

## NEW TAXA AND NOMENCLATURAL CHANGES IN THE NORTH AMERICAN FERN FLORA

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The ferns represent an ancient and diverse lineage in which hybridization and reticulate evolution have been extraordinarily common. Although the phylogenetic history of some fern genera can be reconstructed accurately from traditional morphological studies (e.g., *Osmunda*; see Miller 1971), the majority did not begin to yield their evolutionary secrets until the advent of experimental systematics less than 50 years ago (see Manton 1950). A combination of chromosome and isozyme analyses has proven to be one of the most effective tools in fern systematics (Hauffer 1985), providing insights into the phylogenetic histories of many, seemingly intractable groups. A number of these studies by myself and my colleagues have been published (e.g., Windham 1987a; Paris & Windham 1988; Gastony & Windham 1989; Hauffer & Windham 1991), but analyses done in the last few years have not yet appeared in print. These unpublished studies indicate the need for significant taxonomic changes in several North American fern genera. The following overview of new taxa and nomenclatural changes is presented to expedite the treatment of these genera in *Flora of North America, Vascular Plants of Arizona*, and other ongoing floristic projects.

### ARGYROCHOSMA

When *Argyrochosma* was first recognized as a genus distinct from *Notholaena* (Windham 1987a), only those names in use at the species level were transferred to the new genus. Previous authors (e.g., R. Tryon 1956) had recognized infraspecific taxa in several species, but the transfer of these names to *Argyrochosma* was delayed pending a more thorough review of systematic relationships in the genus. That review is not yet complete, but the impending publication of *Flora of North America* requires that a decision be made concerning the status of infraspecific taxa within *Argyrochosma limitanea* (Maxon) Windham. This species includes two morphologically distinctive taxa that show significant differences in blade shape and degree of dissection. The typical form of *A. limitanea* has broadly ovate-deltate leaf blades that are 4–5-pinnate, with the basal pinnae at least 1/2 as long as the blades. The taxon herein called subsp. *mexicana* has lanceolate to oblong leaf blades that are 3–4-pinnate, with basal pinnae that are 1/4 to 1/3 as long as the blades. These taxa tend to occupy different geographic ranges (R. Tryon 1956; maps 55, 56), and genetic interaction between them in regions of sympatry is precluded by the fact that both are apogamous triploids. Isozyme analyses indicate that the two taxa have different polyploid origins and may be worthy of recognition at the species level. However, evolutionary relationships (and thus proper taxonomic treatment) cannot be resolved until the sexually-reproducing progenitors of these polyploids are found. In the interim, these taxa

are best recognized as subspecies of *A. limitanea*, and the following new combination is proposed.

**Argyrosma limitanea** (Maxon) Windham subsp. **mexicana** (Maxon) Windham, comb. nov. *Notholaena limitanea* subsp. *mexicana* Maxon, Amer. Fern J. 9: 72, 1919.—TYPE: MEXICO, Chihuahua: Santa Eulalia Mts, 15 Sep 1885, Pringle 451 (holotype: US!).

#### CHEILANTHES

During detailed monographic studies of *Cheilanthes* subgenus *Physapteris*, Reeves (1979) ascertained that there were two distinct species included within *Cheilanthes wootonii* Maxon. As Reeves observed, typical representatives of *C. wootonii* have leaf blades that appear glabrous adaxially, abaxial blade scales that are often ciliate only in the proximal half, and rhizome scales that are usually light brown and deciduous on older portions of the rhizome. The taxon Reeves provisionally called *C. yavapensis* was distinguished by having leaf blades that appear sparsely pubescent adaxially, abaxial blade scales that are ciliate for most of their length, and rhizome scales that are dark brown (or bicolorous with a dark central stripe) and persistent. Initial reports (Reeves 1979) that *C. wootonii* and *C. yavapensis* are distinguished by the number of spores per sporangium have proven incorrect, but subsequent analyses have revealed genetic distinctions that reinforce the recognition of two species. Chromosome studies of *C. wootonii* s.s. indicate that this taxon is an apogamous triploid with  $n = 90$  (Windham 1983). *Cheilanthes yavapensis*, on the other hand, has proven to be an apogamous tetraploid with  $n = 120$ . A correlation between chromosome number and spore size provides an additional morphological character distinguishing *C. wootonii* (spores averaging  $< 64 \mu\text{m}$  long) from *C. yavapensis* (spores averaging  $> 64 \mu\text{m}$  long). Although the origin of triploid *C. wootonii* is uncertain, isozyme studies suggest that *C. yavapensis* arose through hybridization between *C. lindheimeri* Hooker (an apogamous triploid quite distinct from *C. wootonii*) and the sexual diploid known as *C. covillei* Maxon (Gastony & Windham 1989). These studies clearly indicate that *C. wootonii* was not involved in the polyploid origin of *C. yavapensis*, and that the similarities between these taxa result from hybrid convergence rather than common ancestry. The distinctive nature of Reeves' *C. yavapensis* is thus confirmed and his manuscript name is here validated.

**Cheilanthes yavapensis** Reeves ex Windham, sp. nov.—TYPE: U.S.A. Arizona: Yavapai Co., small east-wall tributary of Black Canyon at a point 3.09 km SSW of Sheep Gulch Spring and 1.13 km NE of the confluence of Black Canyon and Sycamore Creek, 2485 ft, 18 Nov 1980, *Windham 202* (holotype: UT!; isotypes: ASC! ASU! US!). Fig. 1.

*C. wootonii* Maxon similis, a qua differt laminarum paleis abaxialibus ciliatis fere per longitudinem, segmentis ultimis minoribus adaxialiter pilis dispersis ramosis instructis, laminis ut videtur pubescentibus adaxialiter, paleis rhizomatum furvioribus magis persistentibus, sporis plus quam  $(x) = 64 \mu\text{m}$  longis metientibus, chromosomatum numero  $n = 120$ ; a *C. lindheimeri* Hooker differt laminis ut videtur sparsim (non dense) pubescentibus adaxialiter, paleis abaxialibus laminarum

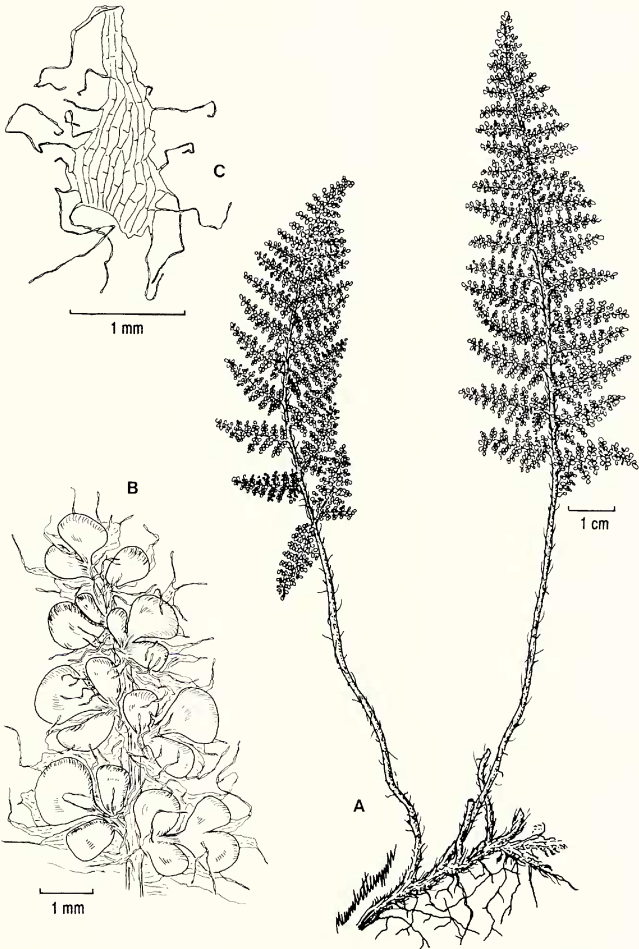


FIG. 1. *Cheilanthes yavapensis*. A. Habit. B. Adaxial view of pinnule; note overtopping cilia of abaxial costal scales and occasional branched hairs that make leaf appear pubescent. C. Abaxial costal scale; note cilia distributed entire length of scale. (Based on Windham (787) & Yatskievych.)

ciliis grossioribus, his non valde intricatis, segmentis ultimis plus quam 1 mm in diametro, rhizomatum paleis brunneis valde appressis magis persistentibus, sporis plus quam  $(x) = 64 \mu\text{m}$  longis metientibus, chromosomatum numero  $n = 120$ .

Plants epipetric. Rhizomes usually long-creeping, 1–3 mm in diameter; rhizome scales lanceolate, strongly appressed, persistent, often bicolorous with a broad, poorly defined, dark brown central stripe and narrow, pale brown margins. Leaves 7–35  $\times$  2–6 cm, scattered along rhizome; croziers non-circinate, hooked. Petioles dark brown, rounded adaxially. Blades oblong-lanceolate to nearly ovate, 4-pinnate proximally; rachises rounded adaxially, with scattered linear-lanceolate scales and sparse monomorphic pubescence. Pinnae appearing sparsely pubescent adaxially, the basal pair not conspicuously larger than adjacent pair, more or less equilateral; costae green adaxially for most of their length; abaxial costal scales lanceolate, the largest 0.4–1.0 mm wide, truncate to cordate at base, without overlapping basal lobes, strongly imbricate and often concealing ultimate segments, with coarse cilia usually distributed entire length of scale. Ultimate segments round to oblong, beadlike, the largest usually 1–2 mm; abaxial surface glabrous or with a few small scales near base; adaxial surface nearly glabrous except for occasional branched hairs; segment margins recurved to form weakly differentiated false indusia. Sporangia containing 32 spores. Spores averaging 64–72  $\mu\text{m}$  long. Chromosome number:  $n = 120$  (from the holotype population and paratypes indicated by \*).

Distribution. U.S.A., Arizona, southern New Mexico, and Trans-Pecos Texas; rocky slopes and ledges, usually on igneous substrates; 500–2400 m.

PARATYPES. U.S.A. ARIZONA: Coconino Co., at base of massive lava flow on the SE slope of Elden Mountain, *Windham* (589) & *Czech*\* (ASC, UC); Gila Co., southwest wall of Sand Tank Canyon in the Sierra Ancha, *Windham* (787) & *Yatskievych*\* (BRY, UT); Graham Co., along small tributary of Jacobson Canyon in the Pinaleno Mts, *Windham* (775) & *Yatskievych* (ARIZ, UT); Maricopa Co., cliff above lower Dripping Springs Canyon, White Tank Mountains Regional Park, *Keil* 6297 (ASU, MEXU, UNM); Yavapai Co., Bradshaw Mts, midway between Cleator and Crown King, *Lehto* 23641 (ASU).—NEW MEXICO: Grant Co., along small tributary of Sawmill Canyon in the Big Burro Mts, *Windham* (769) & *Yatskievych* (NMC, UT, UTC, UTEP).

#### NOTHOLAENA

*Notholaena californica* D. Eaton comprises white and yellow color morphs that show striking differences in the chemical composition of the powdery farina concentrated on abaxial leaf surfaces (Wollenweber 1984). The chemical distinctions between the color morphs were so profound that Wollenweber considered *N. californica* one of the best candidates in *Notholaena* for the recognition of infraspecific taxa. Subsequent chromosome studies further reinforce the differences between the white and yellow morphs. Preliminary data indicate that the white morph consists of sexual diploids and low polyploids (apogamous triploids and possibly tetraploids), whereas the yellow morph appears to consist entirely of high polyploids (apogamous pentaploids). The two color morphs are rarely, if ever, found growing at the same locality, and gene flow in the region of sympatry (southern California) is prevented because both are apogamous in this area. These taxa ultimately may prove worthy of recognition as distinct species, but until the complex evolutionary history of the group is resolved subspecific status seems

most appropriate. The lectotype of *N. californica* (chosen by R. Tryon 1956) and the holotype of the only previously recognized subspecies (*N. californica* subsp. *nigrescens* Ewan) both represent the yellow color morph and it is therefore necessary to apply a new name to the white morph. Given the chromosomal heterogeneity of the white morph and the inevitability of future taxonomic changes, the following description and type citations are based exclusively upon 64-spored, sexually reproducing populations occurring in Baja California.

***Notholaena californica*** D. Eaton subsp. ***leucophylla*** Windham, subsp. nov.—TYPE: MEXICO. Baja California: low granitic hills 4 mi N of Rancho Mesquital, 30 Mar 1961, Wiggins 16187 (holotype: US!; isotypes: DS! MICH! RSA!).

A subsp. *californica* lamina abaxialiter farina albida (non flavida) obtecta, sporangijs 64 sporas capientibus, sporis vulgo minoribus minus quam ( $x$ ) = 55  $\mu$ m longis metientibus differt.

Plants epipetric. Rhizomes compact to short-creeping, usually branched, the branches 3–7 mm in diameter; rhizome scales linear-subulate, weakly bicolorous with a broad, dark brown central stripe and very narrow, poorly defined pale brown margins; scale margins ciliate-denticulate. Leaves 4–15  $\times$  1.5–6 cm. Petioles brown, often longer than blade, rounded adaxially, bearing scattered farinose glands and a few scales near base. Blades broadly pentagonal, 3-pinnate proximally, usually slightly longer than wide; abaxial surface with conspicuous white farina; adaxial surface distinctly glandular. Basal pinnae much larger than adjacent pair, strongly inequilateral, the proximal basiscopio pinnules greatly enlarged. Ultimate segments sessile to subsessile, narrowly adnate to costae or occasionally free; segment margins recurved but rarely concealing mature sporangia. Sporangia containing 64 spores. Spores averaging 44–54  $\mu$ m long.

Distribution. Mexico, Baja California; rocky slopes and cliffs, usually on granitic or volcanic substrates; 100–1100 m.

PARATYPES. Mexico. BAJA CALIFORNIA SUR: 2–3 km inland from Bahía Candelero, Isla Espíritu Santo, Wiggins 16129 (DS, MEXU, MICH, UT).

Gastony and Windham (1989) reported that *Notholaena grayi* Davenp. comprised two cytotypes, a sexual diploid with  $n = 30$  chromosomes and an apogamous triploid showing  $n = 90$ . The two cytotypes are recognizable morphologically because of differences in spore number per sporangium and spore size. Sexual diploid populations produce 32 spores per sporangium, and the spores are relatively small, averaging 44–54  $\mu$ m long. Apogamous triploid collections (including the type of *N. grayi*) yield 16 (or 8) spores per sporangium and, though the spores are quite variable in size, all samples average more than 55  $\mu$ m long. Isozyme studies indicate that the apogamous triploid cytotype is an autopolyploid derivative of the sexual diploid, and Gastony and Windham (1989) suggested that these cytotypes might best be recognized as varieties. Additional work has revealed ecogeographic distinctions between the cytotypes of *N. grayi*; the sexual diploid occupies habitats in and around the Sonoran Desert, and the apogamous triploid occurs primarily in the Chihuahuan Desert. The discovery of a strong geographic component to variation in *N. grayi* argues for subspecific recognition of the taxa involved. The previously undescribed sexual diploid cytotype is characterized as follows.

**Notholaena grayi** Davenp. subsp. **sonorensis** Windham, subsp. nov.—TYPE: MEXICO. Sonora: steep sides of canyon at La Mina Verde, 31 km W of Cumpas, 3600 ft, 23 Sep 1934, *Wiggins 7400* (holotype: US!; isotypes: ARIZ! DS! MICH! UC!).

A subsp. *grayi* sporangia 32 spores capientibus, sporis minus quam  $(x) = 55 \mu\text{m}$  longis metientibus, chromosomatum numero  $n = 30$  differt.

Plants epipetric. Rhizomes compact to short-creeping, usually branched, the branches 3–7 mm in diameter; rhizome scales linear-subulate, uniformly blackish brown or weakly bicolorous with very narrow, poorly defined pale brown margins; scale margins ciliate-denticulate. Leaves 5–25  $\times$  1.5–4 cm. Petioles brown, shorter than or equal to blade, rounded adaxially, glandular-farinoso, bearing scattered hairs and scales. Blades linear-lanceolate, 2-pinnate-pinnatifid proximally, 3–6 times longer than wide; abaxial surface with conspicuous whitish farina throughout and lanceolate, entire scales scattered along rachises and costae; adaxial surface distinctly glandular. Basal pinnae equal to or slightly larger than adjacent pair, more or less equilateral, the proximal basiscopic pinnules not greatly enlarged. Ultimate segments sessile, broadly adnate to costae; segment margins slightly recurved, rarely concealing mature sporangia. Sporangia containing 32 spores. Spores averaging 44–54  $\mu\text{m}$  long. Chromosome number:  $n = 30$  (from paratypes indicated by \*).

Distribution. U.S.A., southern Arizona, and western Mexico south to Jalisco; rocky slopes and cliffs, usually on granitic or volcanic substrates; 1200–2000 m.

PARATYPES. U.S.A. ARIZONA: Cochise Co., Mule Mountains, Box Canyon Ranch, lower end of Box Canyon, *Yatskievych 84-195* (ARIZ, UT); northeast slope of the Huachuca Mts along unnamed tributary of Soldier Creek, *Windham (784) & Yatskievych\** (ASC, KANU, NY); Pima Co., Baboquivari Mts, Baboquivari Canyon, *Gould & Haskell 3228* (ARIZ, MO); Santa Cruz Co., W side of Alamo Canyon, Pajarito Mts, *Windham & Yatskievych 225\** (ASU, RSA, UT).

## PELLAEA

Recent morphological (Windham, unpubl.) and isozyme studies (Gastony 1988) of *Pellaea atropurpurea* (L.) Link and its allies have revealed the existence of apogamous tetraploid hybrids between this species (an apogamous triploid) and diploids within the *P. glabella* Mett. ex Kuhn complex. As a result of their apogamous life cycle, these *P. atropurpurea*  $\times$  *glabella* s.l. hybrids are reproductively competent and range far beyond the limited areas of parental sympatry. In terms of morphology, the hybrids are most similar to *P. atropurpurea*, which contributed three of the four chromosome sets found in somatic cells of the plants (Gastony 1988). The hybrids are easily distinguished from *P. atropurpurea*, however, by having rachises that are sparsely villous (not densely curly-pubescent) on the adaxial surface, pinnules that are usually less than 30 mm long, and spores averaging more than 62  $\mu\text{m}$  long. As an independently reproducing interspecific hybrid, this taxon cannot be included within any previously recognized species of *Pellaea* and is described here as a new nothospecies. It is named in honor of Gerald J. Gastony, Indiana University, in recognition of his contributions to our understanding of evolutionary patterns in many fern genera, especially *Pellaea*.

**Pellaea gastonyi** Windham, sp. nov.—TYPE: CANADA. British Columbia: Kinbasket Mountain by Kinbasket River, NW of Golden, 17 Aug 1953, *Calder & Savile 11976* (holotype: US!; isotypes: DAO! UBC! WTU!). Fig. 2.

*Pellaea atropurpurea* (L.) Link similis, a qua differt rhachidibus sparsim villosis adaxialiter (non dense crispato-pubescentibus), pinnulis vulgo minus quam 30 mm longis, sporis plus quam ( $x$ ) = 62  $\mu$ m longis metientibus; a *P. lyngholmii* Windham pinnis basalibus pinnulis 3–7, nonnullis pinnulis rhachillis longissimis longioribus, frondibus fertilibus plerumque minus quam 6 cm latis differt.

Plants epipetric. Rhizomes compact, 5–10 mm in diameter; rhizome scales linear-subulate, 0.1–0.3 mm wide, uniformly reddish brown or tan, with entire to denticulate margins. Leaves 8–25  $\times$  3–6 cm, slightly dimorphic with sterile leaves shorter than fertile leaves; croziers villous. Petioles reddish purple to dark brown, rounded adaxially, without prominent articulation lines. Blades elongate-deltate to lanceolate, 2-pinnate proximally; rachis straight, rounded adaxially, sparsely villous with long, divergent hairs. Pinnae ascending or perpendicular to rachis, not decurrent on rachis or obscurely so, usually with 3–7 ultimate segments; costae 2–30 mm, usually shorter than ultimate segments. Ultimate segments oblong-lanceolate, 7–30 mm, with obtuse to slightly mucronate apex, sparsely villous along midrib abaxially; segment margins usually recurved on fertile segments, covering less than 1/2 the abaxial surface. Sporangia long-stalked, not intermixed with glandular paraphyses, containing 32 spores. Spores averaging 64–72  $\mu$ m long.

Distribution. Sporadically in western Canada (Alberta, British Columbia, and Saskatchewan) and the central U.S.A. (South Dakota, Wyoming and Missouri); calcareous cliffs and ledges, usually on limestone; 100–1500 m.

PARATYPES. **Canada.** ALBERTA: 6.5 km ESE of Canmore on S side of Grotto Mtn, *Brunton 1289* (CAN, UT).—BRITISH COLUMBIA: east shore of Columbia Lake, *Taylor & Ferguson 3932* (DAO).—SASKATCHEWAN: Cluff Lake area, 58° 21'N, 109° 42'W, *Polson & Hudson 3680B* (DAO, SASK); vicinity of the base of Cornwall Bay, Lake Athabaska, *Raup 6558* (CAN, CAS, US). **U.S.A.** SOUTH DAKOTA: Pennington Co., 6 mi. E of Sheridan Lake, *Stevens 7133* (KANU).—WYOMING: along Moskee Rd 9.6 mi SE of junction of Moskee Rd and I-90, *Gastony 83-68* (IND, UT).

The taxonomic status and evolutionary relationships of taxa constituting the *Pellaea glabella* Mett. ex Kuhn complex have been the source of much debate. In her monograph of *Pellaea* section *Pellaea*, A. Tryon (1957) recognized three varieties of *P. glabella*: an eastern North American apogamous tetraploid (var. *glabella*), a western North American apogamous tetraploid (var. *simplex*), and a western sexual diploid (var. *occidentalis*). An eastern sexual diploid was subsequently discovered by Wagner et al. (1965) but did not receive a formal name (var. *missouriensis*) until 1988.

In the next continent-wide overview of the *P. glabella* complex, Lellinger (1985) treated each of A. Tryon's varieties as a distinct species and relegated the eastern diploid to the status of a minor variant within *P. glabella*. Using primarily isozyme data, Gastony (1988) proposed yet another approach to the taxonomy of this group. Gastony presented evidence that the eastern tetraploid arose as an autopolyploid derivative of the eastern diploid, and that the western tetraploid originated in like manner from the western diploid. Consequently, Gastony (1988) recognized two species in the complex: the eastern North American *P. glabella* (with two varieties) and the western North American *P. occidentalis* (E. Nels.) Rydb. (with two subspecies). In a more recent paper, Gastony et al. (1992) present chloroplast DNA data that appear to support the taxonomic realignments proposed in 1988.

The focal point of controversy in the taxonomic treatment of the *P. glabella* complex relates to the degree of genetic divergence among the various taxa involved. In terms of morphology, many of the key characters used by proponents of

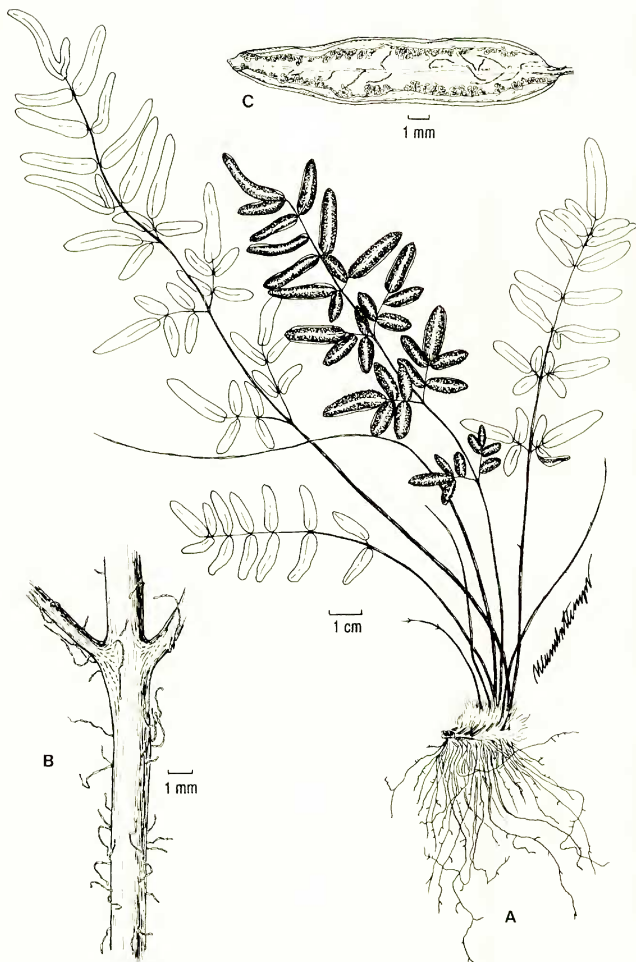


FIG. 2. *Pellaea gastonyi*. A. Habit; note that most costae are shorter than the ultimate segments. B. Adaxial view of portion of rachis; note sparsely villous surface and ascending, obscurely decurrent costae. C. Abaxial view of ultimate segment; note sparsely villous midrib. (Based on Calder & Savile 11976.)



multi-species taxonomies (e.g., Butters 1921; Lellinger 1985) fail singly or in combination. Especially prone to overlap are features of the leaf blade, including size, shape, and degree of dissection. These are strongly influenced by habitat, and heavy dependence on them has resulted in frequent misidentification. Because of the subtle morphological differentiation among taxa, the three-species taxonomy has proven largely unworkable on a continent-wide basis.

The same criticism, however, can be leveled at the two-species taxonomy proposed by Gastony (1988). The only morphological characters that consistently distinguish members of the *P. glabella* complex are spore size, spore number per sporangium, petiole color, and the presence or absence of hairs along pinnule midribs. The first three characters separate taxa *within* Gastony's species, so only the fourth (in combination with geography) can be used to differentiate *between* species. This suggests that *P. occidentalis* and *P. glabella* have not diverged sufficiently to be considered separate species, an interpretation supported both by isozymes (Gastony 1988; Windham, unpubl.) and cp DNA studies (Gastony et al. 1992). Isozyme surveys of section *Pellaea* indicate that *P. occidentalis* and *P. glabella* are less divergent genetically than any other pair of *Pellaea* species in North America. In terms of cp DNA, the maximum patristic distance between *P. occidentalis* and *P. glabella* is 11, which is less than 25% of the estimated distance between the *P. glabella* complex and its sister taxon, *P. atropurpurea*. All of these observations argue against the recognition of *P. occidentalis* and *P. glabella* as distinct species.

One further consideration involves the impact of Gastony's (1988) two-species taxonomy on the treatment of the newly recognized nothospecies *P. gastonyi* (*P. atropurpurea* × *glabella* s.l.). If *P. occidentalis* and *P. glabella* are considered separate species, then independently derived populations of *P. gastonyi* in eastern and western North America must also be treated as distinct, because they would represent hybrids between different parental species. The characters that distinguish *P. occidentalis* and *P. glabella* are so subtle that they are completely obscured in hybrids with *P. atropurpurea*, and eastern and western populations of *P. gastonyi* appear to be morphologically indistinguishable. Considering these facts, a more conservative treatment of the *P. glabella* complex seems warranted, and the four taxa will be treated as subspecies of *P. glabella* in *Flora of North America*. This necessitates the following nomenclatural changes.

***Pellaea glabella*** Mett. ex Kuhn subsp. ***missouriensis*** (Gastony) Windham, stat. nov. *Pellaea glabella* var. *missouriensis* Gastony, Amer. Fern J. 78: 64. 1988.—TYPE: U.S.A. Missouri: Jefferson Co., river bluffs 10 mi W of DeSoto, near jct. of rd H and Big River, *Gastony 83-34-47* (holotype: IND; isotypes: GH, MICH, MO!).

***Pellaea glabella*** Mett. ex Kuhn subsp. ***occidentalis*** (E. Nelson) Windham, comb. et stat. nov. *Pellaea atropurpurea* var. *occidentalis* E. Nelson, Fern Bull. 7: 30. 1899.—TYPE: U.S.A. Wyoming: Laramie Hills, 13 Jun 1896, *Nelson 1919* (holotype: RM!; isotypes: BRY! MO, NY!).

A series of distinctive *Pellaea* populations discovered in central Arizona by M. D. Windham and D. Lyngholm have proven to consist of apogamous tetraploid hybrids between *P. atropurpurea* and *P. truncata* Goodding (Gastony & Yatskievych 1992). As is the case with *P. gastonyi* (described above), these hybrids are reproductively competent and most similar to the apogamous triploid parent, *P. atropurpurea*, which contributed three of the four chromosome sets found in

somatic cells of the plants (Gastony & Yatskievych 1992). The hybrids are easily distinguished from *P. atropurpurea*, however, by having rachises that are sparsely villous (not densely curly-pubescent) on the adaxial surface, mucronate pinnules that are smaller (usually less than 25 mm long) and more numerous, and spores averaging more than 62  $\mu\text{m}$  long. As an independently reproducing interspecific hybrid, this taxon cannot be included within any previously recognized species of *Pellaea* and is described here as a new nothospecies. It is named in honor of Donavon Lyngholm, codiscoverer of this unusual fern, whose tireless efforts in support of wilderness conservation have helped to ensure the continued survival of this and many other rare species.

***Pellaea lyngholmii*** Windham, sp. nov.—TYPE: U.S.A. Arizona: Yavapai Co., SW side of Fay Canyon ca. 1.39 km SSE of the summit of Bear Mountain, 4775 ft, 23 Sep 1990, *Windham (90-420) & Lyngholm* (holotype: UT!; isotypes: ASU! UC! US!). Fig. 3.

*Pellaea atropurpureae* (L.) Link similis, a qua differt rhachidibus sparsim villosis adaxialiter (non dense crispato-pubescentibus), pinnulis vulgo minus quam 25 mm longis, sporis plus quam ( $x$ ) = 62  $\mu\text{m}$  longis metientibus; a *P. gastonyi* Windham pinnis basalibus pinnulis 7–15, pinnulis rhachillis longissimus persaepe brevioribus, frondibus fertilibus plerumque plus quam 6 cm latis differt.

Plants epipetric (rarely terrestrial). Rhizomes compact, 5–10 mm in diameter; rhizome scales linear to subulate, 0.1–0.3 mm wide, uniformly brown or tan, with entire to denticulate margins. Leaves 10–30  $\times$  5–15 cm, slightly dimorphic with sterile leaves shorter and less divided than fertile leaves; croziers villous. Petioles dark brown to reddish purple, rounded adaxially, without prominent articulation lines. Blades elongate-deltate to ovate, 2-pinnate proximally; rachis straight, often slightly flattened adaxially, sparsely villous with long, divergent hairs. Pinnae perpendicular to rachis or slightly ascending, not decurrent on rachis, the largest with 7–15 ultimate segments; costae 25–80 mm, usually longer than ultimate segments. Ultimate segments oblong-lanceolate, 10–25 mm, with slightly mucronate apex, sparsely villous abaxially along midrib; segment margins usually recurved on fertile segments, covering less than 1/2 the abaxial surface. Sporangia long-stalked, not intermixed with glandular paraphyses, containing 32 spores. Spores averaging 64–72  $\mu\text{m}$  long.

Distribution. U.S.A., central Arizona; rocky slopes and ledges in thin, sandy soil associated with sandstone outcrops; 1200–1800 m.

PARATYPES. U.S.A. ARIZONA: Coconino Co., bottom of Damfino Canyon, *Windham (901) & Windham* (UT); Yavapai Co., along small tributary of Dry Creek on NW slope of Capitol Butte, *Windham (721) & Lyngholm* (ARIZ. MO. NMC. UNM, UT); near head of ravine on S side of Fay Canyon, *Windham 7* (ASC).

*Pellaea mucronata* (D. Eaton) D. Eaton encompasses two morphological extremes that tend to occupy different habitats. The typical 3-pinnate form is scattered throughout California and southern Nevada, usually below 1800 m elevation. The 2-pinnate form with ascending, overlapping pinnae is apparently confined to the Sierra Nevada and Transverse Ranges of California at elevations greater than 1800 m. The taxonomic status of these entities remains in dispute, and they are often treated as mere ecological forms. Wagner et al. (1983) indicated that natural hybrids formed between *P. bridgesii* and these two taxa are morphologically distinct, which suggests that the differences observed between these morphotypes of *P. mucronata* are genetically based. Because they represent well-characterized

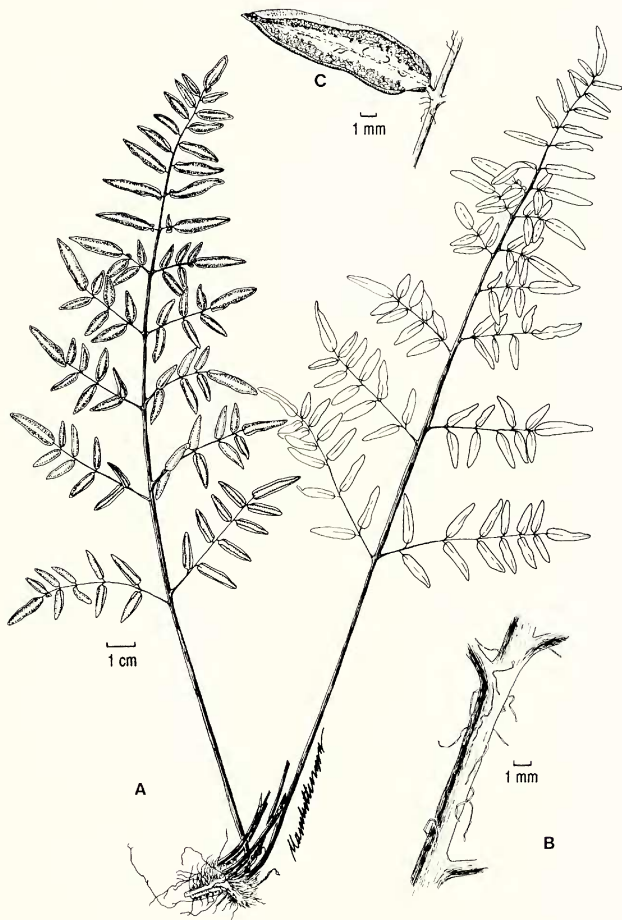


FIG. 3. *Pellaea lyngholmii*. A. Habit; note that most costae are longer than the ultimate segments. B. Adaxial view of portion of rachis; note sparsely villous surface. C. Abaxial view of ultimate segment; note sparsely villous midrib and slightly mucronate apex. (Based on Windham (90-420) & Lyngholm.)

genetic variants that tend to occupy discrete ranges, they will be treated as subspecies in *Flora of North America*, and the following nomenclatural change is necessary.

***Pellaea mucronata*** (D. Eaton) D. Eaton subsp. ***californica*** (Lemmon) Windham, comb. et stat. nov. *Pellaea wrightiana* var. *californica* Lemmon, Ferns Pacific Coast, 10. 1882.—TYPE: U.S.A. California: San Bernardino Mts, 30 May 1876, *Lemmon* (lectotype, designated by A. Tryon, 1957: UC!; isolecotypes: F, GH, US).

As defined by A. Tryon (1957), *Pellaea ternifolia* (Cav.) Link included two varieties: a widespread taxon with ternately dissected pinnae (var. *ternifolia*) and a primarily North American element in which the pinnae are fully pinnate (var. *wrightiana*). Even with the recognition of var. *wrightiana* as a distinct species (following Wagner 1965), *P. ternifolia* remains a highly variable taxon. Within the area covered by *Flora of North America*, there are three genetically distinct taxa characterized by differences in leaf morphology and chromosome number. A population in west Texas consisting of glabrous-leaved diploids with short (< 18 mm) ultimate segments and grooved or flattened petioles appears to represent the typical form of the species (judging from the original description and a photo of the holotype at UT). The most common form occurring in the flora is a glabrous-leaved tetraploid with long (> 18 mm) ultimate segments and more or less terete petioles. The third taxon, a pubescent-leaved tetraploid mentioned by A. Tryon (1972), is apparently very rare in the flora but commonly encountered in Mexico. Isozyme and chromosome studies suggest that both tetraploids are segmental allopolyploids produced by hybridization between typical *P. ternifolia* and other (as yet unidentified) diploid elements within the *P. ternifolia* complex. The two tetraploid taxa have not received formal recognition in the past and are here described as subspecies.

***Pellaea ternifolia*** (Cav.) Link subsp. ***arizonica*** Windham, subsp. nov.—TYPE: U.S.A. Arizona: Cochise Co., SW slopes of the Dragoon Mountains ca. 1.59 km NNE of Granite Spring, 6050 ft, 18 Mar 1981, *Windham 246* (holotype: UT!; isotypes: ASC! ASU! MO! UC! US!).

Subsp. *ternifoliae* similis a qua differt numero majore pinnarum indivisarum ad apicem frondium, nonnullis pinnulis plus quam 18 mm longis, stipitibus adaxialiter convexis vel leviter complanatis distaliter, sporis plus quam  $(x) = 46 \mu\text{m}$  longis metientibus, chromosomatum numero  $n = 58$ ; a subsp. *villosa* Windham pinnis omnino glabris, rhachidibus glabrescentibus pilis paucis perdispersis differt.

Plants epipetric (rarely terrestrial). Rhizomes compact, 5–10 mm in diameter; rhizome scales linear-subulate, 0.1–0.3 mm wide, strongly bicolorous, with a sharply defined, black central stripe and brown, erose-dentate margins. Leaves 10–50 × 3.5–8 cm, monomorphic; croziers sparsely villous to glabrescent. Petioles black or dark purple, rounded or slightly flattened adaxially in distal portion, without prominent articulation lines. Blades linear-lanceolate to ovate, deeply pinnate-pinnatifid proximally; rachis straight, often flattened adaxially, glabrous or with a few widely scattered hairs. Pinnae perpendicular to rachis or slightly ascending, not decurrent on rachis, ternately divided in proximal portion of blade; costae absent. Ultimate segments linear-oblong, 18–40 mm, with a mucronate apex, glabrous throughout; segment margins recurved on fertile segments, rarely covering more than 1/2 the abaxial surface. Sporangia long-stalked, not intermixed with glandular paraphyses, containing 64 spores. Spores averaging 46–53  $\mu\text{m}$  long. Chromosome number:  $n = 58$  (from holotype population and paratypes indicated by \*).

Distribution. U.S.A., southeastern Arizona and Trans-Pecos Texas, and northern Mexico, Chihuahua and Sonora; cliffs and rocky slopes on a variety of acidic substrates including quartzite and granite; 1700–2400 m.

PARATYPES. U.S.A. ARIZONA: Cochise Co., Ramsey Canyon, Huachuca Mts. *Peebles, Harrison & Kearney 3501* (ARIZ); southeast wall of Huachuca Canyon, *Windham 303\** (ASC, CAS, KANU, TEX, UNM, UT); Santa Cruz Co., Madera Canyon, Santa Rita Mts. *Phillips 3000* (ARIZ, US).—TEXAS: Brewster Co., Big Bend National Park, Chisos Mountain Basin Area, canyon along south rim of the Basin, *Tryon & Tryon 5042* (MEXU, UT).

***Pellaea ternifolia*** (Cav.) Link subsp. ***villosa*** Windham, subsp. nov.—TYPE: MEXICO. Hidalgo: rocky hills, Lena Station, 8300 ft, 24 Aug 1905, *Pringle 10025* (holotype: LL!; isotypes: ARIZ! BRY! CAS! COLO! DAO! ENCB! F! GH! IND! KANU! LL! MSC! OKLA! SMU! TEX! UC! US! VT! WIS!).

Subsp. *ternifoliae* et subsp. *arizonicae* Windham similis, a quibus differt pinnis pilis dispersis secus venas principales abaxialiter, rhachidibus villosis apprime axillis pinnarum; insuper differt a subsp. *ternifolia* numero majore pinnarum indivisarum ad apicem, pinnulis plus quam 18 mm longis, stipitibus adaxialiter convexis vel leviter complanatis distaliter, sporis plus quam (x) = 46  $\mu$ m longis metentibus, chromosomatium numero  $n = 58$ .

Plants epipetric (rarely terrestrial). Rhizomes compact, 5–10 mm in diameter; rhizome scales linear-subulate, 0.1–0.3 mm wide, strongly bicolorous, with a black central stripe and brown, erose-dentate margins. Leaves 10–50  $\times$  3–7 cm, monomorphic; croziers densely villous. Petioles black or dark purple, rounded or slightly flattened adaxially in distal portion, without prominent articulation lines. Blades linear-lanceolate, deeply pinnate-pinnatifid proximally; rachis straight, often flattened or slightly grooved adaxially, villous throughout or with hairs concentrated in axils of pinnae. Pinnae ascending or rarely perpendicular to rachis, not decurrent on rachis, ternately divided in proximal portion of blade; costae usually absent. Ultimate segments linear-oblong, 18–40 mm, with a mucronate apex, sparsely villous abaxially along midribs; segment margins usually recurved on fertile segments, often covering more than 1/2 the abaxial surface. Sporangia long-stalked, not intermixed with glandular paraphyses, containing 64 spores. Spores averaging 46–53  $\mu$ m long. Chromosome number:  $n = 58$  (from paratypes indicated by \*).

Distribution. Central and northern Mexico from Puebla north to Durango, Chihuahua and Coahuila, one disjunct locality in the Davis Mountains of west Texas, U.S.A.; rocky slopes and ledges on various (mostly calcareous) substrates; 1800–2700 m.

PARATYPES. Mexico. DURANGO: near km post 14 on Hwy 40 W of Ciudad Durango, *Ranker (829b) & Yatskievych\** (UT).—PUEBLA: Mpio. de Felipe los Angeles, La Candelaria, *Ventura A. 4289\** (MICH).—SAN LUIS POTOSÍ: Sierra San Miguelito, 15 mi W of San Luis Potosí, *Rollins & Tryon 58218\** (GH).

### Pleopeltis

A recent paper by Mickel and Beitel (1987) detailing the extent of hybridization between *Pleopeltis* and *Polypodium* raises questions concerning the circumscription of these genera. The authors recognize five different hybrid taxa, which they assign to the intermediate genus  $\times$ *Pleopodium*. In each case, the *Polypodium*

species involved in the hybridization event belonged to subgenus *Marginaria*, the scaly polypodies. It is important to note that typical members of *Polypodium* (subg. *Polypodium*) are not known to hybridize with either *Pleopeltis* or any species of subg. *Marginaria*.

*Pleopeltis* and the scaly polypodies have long been considered close allies (de la Sota 1966, 1973; Pichi Sermolli 1977; Tryon & Tryon 1982), and they share a number of distinctive morphological traits. Unlike most members of the Polypodiaceae s.s., both *Pleopeltis* and the scaly polypodies have scales scattered over the abaxial surface of the blade. These laminar scales are of a distinctive type (stalked, peltate, and centrally clathrate) otherwise unknown in the Polypodiaceae (Baayen & Hennipman 1987). Another unusual characteristic shared by these groups is the tendency for developing sori to be protected by a "false indusium" composed of overlapping, peltate scales. The discovery of laminar nectaries in both *Pleopeltis* (Windham, unpubl.) and *Polypodium* subg. *Marginaria* (Koptur et al. 1982) provides yet another feature that separates these taxa from most other Polypodiaceae. Similarities in spores, rhizome scales, and venation patterns round out the list of characters suggesting a close evolutionary relationship between these two groups.

The features that distinguish the scaly polypodies from *Pleopeltis* are quite apparent, even to the untrained eye. Leaf blades of the polypodies are deeply pinnatifid, whereas those of *Pleopeltis* are usually simple and entire. There are several exceptions to this rule, however, most notably *Pleopeltis angusta* (the type species of the genus) and *Pleopeltis fallax* (a species recently transferred from *Polypodium* by Mickel and Beitel). The primary character used to separate the two groups involves the attachment of the soral scales, which arise directly from the receptacle in *Pleopeltis* but are peripheral to the sorus in *Polypodium* subg. *Marginaria*. Another distinction frequently mentioned in the literature (Wagner & Wagner 1975; Tryon & Tryon 1982) involves venation patterns in the leaf. Laminar venation patterns tend to be more complex in *Pleopeltis*, and each sorus is served by several veins that form a complex reticulum within the receptacle (Wagner & Wagner 1975). The scaly polypodies, on the other hand, have simpler vascular systems (with fewer anastomoses) and each sorus is supplied by a single vein.

Although the characters that distinguish *Pleopeltis* from the scaly polypodies are conspicuous, their value for generic segregation must be reexamined in light of the hybridization data (Wagner & Wagner 1975). The association of each sorus with several veins in *Pleopeltis* suggests that they may be coenosori, compound structures formed by the fusion of several individual sori (see Wagner 1986). Support for this hypothesis derives from the occurrence of small "islands" of parenchyma within the vascular reticulum of the receptacle, a situation observed in many coenosoral taxa including the closely related *Marginariopsis* (Wagner 1986). If the "sori" of *Pleopeltis* are actually coenosori, then the distinctive receptacular scales could have originated as peripheral scales that became incorporated into the coenosori during soral fusion. This idea finds support in the work of Baayen and Hennipman (1987), who report that the "paraphyses" (receptacular scales) of *Pleopeltis* are unique among polypodioid ferns in being structurally identical to the laminar scales distributed around the sori. These observations suggest that both the complex venation patterns and the receptacular scales of *Pleopeltis* may have arisen through soral fusion. Such fusion could, in turn, be a direct result of blade simplification (the evolution of a simple blade from a pin-

natifid ancestral form). Thus, the three features that distinguish *Pleopeltis* from the scaly polypodies could be viewed as a complex of covarying traits, all of which may trace their origin to a simple change in blade dissection. If this interpretation is correct, it casts serious doubt on the generic separation of *Pleopeltis* and *Polypodium* subg. *Marginaria*.

The foregoing discussion of *Pleopeltis* and *Polypodium* raises an important question concerning the classification of polypodioid ferns: Are the scaly polypodies more closely related to *Polypodium* (as the current classification suggests) or to *Pleopeltis*? This question has been addressed through isozyme and cpDNA analyses (Andrews, Haufler, & Windham, unpubl.) of a small set of species representing each of the three lineages. Although some enzyme loci were too variable to be useful, the most conservative enzymes (such as TPI) indicated that *Pleopeltis* and the scaly polypodies form a cohesive group quite distinct from both temperate and tropical members of subg. *Polypodium*. Similar results were obtained from a preliminary cpDNA analysis, which indicated that *Pleopeltis* and the scaly polypodies were nearly identical to one another but well differentiated from subg. *Polypodium*. Thus, the molecular analyses strongly support the hypothesis that the scaly polypodies are more closely related to *Pleopeltis* than they are to other species of *Polypodium*.

A combination of morphological, molecular, and hybridization data suggests that the classification of this group of polypodioid ferns is in need of revision. As currently defined, *Pleopeltis* appears to be paraphyletic, whereas *Polypodium* is clearly polyphyletic. This problem can be resolved by either submerging *Pleopeltis* into a broadly defined *Polypodium* or redefining *Pleopeltis* to include the scaly polypodies.

The first option would require fewer nomenclatural changes, because most species of *Pleopeltis* have, at one time or another, resided within *Polypodium*; however, this approach substantially increases the heterogeneity of *Polypodium*, which is already large and poorly defined. The inclusion of *Pleopeltis* within *Polypodium* would weaken the case for recognizing other segregate genera, such as *Campyloneurum*, *Microgramma*, and *Phlebodium*, and would result in making *Polypodium* even more heterogeneous. This approach would also reduce the information content of the classification system, because it does not reflect either the close relationship between *Pleopeltis* and the scaly polypodies or their substantial evolutionary divergence from *Polypodium* subg. *Polypodium*.

The second option (redefining *Pleopeltis* to include the scaly polypodies) requires a greater number of nomenclatural changes and increases the heterogeneity of *Pleopeltis*, which can no longer be identified solely by the presence of receptacular scales. When circumscribed to include the scaly polypodies, *Pleopeltis* can still be recognized by a combination of apparent synapomorphies, including the unique laminar scales, the presence (in immature sori) of a "false indusium" composed of overlapping, peltate scales, and the presence of nectaries near the base of the blade. The transfer of the scaly polypodies to *Pleopeltis* makes that genus a natural (probably monophyletic) group and improves prospects for clarifying the definition and phylogenetic relationships of *Polypodium*. The resulting classification also provides a more accurate representation of evolutionary relationships, emphasizing both the clear phylogenetic affinity between *Pleopeltis* and the scaly polypodies and their genetic isolation from *Polypodium* subg. *Polypodium*.

Redefining *Pleopeltis* to include the scaly polypodies seems the best approach to the taxonomic problems outlined above, and that is the course adopted here.

Unresolved problems of synonymy and species boundaries within the scaly polypodies prevent the wholesale transfer of all 40+ species at this time. Until studies of this group are completed, I propose to transfer only those species to *Pleopeltis* that hybridize with species currently included in *Pleopeltis* and occur within (or immediately adjacent to) the region covered by *Flora of North America*.

***Pleopeltis guttata*** (Maxon) E. G. Andrews & Windham, comb. nov. *Polypodium guttatum* Maxon, Contr. U.S. Natl. Herb. 17: 575. 1916.—TYPE: MEXICO, Coahuila: near Saltillo, 15–30 Apr 1898, *Palmer 65* (holotype: US).

***Pleopeltis polypodioides*** (L.) E. G. Andrews & Windham, comb. nov. *Acrostichum polypodioides* L., Sp. pl. 2: 1068. 1753.—TYPE: JAMAICA, collector unknown (lectotype, designated by Weatherby, 1939; Herb. Plukenet, BM).

***Pleopeltis polypodioides*** (L.) E. G. Andrews & Windham var. ***acicularis*** (Weatherby) E. G. Andrews & Windham, comb. nov. *Polypodium polypodioides* (L.) Watt var. *aciculare* Weatherby, Contr. Gray Herb. 124: 33. 1939.—TYPE: COSTA RICA, San Francisco de Guadalupe, *Tonduz 8476* (holotype: GH; isotype: NY).

***Pleopeltis polypodioides*** (L.) E. G. Andrews & Windham var. ***michauxiana*** (Weatherby) E. G. Andrews & Windham, comb. nov. *Polypodium polypodioides* (L.) Watt var. *michauxianum* Weatherby, Contr. Gray Herb. 124: 31. 1939.—TYPE: U.S.A. Virginia: Nansemond Co., Kilby, *Fernald, Long & Fogg 4703* (holotype: GH).

***Pleopeltis thyssanolepis*** (A. Braun ex Klotzsch) E. G. Andrews & Windham, comb. nov. *Polypodium thyssanolepis* A. Braun ex Klotzsch, Linnaea 20: 392. 1847. SYNTYPES: COLOMBIA, *Moritz 22* (B; isosyntype: P), *Otto 896* (B; isosyntype: P).

A northern variant of *Pleopeltis thyssanolepis* described by Wendt (1980) as var. *riograndense* appears to represent a distinct species. It differs from typical representatives of *P. thyssanolepis* in having sparsely scaly petioles and leaves, petiole scales that are mostly ovate or lance-ovate (not suborbicular), mostly free venation with < 40% of the sori within areoles, and basal blade segments that are distinctly alternate. These morphological differences, combined with a tetraploid chromosome number, suggest that this taxon may have originated as a hybrid between *P. thyssanolepis* and *P. guttata*. Recognition as a distinct species within *Pleopeltis* requires the following nomenclatural change.

***Pleopeltis riograndensis*** (Wendt) E. G. Andrews & Windham, comb. et stat. nov. *Polypodium thyssanolepis* A. Braun ex Klotzsch var. *riograndense* Wendt, Amer. Fern J. 70: 6. 1980.—TYPE: U.S.A. Texas: Presidio Co., lower Indian Cave Canyon (side canyon of Dead Horse Canyon), N side of Chinati Mts, 16 Oct 1977, *Butterwick & Lott 3897* (holotype: TEX; isotypes: GH, MEXU).



## POLYPODIUM

Collections of *Polypodium* from the southern Rocky Mountains traditionally have been assigned to a single taxon, variously known as *P. hesperium* Maxon or *P. vulgare* L. var. *columbianum* Gilbert. Martens (1943), Lang (1969), and Windham (1985), however, reported that some specimens from the region have paraphyses (= sporangiasters) scattered among the sporangia. Such sporangiasters are absent from the sori of *P. hesperium* (Lang 1969, 1971), and southern Rocky Mountain collections exhibiting them have been identified as *P. virginianum* L. (Martens 1943), *P. montense* Lang (Lang 1969), or *P. amorphum* Suksdorf (Windham 1985).

As noted by Martens (1943), collections of *Polypodium* with sporangiasters from the southern Rocky Mountains are rather similar to the eastern North American taxon known as *P. virginianum*. The western plants differ from typical representatives of *P. virginianum* in having narrower leaf blades (mostly < 3.5 cm wide) and sporangiasters with fewer glandular trichomes. The Rocky Mountain taxon also shows a strong resemblance to *P. amorphum*, a Pacific Northwest species formerly known as *P. montense*. Plants from the southern Rocky Mountains differ from this species in having sporangiasters with fewer glandular trichomes, strongly tuberculate spores averaging more than 62  $\mu\text{m}$  long, and a chromosome number of  $n = 74$ .

The discovery that the southern Rocky Mountain taxon was tetraploid led Windham (1985) to hypothesize that it arose as a hybrid between a typical form of *P. amorphum* and a "local (i.e., Rocky Mountain) form with strongly tuberculate spores." Recent isozyme analyses support a modified version of this scenario. These studies clearly indicate that the southern Rocky Mountain taxon is an allotetraploid whose parentage includes *P. amorphum*. The other parent (i.e., the variant of *P. amorphum* with strongly tuberculate spores) is the circumboreal diploid now known as *P. sibiricum* Siplivinskij, which extends south in the Rocky Mountains as far as central British Columbia. The involvement of *P. sibiricum* in the origin of the southern Rocky Mountain taxon also explains its resemblance to *P. virginianum*, which originated as a hybrid between *P. sibiricum* and the eastern North American *P. appalachianum* (Haufler & Windham 1991). As an allotetraploid hybrid between *P. amorphum* and *P. sibiricum*, the southern Rocky Mountain taxon cannot be included within any previously recognized species of *Polypodium* and is described here as a nothospecies.

***Polypodium saximontanum*** Windham, sp. nov.—TYPE: U.S.A. Colorado: La Plata Co., E side of Vallecito Creek ca. 2.15 km NNE of its confluence with Fall Creek, 8240 ft, 25 Jun 1990, *Windham (90-231)* & *Windham* (holotype: UT!; isotypes: BRY! COLO! KANU! MO! UC!). Fig. 4.

*Polypodium amorphoi* Suksdorf simile, a quo differt sporangiasteribus trichomatibus paucioribus, sporis tuberculatis plus quam ( $x$ ) = 62  $\mu\text{m}$  longis metientibus, chromosomatium numero  $n = 74$ ; a *P. virginiano* L. laminis plerumque minus quam 3.5 cm latis, sporangiasteribus trichomatibus paucioribus differt; a *P. hesperio* Maxon sori sporangiasteribus instructis, paleis rhizomatium atrobrunneis grosse dentatis et contortis distaliter, paleis abaxialibus rhachidum caducis, lanceolato-

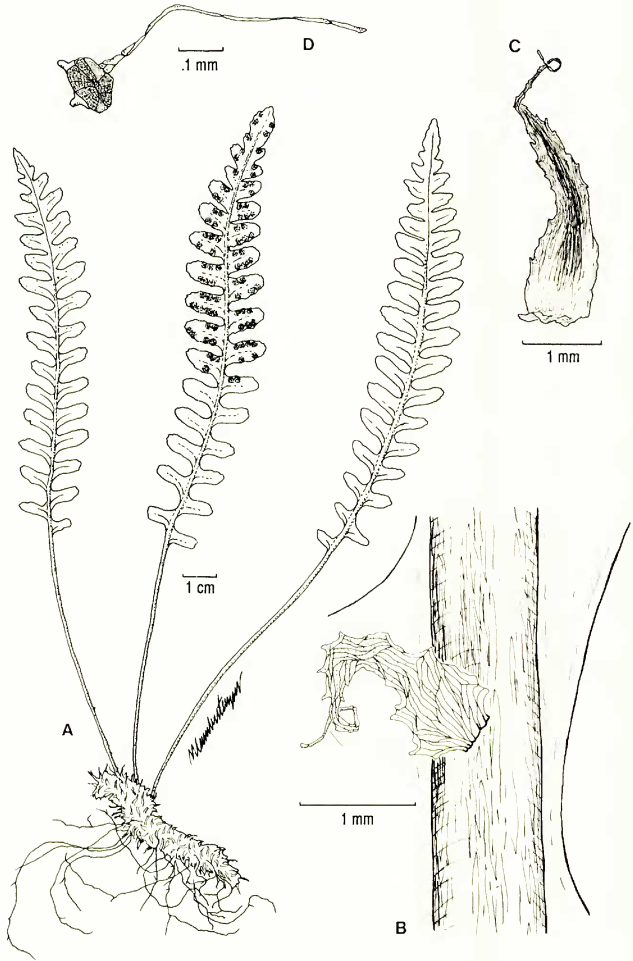


FIG. 4. *Polypodium saximontenum*. A. Habit; note narrow, almost linear leaves and submarginal sori. B. Abaxial view of portion of rachis; note persistent, lanceolate scale. C. Bicolorous rhizome scales with dentate margins and contorted tip. D. Sporangium from sorus; note small number of glands on head. (Based on Windham (90-231) & Windham.)

ovatis plerumque plus quam 6 cellulis in latitudine; a *P. sibirico* Siplivinskij differt soris sporangiasteribus glandulosis instructis, sporis plus quam  $(x) = 62 \mu\text{m}$  longis metientibus, chromosomatum numero  $n = 74$ .

Plants epipetric. Rhizomes creeping, 2–7 mm in diameter, usually whitish pruinose, acrid-tasting; rhizome scales lanceolate, 20–30 cells wide just above the point of attachment, contorted distally, often coarsely dentate, weakly bicolorous with a dark central region and pale brown margins. Leaves 3–27  $\times$  1–4 cm. Petioles slender, 0.75–1.5 mm in diameter. Blades narrowly oblong to linear, deeply pinnatifid, usually widest near the middle, coriaceous to subcoriaceous, with widely scattered glands on both surfaces; rachis sparsely scaly to glabrescent abaxially, glabrous adaxially; rachis scales lanceolate-ovate, usually more than 6 cells wide. Blade segments oblong, 2–8 mm wide, with rounded (rarely broadly acute) apex and entire to crenulate margins; segment midrib glabrous adaxially; veins free, forking 1–2 times, obscure in mature leaves. Sori circular, usually submarginal, 1–2 mm in diameter. Sporangiasters present, fewer than 40 per sorus, the bulbous heads with 2–6 small glandular hairs (rarely glabrous). Spores averaging 62–70  $\mu\text{m}$  long, conspicuously tuberculate with blunt projections 3–5  $\mu\text{m}$  in height. Chromosome number:  $n = 74$  (from the paratypes indicated by \*).

Distribution. U.S.A., Colorado, north-central New Mexico, southeastern Wyoming and the Black Hills of South Dakota; cracks and ledges on rock outcrops, apparently confined to granitic and gneissic substrates; 1800–3000 m.

PARATYPES. U.S.A. COLORADO: Gunnison Co., small tributary of Spring Creek, *Windham 363\** (ASC, UBC); SE side of the Taylor River, *Windham 361\** (ARIZ, ASC, UNM), *Windham 364\** (ASC, ASU, UTC); W wall of Spring Creek Canyon, *Windham 362\** (ASC, UT); Saguache Co., along Cochetopa Creek, *Windham 359\** (ASC, COLO).—NEW MEXICO: Rio Arriba Co., vicinity of Brazos Canyon, *Standley & Bollman 10626, 11195* (US).—WYOMING: Carbon Co., Platte River Canyon, *Dorn 4397, 4398* (RM).

### Woodsia

The application of modern biosystematic techniques to the study of North American species of *Woodsia* has revealed a complex web of evolutionary relationships (Windham 1987b) and the existence of several undescribed taxa. The most significant changes involve the *W. mexicana* Fée complex, an extraordinarily heterogeneous assemblage occurring in a wide range of habitats from South Dakota to central Mexico. Reexamination of the type specimens and original descriptions for taxa in the *W. mexicana* complex reveals that *W. mexicana* s.s. is absent from the region covered by *Flora of North America*. Isozyme and chromosome studies of North American collections traditionally identified as *W. mexicana* indicate that they represent three undescribed species here recognized as *W. phillipsii*, *W. neomexicana*, and *W. cochisensis*.

Specimens of *W. phillipsii* have been identified consistently as *W. mexicana* and have been considered typical of that species by many authors (e.g., Brown 1964). Rediscovery of the type specimen of *W. mexicana* (Windisch 1982) and careful examination of Fée's original description reveal the fallacy of this interpretation. *Woodsia phillipsii* differs from *W. mexicana* in having 1) long, completely filamentous indusial segments, 2) a greater number of indusial segments per sorus, 3) multicellular (often filamentous) translucent projections on pinnule margins, 4) glandular hairs with relatively thin stalks, 5) a greater number of

pinnules per pinna, 6) enlarged hydathodes readily visible on the adaxial leaf surface, and 7) smaller spores averaging 37–44  $\mu\text{m}$  long. In addition, plants of *W. mexicana* from eastern Mexico proved to be tetraploids (Windham, unpubl.), whereas chromosome counts derived from *W. phillipsii* are consistently diploid. Isozyme analyses indicate that *W. phillipsii* is the basic diploid of the *W. mexicana* group and was involved, as one parent, in the allopolyploid origins of *W. neomexicana*, *W. cochisensis*, and *W. mexicana*; as such, it should be considered a separate species. It is named in honor of Walter S. Phillips, a pioneer in the study of Arizona ferns, whose collections and ideas have proven invaluable to subsequent researchers.

**Woodsia phillipsii** Windham, sp. nov.—TYPE: U.S.A. Arizona: Cochise Co., Rucker Canyon, Chiricahua Mts, canyon sides in pine woods, 6500 ft, 7 Oct 1945, *Phillips 2854* (holotype: GH!; isotypes: ARIZ! ASC! UBC! US!). Fig. 5.

*Woodsiae mexicanae* Fée et *W. neomexicanae* Windham similis, a quibus differt marginibus pinnularum projecturis multicellularibus saepe filamentosis translucentibus e dentibus exorientibus, pinnis plerumque 7–18 paribus segmentorum non imbricatorum, gradatim attenuatis ad apicem anguste acutum, sporis minus quam (x) = 44  $\mu\text{m}$  longis metientibus, chromosomatum numero  $n = 38$ ; insuper a *W. mexicana* Fée differt segmentis indusiorum basi filamentosis, pilis gracilibus ad apicem cellula inconspicue tumida et glandulosa terminatis.

Plants epipetric (rarely terrestrial). Rhizomes compact to short-creeping, the individual branches usually 3–8 mm wide, with few to many persistent petiole bases of unequal lengths; rhizome scales narrowly lanceolate, often uniformly brown but at least some distinctly bicolorous with a dark central stripe and pale brown margins. Leaves 5–35  $\times$  1.5–6 cm. Petioles often somewhat brittle, light brown or straw-colored when mature (occasionally darker at the base). Blades lanceolate, usually 2-pinnate proximally, sparsely to moderately glandular but never viscid, the glandular hairs with thin stalks and slightly expanded tips; rachises with scattered glandular hairs and narrow scales. Pinnae elongate-deltate to elliptic, longer than wide, often attenuate to a narrowly acute apex, the largest divided into 7–18 pairs of distinct, well-separated pinnules; abaxial and adaxial surfaces somewhat glandular, devoid of eglandular hairs or scales. Pinnules dentate, often shallowly lobed; pinnule margins somewhat thickened, often lustrous adaxially, sparsely glandular, appearing ciliate due to the presence of multicellular translucent projections on teeth that are often prolonged to form twisted filaments; vein tips usually enlarged to form whitish hydathodes visible adaxially. Indusia of narrow, filamentous segments, these uniseriate for most of their length, often greatly surpassing mature sporangia, composed of cells that are more or less isodiametric. Spores averaging 37–44  $\mu\text{m}$  long. Chromosome number:  $n = 38$  (from the paratypes indicated by \*).

Distribution. U.S.A., southern Arizona, southern New Mexico, and Trans-Pecos Texas, and northern Mexico, Chihuahua and Sonora; cliffs and rocky slopes, usually on quartzite or various igneous substrates; 1600–3200 m.

PARATYPES. **Mexico.** CHIHUAHUA: Mpio. Guachochic, N of Basiguare, *Bye 8039* (COLO); Tecolote 10 mi W of Chinatu, *Correll & Gentry 23006* (LL, MO, US). **U.S.A. ARIZONA:** Cochise Co., SE wall of Huachuca Canyon, *Windham 298\** (UT), *Windham 302\** (ASC, ASU).—**NEW MEXICO:** Grant Co., S side of Iron Creek in the Mimbres Mts, *Windham (611) & Hauffer* (NMC, UC, UT, UTEP); Hidalgo Co., Animas Mts, upper Indian Creek Canyon, *Wagner 1757* (UNM).—**TEXAS:** Brewster Co., on trail from Boot Spring to South Rim, *Warnock 1105* (TEX, US).

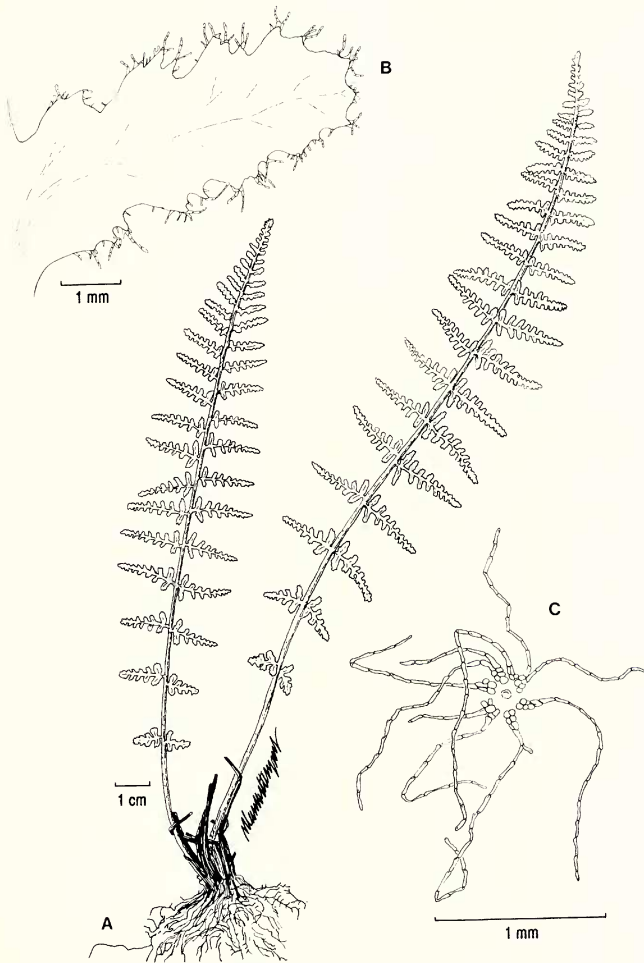


FIG. 5. *Woodsia phillipsii*. A. Habit; note attenuate pinnae divided into numerous, well-separated pinnules. B. Adaxial view of pinnule showing multicellular, filamentous projections on margin. C. Sorus with sporangia removed; note long, filamentous indusial segments. (Based on Windham (611) & Haufler.)

*Woodsia neomexicana* has also been associated with *W. mexicana*, though occasional specimens have been misidentified as *W. oregana*. The latter tendency is not surprising because isozyme data indicate that *W. neomexicana* represents an allotetraploid hybrid between *W. phillipsii* and a diploid member of the *W. oregana* complex. Similarities between *W. neomexicana* and *W. mexicana* probably result from the fact that they share a genome derived from *W. phillipsii*. Nevertheless, *W. neomexicana* differs from *W. mexicana* in having longer, completely filamentous indusial segments, a greater number of indusial segments per sorus, leaf blades that are glabrescent or sparsely glandular, and glandular hairs with relatively thin stalks. Features distinguishing *W. neomexicana* from *W. phillipsii* and *W. oregana* are summarized in the the diagnosis presented below. As a fertile allotetraploid hybrid between the basic diploid member of the *W. mexicana* complex and *W. oregana*, *W. neomexicana* should be recognized as a distinct species, characterized as follows.

***Woodsia neomexicana*** Windham, sp. nov.—TYPE: U.S.A. New Mexico: Socorro Co., along small tributary of Water Canyon in the Magdalena Mts ca. 5.84 km SE of the summit of North Baldy, 7050 ft, 23 Aug 1990, *Windham (90-365)* & *Rabe* (holotype: UT!; isotypes: ARIZ! ASU! BRY! COLO! GH! MICH! MO! NMC! NY! TEX! UC! UNM! US!). Fig. 6.

*Woodsiae mexicanae* Fée similis, a qua differt segmentis indusiorum filamentosis e basi, laminis glabrescentibus vel sparsim glandulosis, pilis gracilibus ad apicem cellula inconspicue tumida et glandulosa terminatis; a *W. oregana* D. Eaton differt stipitibus pallide brunneis vel stramineis ubique, filamentis indusiorum sporangia matura excedentibus, marginibus pinnularum projecturis translucen- tibus e dentibus exorientibus; a *W. phillipsii* Windham differt marginibus pinnularum projecturis translucen- tibus 1–2-cellularibus (raro multicellularibus) e denti- bus, pinnis plerumque segmentis minus quam 7-jugis imbricatis, versus apicem abrupte angustatis apice late rotundatis, sporis plus quam  $(x) = 44 \mu\text{m}$  longis metientibus, chromosomatum numero  $n = 76$ .

Plants epipetric (rarely terrestrial). Rhizomes compact, the individual branches usually 5–9 mm wide, with few to many persistent petiole bases of unequal lengths; rhizome scales narrowly lanceolate, often uniformly brown but at least some distinctly bicolorous with a dark central stripe and pale brown margins. Leaves 4–30  $\times$  1.5–6 cm. Petioles often somewhat brittle, light brown or straw-colored when mature (occasionally darker at very base). Blades linear to lanceolate, usually pinnate-pinnatifid proximally, glabrescent to sparsely glandular but never viscid, the glandular hairs with thin stalks and slightly expanded tips; rachises with scattered glandular hairs and rare, hairlike scales. Pinnae ovate-deltate to elliptic, longer than wide, abruptly tapered to a rounded or broadly acute apex, the largest divided into 3–7 pairs of closely spaced pinnules; abaxial and adaxial surfaces glabrescent to sparsely glandular, devoid of eglandular hairs or scales. Pinnules dentate, often shallowly lobed; pinnule margins thin, nonlustrous, with widely scattered glands and 1–2-celled translucent projections on most teeth; vein tips occasionally enlarged to form whitish hydathodes visible adaxially. Indusia of narrow filamentous segments, these uniseriate for most of their length, usually surpassing the mature sporangia, composed of cells that are more or less isodiametric. Spores averaging 44–52  $\mu\text{m}$  long. Chromosome number:  $n = 76$  (from the paratypes indicated by \*).

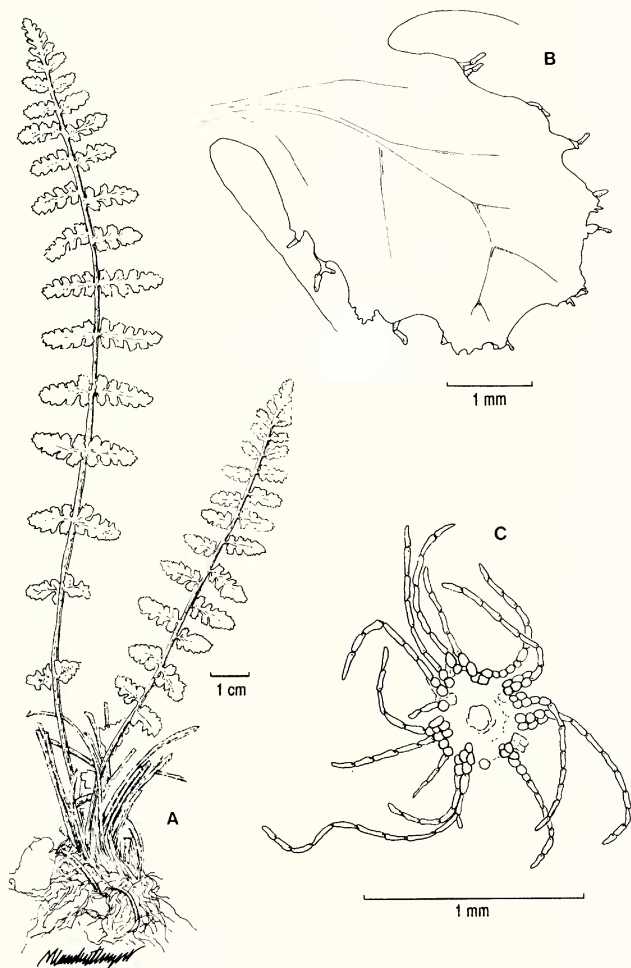


FIG. 6. *Woodsia neomexicana*. A. Habit; note rounded pinna apices and small number of closely spaced pinnules. B. Adaxial view of pinnule showing 1-2-celled projections on margins. C. Sorus with sporangia removed; note long, filamentous indusial segments. (Based in Windham (90-365) & Rabe.)

Distribution. U.S.A., New Mexico, Arizona, southern Colorado, western Oklahoma, and Trans-Pecos Texas, one disjunct population in eastern South Dakota; cliffs and rocky slopes, usually on sandstone, quartzite, or various igneous substrates; 300–3500 m.

PARATYPES. U.S.A. ARIZONA: Coconino Co., cliffs W of Lenox Park, San Francisco Peaks, *Windham 195\** (ARIZ, ASC); Gila Co., below Hi View Point on the Mogollon Rim, *Windham 178* (ASC).—COLORADO: La Plata Co., along trail on W side of Vallecito Creek, *Windham (90-247) & Windham* (COLO, UT, UTC).—NEW MEXICO: Colfax Co., vicinity of Ute Park, *Standley 13832* (US).—OKLAHOMA: Caddo Co., Red Rock Canyon State Park near Hinton, *Lellingier 214* (US).—TEXAS: Jeff Davis Co., across rd from "Point of Rocks" roadside park on scenic drive about 11 mi from Ft. Davis, *Correll 33688* (ENCB, LL, NCU); Presidio Co., North Chinati Mountains, *Wornock 19239* (SRSC).

Specimens of *W. cochisensis* traditionally have been identified as *W. plummerae* Lemmon or (less often) *W. mexicana*. The association with *W. plummerae* stems from the widely held belief that the broad indusial segments and somewhat glandular blade of *W. cochisensis* exclude it from *W. mexicana*. To the contrary, reexamination of the type specimen and original description of *W. mexicana* reveals that these features are characteristic of that species and thus do not serve to distinguish it from either *W. plummerae* or *W. cochisensis*. The three taxa are clearly distinct in other features, however, and worthy of recognition as separate species. *Woodsia cochisensis* differs from *W. plummerae* in having 1) petioles that are light brown or stramineous throughout, 2) leaf blades that are sparsely to moderately glandular and never viscid, 3) glandular hairs with thin stalks and inconspicuously swollen tips, 4) pinnule margins that are usually thickened and lustrous on the adaxial surface, and 5) vein tips enlarged to form hydathodes readily visible on the adaxial surface. It differs from *W. mexicana* in having fewer, narrower glands on the leaf, pinnule margins that are usually thickened and lustrous on the adaxial surface, and well-developed hydathodes readily visible on the adaxial surface. *Woodsia cochisensis* is easily distinguished from other North American members of the *W. mexicana* group (*W. phillipsii* and *W. neomexicana*) by having indusial segments that are broad and non-filamentous for much of their length. Isozyme and chromosome studies suggest that *W. cochisensis* is an allotetraploid that originated through hybridization between *W. phillipsii* and an undescribed Mexican diploid. As such, it should be considered a distinct species characterized as follows.

***Woodsia cochisensis*** Windham, sp. nov.—TYPE: U.S.A. Arizona: Cochise Co., SE wall of Huachuca Canyon in the Huachuca Mts ca. 2.85 km SE of Blacktail Spring, 6000 ft, 31 Aug 1985, *Windham (781) & Yatskievych* (holotype: UT!; isotypes: ARIZ! ASU! MICH! UC! US!). Fig. 7.

*Woodsiae plummerae* Lemmon similis, a qua differt stipitibus pallide brunneis vel stramineis ubique, laminis sparsim vel moderate glandulosis, haud viscidis, pilis gracilibus ad apicem inconspicue tumidis glandulosis, marginibus pinnularum plerumque incrassatis, adaxialiter nitidis, apicibus venarum dilatatis et formantibus hydathodo albido adaxialiter; a *W. mexicana* Fée differt glandulis paucioribus et angustioribus in lamina, marginibus pinnularum plerumque incrassatis et nitidis adaxialiter, hydathodis manifestis; a *W. phillipsii* Windham et *W. neomexicana* Windham segmentis indusiorum latis non filamentosis praeter apicem differt.



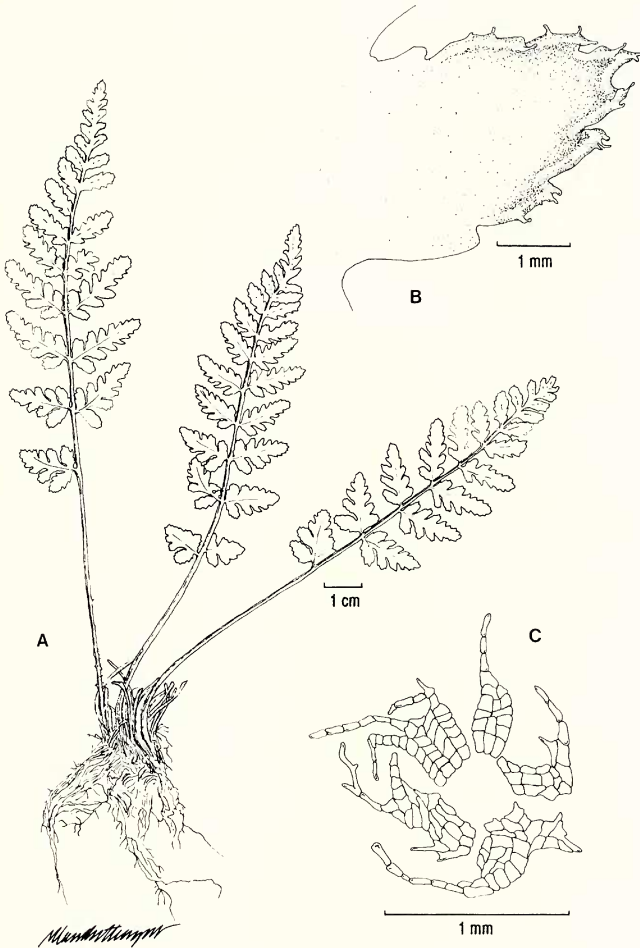


FIG. 7. *Woodsia cochisensis*. A. Habit. B. Adaxial view of pinnule showing thickened margins with scattered glands and 1-2-celled projections. C. Sorus with sporangia removed; note relatively broad indusial segments that are multiseriate proximally but often divided and uniseriate distally. (Based on Windham (781) & Yatskievych.)

Plants epipetric (rarely terrestrial). Rhizomes compact, the individual branches usually 4–9 mm wide, with a few persistent petiole bases of unequal lengths; rhizome scales narrowly lanceolate, often uniformly brown but at least some distinctly bicolorous with a dark central stripe and pale brown margins. Leaves 5–25 × 1.6–6 cm. Petioles often somewhat brittle, light brown or straw-colored when mature (occasionally darker at very base). Blades narrowly lanceolate to ovate, pinnate-pinnatifid to 2-pinnate proximally, sparsely to moderately glandular but never viscid, the glandular hairs with thin stalks and slightly expanded tips; rachises with glandular hairs and occasional narrow scales. Pinnae ovate-deltate to elliptic, longer than wide, abruptly tapered to a rounded or broadly acute apex (rarely attenuate), the largest divided into 4–9 pairs of closely spaced pinnules; abaxial and adaxial surfaces glandular, devoid of eglandular hairs or scales. Pinnules dentate, often shallowly lobed; pinnule margins usually thickened, lustrous adaxially, sparsely glandular, with 1–2-celled translucent projections on some teeth; vein tips enlarged to form whitish hydathodes visible adaxially. Indusia of relatively broad segments, these multiseriate much of their length but usually divided and uniseriate distally, often surpassing the mature sporangia, composed of cells that are more or less isodiametric. Spores averaging 43–49  $\mu\text{m}$  long. Chromosome number:  $n = 76$  (from the holotype population).

Distribution. U.S.A., southern Arizona and southwestern New Mexico, and northern Mexico, Chihuahua and Sonora; shaded ledges and alcoves near springs and seeps, usually on granitic or volcanic substrates; 1000–2200 m.

PARATYPES. **Mexico.** CHIHUAHUA: Barranca de Batopilas between La Bufa and Wimivo, *Bye 6086* (COLO). **U.S.A. ARIZONA:** Cochise Co., unnamed tributary of Stronghold Canyon East, Dragon Mts, *Windham 309* (ASC); Pima Co., Baboquivari Mts, *Peebles, Harrison & Kearney 3800* (ARIZ, MO); Rincon Mts, *Harrison & Kearney 7977* (ARIZ, US); south wall of Box Canyon, Santa Rita Mts, *Windham 167* (ASC, ASU, KANU); Santa Cruz Co., Sycamore Canyon, *Goodding & Goodding 423* (ARIZ, RM, US); Tumacacori Mts, Rock Corral Spring, *Fletcher 3899* (UNM).

Recent chromosome studies reveal that *Woodsia obtusa* comprises two cytotypes that show evidence of morphologic and ecogeographic differentiation. The tetraploid cytotype is found throughout the eastern United States, commonly occurring on limestone. The diploid cytotype occurs at the western edge of the species range and is usually found on sandstone or granite. The geographically restricted diploid taxon differs from the widespread tetraploid in having leaf blades that are often finely cut and nearly tripinnate, rhizomes that are short- to long-creeping and usually less than 5 mm in diameter, and smaller spores averaging less than 42  $\mu\text{m}$  long. Chromosome and isozyme data suggest that the tetraploid cytotype of *W. obtusa* probably was derived directly from the diploid cytotype through autopolyploidy. Although Sprengel did not designate a type specimen, the original description and the collection locality cited (Pennsylvania) leave little doubt that the type material of *Woodsia obtusa* was tetraploid. It appears that none of the published names in *Woodsia* are applicable to the diploid cytotype of this species, which is here described as a new subspecies.

***Woodsia obtusa*** (Sprengel) Torrey subsp. ***occidentalis*** Windham, subsp. nov.—  
TYPE: U.S.A. Texas: Llano Co., W side of Inks Lake, on hillside in granite area, 16 Apr 1945, *Lundell 13484* (holotype: LL!; isotypes: LL! RM!).

A subsp. *obtusata* differt pinnulis proximalibus pinnarum infimarum profunde lobatis vel pinnatifidis, laminis saepe subtiliter incisae fere tripinnatis, rhizomatibus brevi- vel longi-repentibus plerumque minus quam 5 mm diametro, sporis minus quam  $(x) = 42 \mu\text{m}$  longis metientibus, chromosomatum numero  $n = 38$ .

Plants epipetric or occasionally terrestrial. Rhizomes short- to long-creeping, the individual branches usually 3–5 mm wide, with a few persistent petiole bases of unequal length; rhizome scales often uniformly brown but at least some distinctly bicolorous with a dark central stripe and pale brown margins. Leaves 8–40  $\times$  2.5–10 cm. Petioles often somewhat brittle, light brown or straw-colored when mature (occasionally darker at very base). Blades lanceolate to narrowly ovate, usually 2-pinnate-pinnatifid proximally, moderately glandular and rarely somewhat viscid, most of the glandular hairs with thick stalks and distinctly bulbous tips; rachises with glandular hairs and scattered, narrow scales. Pinnae ovate-deltate to elliptic, longer than wide, often attenuate to a narrowly acute apex, the largest divided into 5–14 pairs of distinct, well-separated pinnules; abaxial and adaxial surfaces glandular, devoid of eglandular hairs or scales. Pinnules dentate, the proximal ones usually deeply lobed; pinnule margins thin, nonlustrous, sparsely to moderately glandular, lacking cilia or translucent projections on the teeth; vein tips usually enlarged to form whitish hydathodes visible adaxially. Indusia of relatively broad, nonfilamentous segments, these multiseriate throughout, concealed by or slightly surpassing the mature sporangia, composed of cells that are more or less isodiametric. Spores averaging 35–42  $\mu\text{m}$  long. Chromosome number:  $n = 38$ .

Distribution. U.S.A., Oklahoma, central Texas, southeastern Kansas, northeastern Arkansas, and the extreme southwestern corner of Missouri; cliffs and rocky slopes, especially on sandstone and granitic substrates; 200–500 m.

PARATYPES. U.S.A. KANSAS: Woodson Co., T26S, R14E, NE1/4, sec. 14, in sandy soil of a rocky wooded hillside in uplands, *Lathrop 637* (GH, KANU, US).—OKLAHOMA: Comanche Co., along trail near top of Elk Mtn, Wichita Mountains Wildlife Refuge, *McMurry 1203* (OKL, OKLA); Johnston Co., "Devil's Den" near Tishomingo, *Palmer 39442* (GH, MO, US).—TEXAS: Burnet Co., Inks Lake State Park, *Hartman 918* (KANU); Granite Mountain, *Palmer 10260* (DS, MO); Gillespie Co., Bear Mountain, *Correll & Correll 12753* (COLO, LL, MICH, SMU, UC).

In his monograph of the genus *Woodsia*, Brown (1964) divided *W. oregana* into two varieties: a diploid (var. *oregana*) thought to span the continent and a tetraploid (var. *cathcartiana*) supposedly restricted to the vicinity of Taylor's Falls on the Minnesota-Wisconsin border. The strong morphological resemblance between these two taxa led Brown to hypothesize that var. *cathcartiana* was an autotetraploid derivative of var. *oregana*. Subsequent chromosome and isozyme work on *W. oregana* has substantially altered our understanding of the distribution and relationships of these taxa. Chromosome surveys of 30 populations scattered across the continent reveal that the tetraploid cytotype of *W. oregana* is actually more common and widespread than the diploid, extending diagonally across North America from California to eastern Canada. Diploid populations, on the other hand, are apparently confined to the Pacific Northwest. The two taxa are nearly allopatric, and isozyme data indicate that var. *cathcartiana* is definitely not an autotetraploid derived from known diploid populations. Although the morphological features that distinguish var. *oregana* and var. *cathcartiana* are subtle, the sharp ecogeographic and genetic discontinuities observed suggest that these taxa should be recognized at a higher taxonomic level. They will be treated as subspecies in *Flora of North America*, which requires the following nomenclatural change.

**Woodsia oregana** D. Eaton subsp. **cathcartiana** (Robinson) Windham, stat. nov.  
*Woodsia cathcartiana* B. L. Robinson, *Rhodora* 10: 30. 1908.—TYPE: U.S.A.  
Minnesota: Taylor's Falls of the St. Croix River, 1874, *Cathcart s.n.* (holo-  
type: GH!).

In the original description of *Woodsia oregana*, Eaton (1865) mentioned two syntypes: 1) Dalles of the Columbia River, *Major Raines* in 1855, and 2) Montium Scopulosorum sub. lat. 39°–41°, *Hall & Harbour 690a*. Examination of the original specimens in the Eaton Herbarium at Yale University reveals that the first collection represents the Pacific Northwest diploid cytotype of *W. oregana*, whereas the second belongs to the widespread tetraploid taxon here called *W. oregana* subsp. *cathcartiana* (Robins.) Windham. In order to stabilize the nomenclature of *W. oregana* and maintain current application of infraspecific names, the first of the two specimens cited by Eaton is here chosen as the lectotype of the species.

**Woodsia oregana** D. Eaton, *Canad. Naturalist & Quart. J. Sci.*, n.s. 2: 90. 1865.—  
TYPE: U.S.A. Oregon: Dalles of the Columbia River, *Major Raines* in  
1855 (lectotype, here designated: Y!; isolectotypes: GH, K).

*Woodsia scopulina* D. Eaton shows substantial variation in leaf size, shape, and dissection, and in the abundance of multicellular hairs on the pinnae. Although much of this variation seems to be environmentally induced, chromosome and isozyme studies have identified three morphogenetic variants worthy of taxonomic recognition. The most distinctive taxon is represented by a series of populations confined to montane habitats in the southeastern United States. Plants found in this region differ from other collections of *W. scopulina* in having 1) narrowly lanceolate rhizome scales that are mostly bicolorous with pale brown margins and a continuous, dark central stripe, 2) broad (non-filamentous) indusial segments, and 3) some blade hairs composed of five or more cells.

Taylor (1947) recognized the distinctive nature of these eastern populations and described them as a new species, *Woodsia appalachiana*. Brown (1964: 98), however, placed this name in synonymy under *W. scopulina*, stating that "the differences are not constant and are so minor that I am not considering even varietal status for this entity." Contrary to Brown's assertion, the differences between the Appalachian taxon and typical representatives of *W. scopulina* from western North America are both stable and significant. The only apparent connection between these two entities consists of scattered populations in the Great Lakes region and western United States that preliminary data suggest may have originated through hybridization. Because of their geographic isolation and morphological distinctiveness, the Appalachian/Ozarkian populations of *W. scopulina* will be treated as a distinct subspecies in *Flora of North America*, which necessitates the following nomenclatural change.

**Woodsia scopulina** D. Eaton subsp. **appalachiana** (Taylor) Windham, stat. nov.  
*Woodsia appalachiana* T. M. C. Taylor, *Amer. Fern J.* 37: 88. 1947.—  
TYPE: U.S.A. West Virginia: on a mountain 4 mi N of Old Sweet, 14 Sep  
1903, *Steele & Steele 306* (holotype: GH!).

As mentioned above, collections of *Woodsia scopulina* from the Great Lakes region tend to bridge the geographic and morphologic gap between subsp. *appa-*

*lachiana* and subsp. *scopulina*. Preliminary evidence suggests that these plants are tetraploid hybrids genetically isolated from diploid populations of *W. scopulina*. They are most similar to subsp. *scopulina*, from which they differ in having larger spores (averaging  $> 50 \mu\text{m}$  long) and some rhizome scales that are weakly bicolorous with clusters of sclerotic cells near the center that form a narrow, usually discontinuous, dark central stripe. The Great Lakes taxon also occurs sporadically in western North America, where it is sympatric with subsp. *scopulina*. Despite regional sympatry, these two taxa are rarely found growing together, suggesting that they differ in ecological tolerances and/or habitat requirements. Although the morphological features that distinguish the Great Lakes taxon are subtle, evidence of strong genetic and ecogeographic isolation suggest that it is worthy of formal taxonomic recognition. None of the names currently available in *Woodsia* are applicable to this taxon, which is here described as a new subspecies.

***Woodsia scopulina*** D. Eaton subsp. ***laurentiana*** Windham, subsp. nov.—TYPE: CANADA. Quebec: Gaspé Co., Tourelle, on sandstone sea-cliffs, 19–21 Aug 1905, Collins & Fernald 25351 (holotype: GH!; isotypes: CAN! CAS! GA! GH! MICH! NY! POM! UC! US!).

A subsp. *scopulina* sporis plus quam ( $x$ ) =  $50 \mu\text{m}$  longis metientibus, paleis rhizomatum interdum infirme bicoloribus prope centrum fuscatis fasciculis angustatis plerumque discontinuis cellularum scleroticarum differt; a subsp. *appalachiana* (Taylor) Windham paleis rhizomatum lanceolato-ovatis infirme (non valde) bicoloribus, pilis raro plus quam 5 cellulis longis in pinnis, segmentis indusiorum angustioribus et saepe filamentosis distaliter, sporis plus quam ( $x$ ) =  $50 \mu\text{m}$  longis metientibus differt.

Plants epipetric (rarely terrestrial). Rhizomes compact, the individual branches usually 5–10 mm wide, with few to many persistent petiole bases of unequal lengths; rhizome scales ovate-lanceolate, most uniformly brown but at least some with clusters of dark, sclerotic cells near the center forming a narrow, usually discontinuous stripe. Leaves 9–35  $\times$  1–8 cm. Petioles relatively brittle and easily shattered, reddish brown to dark purple proximally when mature. Blades lanceolate to linear-lanceolate, 2-pinnate proximally, moderately glandular and rarely somewhat viscid, the glandular hairs with thick stalks and distinctly bulbous tips; rachises usually with abundant glandular and eglandular hairs. Pinnae lanceolate-deltate to ovate, longer than wide, usually gradually tapered to an acute apex (occasionally attenuate), the largest divided into 5–14 pairs of more or less closely spaced pinnules; abaxial and adaxial surfaces glandular and sparsely villous with long, eglandular hairs concentrated near the midribs. Pinnules dentate, often shallowly lobed; pinnule margins thin, nonlustrous, glandular and sparsely ciliate with long, eglandular hairs; vein tips slightly (if at all) enlarged, barely visible adaxially. Indusia of relatively narrow segments, these multiseriate proximally but often divided into uniseriate filaments distally, concealed by or slightly surpassing the mature sporangia, composed of cells that are more or less isodiametric. Spores averaging 50–57  $\mu\text{m}$  long. Chromosome number:  $n = 76$  (in collections from the western U.S.A.).

Distribution. Bimodal distribution with a cluster of populations in the Great Lakes/St. Lawrence region (Ontario, Quebec, and Minnesota) and scattered records in western North America (Alberta and British Columbia south to California and possibly Arizona); cliffs and rocky slopes on a variety of substrates including both granite (acidic) and limestone (basic); 0–3000 m.

PARATYPES. **Canada**, ONTARIO: Nipissing District, Algonquin Provincial Park, ca. 300 yds due E of campsite at N end of Hilliard Lake, *Britton s.n.* (CAN, DAO, OAC, TRT); Thunder Bay District, E side of Cloud Bay, *Garton 18531* (CAN, DAO, LKHD); Laverendrye Provincial Park, E shore of North Fowl Lake, *Brunton 6862* (CAN, OAC, UT).—Quebec: Gaspé Co., Gulf of St. Lawrence, Christie, *Fernald & Pease 24800* (CAN, GH, MICH, NY, US). **U.S.A.**, MINNESOTA: Cook Co., face of cliff north of center of East Pike Lake, *Burns & Hendrickson 231* (COLO, MIN, MO, RM); St. Louis Co., near Grand Portage, north shore of Lake Superior, *Wiggins 14945* (DS).

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