut, N & S sides of Vt. Rte. 58, ca. 0.5 mi. W of Vt. Rte. 100, 275 m, *Dann & Zika 6156* (VT); dunite roadcut, E side of Vt. Rte. 100, at the Lowell town line, 260 m, *Paris 888 & 889* (VT); E- and W-facing dunite outcrops, Brown's Ledges, 450 m, *Dann & Zika 6168 & 6169* (VT); **Westfield:** dunite knob near Mineral Springs Brook, 245 m, *Dann 8323* (VT); Franklin Co.: **Montgomery:** *Mrs. Jolley s.n.* in 1924 (GH).

Adiantum viridimontanum, the Green Mountain maidenhair fern, is the allotetraploid derivative of a hybrid between *A. pe-*

datum sensu stricto and *A. aleuticum* (Paris and Windham, 1988). The species reproduces sexually and 64 normal spores are formed at meiosis. Presumed to be of recent origin, it is at present known from only five locations, all on serpentine, in north-central Vermont. Mrs. F. L. Jolley first located the plant (identified as *A. pedatum* var. *aleuticum*) in 1922, at the asbestos mine on Belvidere Mountain. The other four stations were found by Vermont botanists Peter Zika and Kevin Dann (Zika and Dann, 1985). Mrs. Jolley's 1924 Montgomery station has not been relocated. Additional populations of the species may eventually be discovered elsewhere in Vermont and southern Québec, particularly in the vicinity of the asbestos mines in the Black Lake area of Megantic Co.

NEW COMBINATION

Adiantum aleuticum* (Ruprecht) Paris, *stat. et comb. nov.

- Adiantum pedatum* L. var. *aleuticum* Ruprecht, *Distr. crypt. vasc. Ross.* 3: 49. 1845. LECTOTYPE (here chosen): Unalaska, *Chamisso* (fragment ex LE, NY!). The remaining syntype is: Kadiak, Langsdorf. *A. pedatum* L. ssp. *aleuticum* (Ruprecht) Calder & Taylor, *Canad. J. Bot.* 42: 1388. 1965.
- A. pedatum* L. var. *subpumilum* Wagner in Wagner & Boydston, *Canad. J. Bot.* 56: 1727. 1978. TYPE: British Columbia: Brooks Peninsula, NW Vancouver Island, 27 June, 1977. *J. Pojar & F. Boas 770191* (HOLOTYPE: MICH; ISOTYPES: v, UBC!). *A. pedatum* L. subsp. *subpumilum* (Wagner in Wagner & Boydston) Lellinger, *Amer. Fern J.* 74: 62. 1984.
- A. pedatum* L. ssp. *calderi* Cody, *Rhodora* 85: 93. 1983. TYPE: Québec, Gaspé County, cold, sheltered ravines, Mt. Albert, 14 August, 1905. *J. F. Collins & M. L. Fernald s.n.* (HOLOTYPE: DAO; ISOTYPE: GH!).
- Adiantum boreale* K. Presl, *Tent. Pterid.* 158. 1836, *nom. nud.* Collection cited: Unalaska, *Chamisso*.

Adiantum aleuticum is the common maidenhair of the Sierra Nevadas, the Cascades, and the Coast Range, from central California north to Glacier Bay, Alaska, and west through the Aleutian Islands. Disjunct populations occur in the northern Rocky Mountains of Idaho, where it is part of the Cascadian floristic element there (Alverson, 1989), and on serpentine in southeastern Canada and northeastern U.S.A. Collections have also been reported from dolomites in Newfoundland (cited in Cody, 1983); these reports may be in error, as the taxon does not occur on dolomites elsewhere in northeastern North America.

Adiantum aleuticum occurs in a variety of habitats throughout its range. In western North America, it is most common in humid,

wooded ravines and on creek banks, but it is also found on sunny talus slopes, serpentine barrens, wet rock fissures, and coastal headlands. In eastern North America it is limited to serpentine. Although there are morphological differences among populations in these diverse habitats, the differences are not consistent or predictable. More significantly, genetic divergence among populations in these various habitats is limited, as shown by the results of chloroplast DNA and isozyme studies of the group (Paris and Stein, 1989). In consequence, infraspecific taxa are not here recognized within *A. aleuticum*.

KEY TO THE *ADIANTUM PEDATUM* COMPLEX IN
NORTH AMERICA

The following key is written to work equally well with living or preserved materials; characters not observable in most herbarium specimens are therefore excluded. Problematic individuals may be backcross or diploid hybrids and should be examined for abortive spores.

1. Medial ultimate segments \pm oblong; blade lax-arching, flabellate; plants generally growing in shade 2.
2. Medial ultimate segments usually less than 3.2 times as long as broad, the apices with rounded, crenulate or crenato-denticulate lobes, these separated by shallow sinuses 0.1–2.0 (–3.7) mm deep, incisions in acroscopic margin narrow, generally less than 1.0 mm broad, borne on stalks ca. 0.6–0.9 mm; eastern North America
. *A. pedatum*
2. Medial ultimate segments usually more than 3.2 times as long as broad, the apices with angular, sharply denticulate lobes, these separated by deeper sinuses 0.6–4.0 mm, incisions in acroscopic margin broader, mostly greater than 1.0 mm broad, borne on stalks up to 0.6 mm long; western North America *A. aleuticum*
1. Medial ultimate segments \pm long-triangular; blade arching to stiffly erect, flabellate to funnel-shaped; plants generally growing in exposed situations 3.
3. Medial ultimate segments borne on stalks shorter than 0.9 mm; false indusia mostly less than 3.5 mm long; spores mostly less than 47 μ m diam.; western North America, disjunct on serpentine in eastern North America
. *A. aleuticum*

3. Medial ultimate segments borne on stalks generally longer than 0.9 mm; false indusia longer, the longest frequently exceeding 3.5 mm; spores mostly greater than 47 μm diam.; serpentine outcrops in north-central Vermont *A. viridimontanum*

PATTERNS OF VARIATION AND TAXONOMIC CHARACTERS

Although *Adiantum pedatum* and its allies occur in a region whose flora is among the best known in the world, a satisfactory taxonomic treatment of the group has so far eluded botanists despite several worthy efforts in that direction. Disagreement has occurred because patterns of variation within the *A. pedatum* group are complex, and there is a general incongruence of the genetic and phenetic units within it, especially in *A. aleuticum*. Nevertheless, the species are distinct and can be reliably separated using standard morphological characters (Table 1).

Intraspecific Variation in *Adiantum aleuticum*

A particular challenge to the maidenhair-fern taxonomist has been presented by *Adiantum aleuticum*, a species in which phenotypic plasticity is superimposed on abundant genetic variation. Based on field observations (my own and others', e.g., Fernald, 1905; Alverson, pers. comm.), degree of exposure, particularly to light, is the key environmental variable to which morphology is responding in that species. In full sun, *A. aleuticum* has stiffly erect, funnel-shaped leaf blades and small ultimate segments twisted on their stalks; in the shade it bears a greater resemblance to *A. pedatum*, with lax-arching leaf blades and larger ultimate segments borne in the plane of the blade. Morphological variation in *A. aleuticum* presents itself as an array of forms that grade insensibly into one another according to degree of insolation; there are no gaps delimiting subspecies. Nevertheless, several subspecific taxa have been recognized and so deserve comment.

The serpentine maidenhair fern, referred by Fernald (1905) to *Adiantum pedatum* var. *aleuticum*, was recognized by Cody (1983) as a distinct taxon, *A. pedatum* subsp. *calderi*. Considering the evidence, I concur with Fernald, though I recognize *aleuticum* as specifically distinct from *pedatum*, as stated previously. To fairly evaluate the status of the serpentine maidenhair fern, it must be

considered in the context of the species as a whole. In eastern North America, the serpentine and the non-serpentine maidenhair ferns represent different species. The former, part of *A. aleuticum*, is almost always stiffly erect, whereas the latter, *A. pedatum*, is lax-arching. Thus the two are seldom confused, although species boundaries have been blurred to some extent by hybridization and allopolyploidy. In western North America, however, maidenhairs are all part of the ecologically diverse and morphologically variable *A. aleuticum*; in the west, plants on serpentine are dubiously distinct from those in exposed but non-serpentine localities. Compare, for instance, a serpentine collection (e.g., Paris 268, [VT], Scheele Mine, Twin Sisters Mountain, Washington) with one from an exposed non-serpentine site (e.g., Van Dyke 67, [GH], Unalaska, Alaska—the type locality for subsp. *aleuticum*). Both collections have leaf blades equivalently small and stiffly erect, with ultimate segments twisted on their stalks. By contrast, plants growing in shaded microsites on serpentine barrens (e.g., Paris XX.C, [VT], Horse Mountain, Trinity Mountains, California) have lax leaves similar to plants in wooded non-serpentine sites (e.g., Paris 274, [VT], Perry Creek Trail, Mt. Baker–Snoqualmie National Forest, Washington). Although variation in characters such as stature and leaf attitude is obviously related to habitat in *A. aleuticum*, such variation is not entirely the result of phenotypic plasticity. Results of common garden trials show that the distinctive characters of plants from serpentine areas and other exposed sites persist to some extent in common culture, indicating that the character state differences have a genetic basis. Thus it appears that ecotypic differentiation is occurring under different light regimes in *A. aleuticum*; the maidenhairs of serpentine soils and other open, sunny sites on lithosolic substrates might best be considered a set of ecotypes. Recognition of the serpentine maidenhair as a distinct subspecies, however, is untenable.

Another taxon that has been recognized in the lineage now designated *Adiantum aleuticum* is *A. pedatum* subsp. *subpumilum* (Wagner *in* Wagner and Boydston) Lellinger, a dwarf maidenhair of coastal cliffs in the Pacific Northwest. This taxon, well known to horticulturalists, was only recently (in 1977) located in nature; currently three stations are known. Plants referred to subsp. *subpumilum* are diminutive in stature and have imbricate ultimate segments with excavate basiscopic margins, characters for which

Table 1. Comparison of *Adiantum pedatum*, *A. aleuticum*, and *A. viridimontanum*. The eastern serpentine maidenhair (part of *A. aleuticum*) is also shown separately (ES). Asterisks mark the characters that best discriminate species. Nu-

Character	Species	
	<i>A. pedatum</i>	<i>A. aleuticum</i>
PLANT HEIGHT	40–75 cm	15–110 cm
RHIZOME		
*Internode length	2.0–10.0 mm	1.0–5.0 mm
*Branching	occasionally to frequently (rhizome not congested)	occasionally to frequently (rhizome congested or not)
LEAF		
Attitude	lax-arching	lax-arching to stiffly erect
BLADE		
Shape	flabellate	flabellate to funnel-shaped
Recurvature, highest order axes of basal pinnae	recurved toward petiole	recurved to spreading or ascending
Dissection, basal pinnae	3–9-pinnate	(1–) 2–7-pinnate
Rachis, length relative to axis of first basal pinna	0–30 mm	0–54 mm
Apex	obtuse to acute	acute to occasionally obtuse
MEDIAL ULTIMATE SEGMENTS		
Shape	oblong	oblong, long-triangular, or occasionally reniform
Length	14–26 (–28) mm	6–34 mm
Width	5–9 mm	4–9 mm
L/W ratio	2.2–3.7 (–4.0)	1.4–4.4 (–4.8)
Attitude	in plane of blade	in plane of blade in shade, twisted out of plane in full sun
Breadth of incisions, acroscopic margin	0.0–0.9 (–1.1) mm	0.2–3.0 mm
Basiscopic margin	straight	straight, oblique, or occasionally excavate
Apex	obtuse, with rounded, crenulate, or crenatodenticulate lobes, these separated by shallow sinuses	obtuse, with angular, sharply denticulate lobes, these separated by deeper sinuses; or acute, entire

merals in the righthand column indicate treatments in which a given character was used in keys or diagnoses. 1 = Ruprecht, 1845; 2 = Fernald, 1950; 3 = Calder and Taylor, 1968; 4 = Cody, 1983; 5 = Lellinger, 1985.

Species		Treatments
<i>A. aleuticum</i> (ES)	<i>A. viridimontanum</i>	
15–59 (–64) cm	30–75 (–90) cm	1, 4
1.0–2.0 mm frequently (rhizome congested)	4.0–7.5 mm occasionally (rhizome seldom congested)	2, 3, 4 2
mostly stiffly erect	arching to stiffly erect	2, 3, 4, 5
mostly funnel-shaped mostly ascending	flabellate to funnel-shaped usually spreading to ascending	2 2, 3, 4, 5
1–6 (–7)-pinnate	(2–) 3–7-pinnate	1, 3
0–30 mm	3–45 mm	
acute to occasionally obtuse	acute	5
long-triangular	long-triangular	
6–18 (–21) mm 3–7 (–8) mm 1.4–3.0 (–3.5)	9–23 mm 4–8 mm (1.4–) 1.7–3.5	2, 3, 4, 5
in plane of blade in shade, twisted out of plane in full sun	in plane of blade in shade, twisted out of plane in full sun	2
0.0–0.9 (–1.1) mm	0.0–1.0 (–1.2) mm	3, 4
oblique	oblique	
acute, entire	acute, usually entire	3, 5

Table 1. Continued.

Character	Species	
	<i>A. pedatum</i>	<i>A. aleuticum</i>
Color	bright green	bright to bluish-green, occasionally glaucous
Texture	weakly herbaceous to herbaceous	herbaceous to chartaceous
*Stalk length	0.5–1.5 (–1.7) mm (\bar{x} = 0.9 mm)	0.2–0.9 (–1.3) mm (\bar{x} = 0.6 mm)
FALSE INDUSIUM		
Length	1.0–3.0 mm	0.2–3.5 (–6.0) mm
Width	0.3–1.0 mm	0.2–1.3 mm
*SPORE SIZE (diameter)	32–42 (–46) μm (\bar{x} = 37.0 μm)	(31–) 34–53 μm (\bar{x} = 43.6 μm)
CHROMOSOME NUMBER	$n = 29$	$n = 29$
HABITAT	deciduous woodlands, often on humus-covered talus	moist, wooded ravines, serpentine areas, coastal cliffs, etc.

the plants breed true (Wagner and Boydston, 1978). Although the dwarf maidenhairs differ from other members of the species in several noteworthy characteristics, observations of the plants in nature call their subspecific status into question. At the one station I have visited, typical “subpumilum-type” plants occur on cliff faces exposed to the sea, but away from the cliffs and back up the canyons, plants look more like normal *A. aleuticum*. Between the two extreme forms, a range of intermediates exists. This pattern of variation along an environmental gradient suggests that the dwarf plants of the cliff faces represent an ecotype, not a subspecies. In consequence, subsp. *subpumilum*, like subsp. *calderi*, is not maintained in the present treatment.

Interspecific Comparisons

In eastern North America, *Adiantum pedatum sensu stricto* and *A. aleuticum* are most reliably distinguished using attributes of the ultimate segments, though they also differ in size, rhizome habit, leaf attitude, texture, color, dissection, mean spore size, and habitat preference (Table 1). More problematic is distinguishing

Table 1. Continued.

Species		
<i>A. aleuticum</i> (ES)	<i>A. viridimontanum</i>	Treatments
usually bluish-green, glaucous	bright to bluish-green	2, 3, 4, 5
mostly chartaceous	firm-herbaceous to chartaceous	2
0.3–1.3 mm (\bar{x} = 0.7 mm)	(0.4–) 0.6–1.5 (–1.9) mm (\bar{x} = 1.1 mm)	
0.8–2.9 (–3.4) mm	2.0–5.0 (–10.0) mm	2, 3, 4, 5
0.5–1.3 mm	0.6–1.4 mm	
(31–) 34–52 (–53) μm (\bar{x} = 43.0 μm)	(35–) 41–62 (–69) μm (\bar{x} = 51.4 μm)	
n = 29	n = 58	
serpentine	serpentine	

A. pedatum from *A. aleuticum* as it appears in moist, wooded ravines, its most common habitat in the American West. Although the western maidenhair fern (as *A. pedatum* ssp. *aleuticum*) has been described as having “branches (of the fronds) usually strongly ascending” (Calder and Taylor, 1968; Cody, 1983), that character is by no means diagnostic: in the shade, *A. aleuticum* has a lax-arching leaf blade much like that of *A. pedatum*. The species can be distinguished, however, using characters of the medial ultimate segments. Medial ultimate segments of *A. aleuticum* are relatively long and narrow, with broad incisions in the acroscopic margin that give them a “saw-toothed” appearance. Segment apices have angular lobes with sharply denticulate margins. Medial ultimate segments of *A. pedatum*, by contrast, are broader relative to their length, have narrower, less prominent incisions, and their apices are round-lobed with crenulate or crenato-denticulate margins. The two species also differ in several attributes of the leaf blade: in *A. aleuticum*, the leaf is less dissected (i.e., has fewer “branches”), the rachis tends to be conspicuously longer than the axes adjacent to it, and the segments on each axis taper to an acute apex. These characteristics, taken together, suggest a human hand. For this reason, *A. aleuticum* is sometimes called the “five-

finger fern," a name never applied to *A. pedatum*, which has a decidedly more fan-shaped leaf blade. The two species also differ in rhizome habit and in spore size (Table 1).

Structural variation in response to light level, common in *Adiantum aleuticum*, also occurs in the tetraploid *A. viridimontanum*. Intermediate (*sensu* Barrington, 1986) between its progenitor diploids in most structural characters, the tetraploid bears a generally greater resemblance to *A. aleuticum* as it appears on serpentine and other exposed sites, having stiffly erect, funnel-shaped leaf blades and small ultimate segments twisted on their stalks (e.g., *Paris* 856, VT, GH, US). In the shade, however, it bears a greater resemblance to *A. pedatum*, with lax-arching, fan-shaped leaf blades and larger ultimate segments borne in the plane of the blade (e.g., *Paris* 208, VT). *Adiantum viridimontanum* is best separated from both *A. pedatum* and *A. aleuticum* by its longer false indusia, which often exceed 3.5 mm, by the longer stalks of the ultimate segments, and by its larger spores (mean diameter = 51.3 μm).

ACKNOWLEDGMENTS

I thank Ed Alverson, David Barrington, Philip Cook, Kevin Dann, Christopher Haufler, Bruce Howlett, Doug Hunter, Arthur Kruckeberg, Diana Stein, Rolla Tryon, Herb Wagner, Michael Windham, and Peter Zika for their invaluable contributions to this work, and curators at A, GH, MO, NHA, NY, PH, and SFS for the loan of specimens. David Barrington prepared Figure 1. Special thanks go to Mr. Howard Manosh of the Vermont Asbestos Group for permission to collect in the old mine at Belvidere Mountain. This work was supported in part by NSF Dissertation Improvement Grant BSR-8800938 to David S. Barrington, and in part by a Grant-in-Aid of Research from Sigma Xi, the Scientific Research Society, to the author.

LITERATURE CITED

- ALVERSON, E. R. 1989. *Cryptogramma cascadiensis*, a new parsley-fern from western North America. *Amer. Fern J.* 79: 95-104.
- BARRINGTON, D. S. 1986. The morphology and cytology of *Polystichum* \times *potteri* *hybr. nov.* (= *P. acrostichoides* \times *P. braunii*). *Rhodora* 88: 297-313.

- CALDER, J. A. AND R. L. TAYLOR. 1968. Flora of the Queen Charlotte Islands. Part I. Systematics of the Vascular Plants. Research Branch, Canad. Dept. Agric. Monogr. No. 4, pt. 1. Queen's Printer, Ottawa.
- CODY, W. J. 1983. *Adiantum pedatum* ssp. *calderi*, a new subspecies in north-eastern North America. *Rhodora* 85: 93–96.
- FERNALD, M. L. 1905. An alpine *Adiantum*. *Rhodora* 7: 190–192.
- . 1925. Persistence of plants in unglaciated areas of boreal America. *Mem. Amer. Acad. Arts* 15: 239–342.
- . 1950. Gray's Manual of Botany, 8th ed. American Book Co., New York.
- GAWLER, S. C. 1983. Note on *Adiantum pedatum* L. ssp. *calderi*. *Rhodora* 85: 389–390.
- HAUFLER, C. H. 1987. Electrophoresis is modifying our concept of evolution in the homosporous pteridophytes. *Amer. J. Bot.* 74: 953–966.
- JOLLEY, L. F. 1922. A variety of maidenhair fern new to Vermont. *Joint Bull. Vermont Bot. and Bird Clubs* 8: 40–41.
- LELLINGER, D. B. 1985. A Field Manual of the Ferns and Fern Allies of the United States and Canada. Smithsonian Institution Press, Washington, DC.
- MOUSLEY, H. 1923. The alpine maidenhair fern (*Adiantum pedatum* L. var. *aleuticum* Rupr.) at Hatley, Stanstead County, Quebec. *Canad. Field-Naturalist* 27: 84–85.
- PARIS, C. A. 1989. Maidenhair fern biogeography and M. L. Fernald's hypothesis of a Gaspé refugium. *Rhodora* 91: 143. (abstract)
- AND D. B. STEIN. 1989. Evolutionary genetics of the *Adiantum pedatum* complex: phylogeny and biogeography. *Amer. J. Bot.* 76: 205–206. (abstract)
- AND M. D. WINDHAM. 1988. A biosystematic investigation of the *Adiantum pedatum* complex in eastern North America. *Syst. Bot.* 13: 240–255.
- RUGG, H. G. 1922. *Adiantum pedatum* var. *aleuticum* in New England. *Amer. Fern J.* 12: 128–130.
- RUPRECHT, F. J. 1845. *Distributio cryptogamarum vascularium in Imperio Rossico*. Buchdruckerei der Kaiserlichen Akademie der Wissenschaften, St. Petersburg.
- SLOSSON, M. 1906. *How Ferns Grow*. Henry Holt, New York.
- TRYON, R. M., JR. 1960. A glossary of some terms relating to the fern leaf. *Taxon* 9: 104–109.
- WAGNER, W. H., JR. 1952. Types of foliar dichotomy in living ferns. *Amer. J. Bot.* 39: 578–592.
- . 1956. A natural hybrid, × *Adiantum tracyi* C. C. Hall. *Madroño* 13: 195–205.
- AND K. E. BOYDSTON. 1978. A dwarf coastal variety of maidenhair fern, *Adiantum pedatum*. *Canad. J. Bot.* 56: 1726–1729.
- ZIKA, P. F. AND K. T. DANN. 1985. Rare plants on ultramafic soils in Vermont. *Rhodora* 87: 293–304.

PRINGLE HERBARIUM
DEPARTMENT OF BOTANY
UNIVERSITY OF VERMONT
BURLINGTON, VT 05405-0086