Toward a monophyletic Cheilanthes: The resurrection and recircumscription of Myriopteris (Pteridaceae)

Amanda Lee Grusz¹, Michael Dennis Windham¹

¹ Department of Biology, Duke University, Box 90338, Durham, NC 27708–0338, USA

Corresponding author: Amanda Lee Grusz (alg3@duke.edu)

Abstract
The fern genus Cheilanthes (Pteridaceae) has perplexed taxonomists for more than two centuries. Complex patterns of evolution involving rampant morphological convergence, polyploidy, hybridization, and apomixis have made the taxonomy of this group especially difficult. Fortunately, recent phylogenetic analyses have helped to clarify relationships among cheilanthoid taxa. Based on these findings, we here formalize an updated taxonomy for one monophyletic clade comprising 47 primarily North and Central American taxa usually included in Cheilanthes. Because the type species of Cheilanthes (C. micropteris) is only distantly related to this clade, we resurrect the genus Myriopteris to accommodate these taxa, and present a revised circumscription for the group, including 36 new combinations.

Keywords
Cheilanthes, cheilanthoid, myriopterid, myriopteroid, nomenclature, taxonomy

Introduction
A “practical and natural” generic classification of cheilanthoid ferns (Pteridaceae) has eluded taxonomists for more than 200 years and was viewed by Tryon and Tryon (1982) as one of the most contentious issues in fern systematics. Central to the problem is the circumscription of the large genus Cheilanthes, which all molecular studies with sufficient sampling indicate is polyphyletic (see Gastony and Rollo 1998; Kirkpatrick 2007; Prado et al. 2007; Schuettpelz et al. 2007; Zhang et al. 2007; Rothfels et al. 2008; Eiserhardt et al. 2011). Since the initial description of Cheilanthes (Swartz...
1806) encompassing 16 species, various authors have moved hundreds of taxa into (e.g., Domin 1913; Mickel 1979) and out of (e.g., Fée 1852; Smith 1875; Ching 1941) the genus. Of the ca. 500 validly published species names in *Cheilanthes*, some 60% have, at some point, resided in other genera. The lack of definitive taxonomic characters in this group often is attributed to widespread convergent evolution in the drought-prone habitats occupied by these ferns (Tryon and Tryon 1973, 1982), and the problem is likely insoluble based on morphology alone. However, the same genetic evidence that highlights shortfalls in the current classification provides a key to solving this puzzle. As DNA sequence data proliferate and morphological features are reexamined in light of molecular phylogenies, it eventually becomes possible to recognize monophyletic assemblages of species that can be circumscribed as genera. We now have reached this point with certain groups of cheilanthoid ferns, at least in terms of removing taxa and clades that cannot reasonably be included within *Cheilanthes* (Link-Perez et al. 2011; Li et al. 2012).

Here, we focus on the primarily New World lineage previously referred to as the “American *Cheilanthes*” (Kirkpatrick 2007), myriopteroid (Rothfels et al. 2008), or myriopterid (Windham et al. 2009; Eiserhardt et al. 2011) ferns. Limited sampling in each of those analyses indicated that these ferns might represent a well-supported, monophyletic group, an assumption fully supported by the more complete (85%) taxon sampling of Grusz et al. (in review). In addition to suggesting the monophyly of the myriopterid lineage, the analyses of Rothfels et al. (2008) and Eiserhardt et al. (2011) conclusively demonstrated that this clade was quite distantly related to the type species of *Cheilanthes*, *C. micropteris* (results summarized in Fig. 1). This improved understanding of phylogenetic relationships among cheilanthoid ferns necessitates a taxonomic revision that can be achieved by one of two options: 1) all taxa derived from the most recent common ancestor of *C. micropteris* and the myriopterid ferns could be assigned to a single genus (which would not be called *Cheilanthes* because of the priority of *Hemionitis*), or 2) myriopterid ferns could be transferred to a different genus, reflecting their phylogenetic distinction from *Cheilanthes s.s*. The first option would require 400+ new combinations in *Hemionitis* (or the conservation of *Cheilanthes* against it followed by more than 100 new combinations in that genus). It would also subsume a number of cohesive, well-characterized genera that are clearly distinct based on morphological, molecular, and cytological grounds, including *Adiantopsis* (Link-Pérez et al. 2011), *Argyrochosma* (Windham 1987; Sigel et al. 2011), *Astrolepis* (Beck et al. 2010), *Doryopteris* (Yesilyurt 2004), *Gaga* (Li et al. 2012), and *Notholaena* (Rothfels et al. 2008). This approach would maximize the number of nomenclatural changes while simultaneously obscuring well-documented phylogenetic relationships, resulting in the inclusion of all but six cheilanthoid species in one genus. Because we consider this option untenable, we have, instead, chosen to remove the myriopterid ferns from *Cheilanthes*.

When any species or clade is removed from *Cheilanthes*, the first issue that must be addressed involves their relationship to *Allosorus pusillus* (Willd. ex Bernh.) Bernh. [= *Cheilanthes pteridioïdes* (Reich.) C. Chr.]. This species was designated the lectotype
Toward a monophyletic *Cheilanthes*: The resurrection and recircumscription... of *Allosorus* Bernh. by Pichi-Sermolli (1953), a choice subsequently validated by the ICBN when *Cheilanthes* was conserved over *Allosorus* (Appendix II of the Montreal Code, Stafleu et al. 1961). The only phylogenetic study published to date that includes the type species of both *Allosorus* and *Cheilanthes* is that of Eiserhardt et al. (2011). In that analysis, it is unclear whether the divergence between *C. maderensis* (= *C. pteridioides*; see Nardi and Reichstein 1985; Rothfels et al. 2012) and *C. micropteris* is sufficient to justify the recognition of two genera. The two taxa appear in distinct, well-supported clades (clade A vs. clade C in fig. 2B of Eiserhardt et al. 2011), but
deeper relationships are poorly resolved and both clearly belong to the rapidly diversifying hemonitid lineage (clade H). The unequivocal assignment of *Allosorus* to the hemonitids by Eiserhardt et al. (2011) does, however, prevent the application of this generic name to the myriopterid clade. Any attempt to expand *Allosorus* to include myriopterids would encompass both *Cheilanthes* (conserved over *Allosorus*) and *Hemionitis* (which has priority over both).

One potentially viable option for generic placement of the myriopterid clade would be to include it within a revised circumscription of *Pellaea* Link. All recent phylogenetic studies with adequate sampling of the two groups (e.g., Kirkpatrick 2007; Rothfels et al. 2008; Eiserhardt et al. 2011) strongly support the position of myriopterids as the sister group of the pellaeid clade, which includes *Pellaea atropurpurea*, the lectotype of the oldest generic name applicable to that clade. We are not in favor of expanding the definition of *Pellaea* to encompass the myriopterids for a variety of reasons. First, the two are quite distinct, both in terms of phylogenetic divergence and morphology. The myriopterids have substantially smaller ultimate segments, pubescent and/or scaly (vs. mostly glabrous) leaf blades, and sporangia that are confined to vein tips (vs. distributed along the veins near the segment margins). Because of these differences, the two groups generally have not been considered closely related, and most myriopterids would require new combinations in *Pellaea*. Adding to this nomenclatural upheaval is the fact that other well-defined genera, including *Argyrochosma* (Sigel et al. 2011) and *Astrolepis* (Beck et al. 2010), would be subsumed within such a circumscription of *Pellaea*, which would require additional new combinations and serve only to further undermine the distinctions among the major genera of cheilanthoid ferns.

If the expansion of *Pellaea* is ruled out, there remain three other generic names typified by species belonging to the myriopterid clade: 1) *Myriopteris*, described by Fée (1852) and typified by *M. marsupianthes* Fée; 2) *Cheilosoria*, named by Trevisan (1877) and lectotypified by Copeland (1947) based on *C. allosuroides* (Mett.) Trev.; and 3) *Pomataphytum*, published by Jones (1930) and typified by *P. pocillatum* M. E. Jones (= *M. lendigera*). Phylogenetic reconstructions (Grusz et al. in review) confirm that the type species of *Myriopteris* and *Pomataphytum* fall within a single, well-supported clade. In fact, the diploid species *M. marsupianthes* is thought to be one of the parents of sexual tetraploid *M. lendigera* (see Mickel and Smith 2004). Thus, the generic name *Pomataphytum* is appropriately considered a taxonomic synonym of the earlier described *Myriopteris* and can be eliminated as a potential name for the myriopterid clade. Copeland’s (1947) lectotype of *Cheilosoria* belongs to the well-supported and morphologically distinctive alabamensis clade that diverges earlier in the myriopterid phylogeny (Grusz et al. in review), and the name *Cheilosoria* could be used for this particular group if the myriopterids were subdivided into two or more genera. However, *Myriopteris* predates *Cheilosoria* by 25 years and, when these species are assigned to a single genus (our preferred approach), *Myriopteris* is the correct generic name for the inclusive myriopterid clade.
Historical use of the name Myriopteris

The original concept of *Myriopteris* (Fée 1852) included 11 species, these split between two sections (*Eumyriopteris* and *Cheilanthastrum*) distinguished by the presence or absence of a well-developed, inframarginal false indusium. The Latin and French descriptions of the genus are only partly overlapping; shared elements include the highly divided fronds, the small, orbicular ultimate segments with recurved margins ("formant un bourrelet très-contracté"), and a tendency to be covered by hairs and/or scales. *Myriopteris* was accepted and significantly expanded by J. Smith (1875: 280) who stated "the genus consists of about 20 species, distinguished from *Notholaena* and *Cheilanthes* by their small, concave, lenticular segments." The segregation of *Myriopteris* from *Cheilanthes* was, however, rejected by most subsequent authors (e.g., Christensen 1906; Copeland 1947; Lellinger 1965; Tryon and Tryon 1982; Kramer et al. 1990), with two notable exceptions. Pichi-Sermolli (1977) advocated a narrowed circumscription of the genus, including only the two species with prominent false indusia, viz., *M. marsupianthes* and *M. lendigera*. As shown by Grusz et al. (in review), this definition of *Myriopteris* is phylogenetically indefensible because it excludes *M. mexicana*, the apparent maternal progenitor of allotetraploid *M. lendigera*. About the same time Pichi-Sermolli was narrowing the definition of *Myriopteris*, Löve and Löve (1977) expanded it slightly by proposing a new combination for the species known as *Cheilanthes covillei* Maxon. This was done without explanation, though almost certainly reflects the fact that this species has the small, bead-like ultimate segments emphasized in earlier circumscriptions of the genus.

Although this “microphyllous” leaf morphology is common within *Myriopteris*, it does not characterize the entire clade (Grusz et al. in review) and has evolved independently in other cheilanthoid lineages. Thus, the possession of small, bead-like ultimate segments does not constitute a synapomorphy for the genus as defined herein. In fact, our list of excluded names (see Taxonomic Treatment) includes seven taxa with bead-like segments previously ascribed to *Myriopteris* but more closely related to *Cheilanthes* s.s. (Windham et al. unpublished). Because all morphological characters used by previous authors to define *Myriopteris* are subject to strong, positive selection in xeric-adapted cheilanthoid lineages (Hevly 1963), it is not surprising that none of them uniquely define the genus. The totality of evidence, however, indicates that the myriopterids represent a deeply divergent clade that cannot reasonably be combined with any other in a single genus. Therefore, we propose to resurrect *Myriopteris* and recircumscribe it to encompass the entirety of this well supported cheilanthoid lineage.

Distinguishing *Myriopteris* Fée emend. Grusz & Windham from *Cheilanthes* s.s.

Ideally, morphological and/or cytological synapomorphies would substantiate phylogenetic relationships inferred from DNA sequence data. However, easily observed synapomorphies distinguishing the various clades of cheilanthoid ferns are few, and
homoplastic characters abound. To paraphrase Sir William Hooker (1852: 75), “Vain is the attempt to form a definite character which shall decide the limits of [Cheilanthes],” a statement that applies equally well to Myriopteris. Highly divided (decompound) leaf blades with small ultimate segments are scattered across the cheilanthoid tree and, indeed, are characteristic of ferns in general, and an indument of hairs and/or scales is one common strategy among plants used to reduce water loss in xeric habitats (Hevly 1963). Other characters useful for species-level identification within myriopterids, such as vernation, are, without exception, shared with other distantly related cheilanthoid ferns.

Molecular analyses spanning the diversity of cheilanthoid species (Windham et al. unpublished) illuminate one particularly useful character distinguishing Myriopteris, as defined herein, from Cheilanthes s.s. The taxa most closely related to the type species of the latter [C. micropteris plus all Australian Cheilanthes and a group of South American species including the C. scariosa (Sw.) C. Presl complex of Tryon and Tryon (1982), C. obducta Mett. ex Kuhn, and C. fractifera R. M. Tryon] have 32 small spores per sporangium when sexual, and 16 large spores per sporangium when apomictic. This intriguing cytological synapomorphy results from the elimination of a premeiotic mitosis in the cell lineages generating the sporocytes (Windham et al. unpublished). Aside from a few species of the distantly related genus Notholaena, all other cheilanthoid ferns so far examined (including every Myriopteris species; Grusz et al. in review) produce 64 small spores per sporangium in sexual individuals and 32 large spores per sporangium in apomicts. This character appears to provide an absolute separation between Myriopteris and Cheilanthes s.s., and is easily observed using a dissecting microscope. In combination with differences in spore ornamentation (see Tryon and Lugardon 1991), leaf venation (Pryer et al. 2010), and geographic distribution, this feature provides a clear distinction between the two genera. For diagnostic purposes, then, Myriopteris Fée emend. Grusz & Windham differs from Cheilanthes s.s. (i.e., C. micropteris and its close relatives) in its production of 64 small or 32 large (vs. 32 small or 16 large) spores per sporangium; mostly cristate or rugulose (vs. echinate, granulose, or verrucate) spore ornamentation; a lack of obvious vein endings near the margins of the ultimate segments (vs. often prominent hydathodes), and a largely North and Central American (vs. exclusively South American/Old World) distribution.

**Taxonomic treatment**

**Myriopteris Fée emend. Grusz & Windham**

http://species-id.net/wiki/Myriopteris

**Type.** Myriopteris marsupianthes Fée, Mém. Fam. Foug. 5: 149, t. 12A. f. 1. 1852

**Description.** Plants rupestral or terrestrial. Rhizomes compact to long-creeping, ascending or horizontal, scaly. Rhizome scales lanceolate to acicular, concolorous (tan
to dark brown) or bicolorous (with dark central stripe and brown margins). Leaf vernation non-circinate to circinate. Petioles castaneous to black, scaly and/or pubescent, rarely almost glabrous. Rachises terete or flattened or grooved adaxially, with indument similar to that of the petioles. Blades 2- to 4-pinnate (rarely pinnate-pinnatifid), lanceolate to ovate-deltate, occasionally linear or pentagonal; adaxial surfaces glabrous or pubescent; abaxial surfaces scaly and/or pubescent or rarely glabrous. Ultimate segments round to oblong-ovate, minute to >1 cm long, the veins obscure and not ending in prominent hydathodes. Segment margins usually recurved, with a poorly differentiated false indusium (strongly differentiated in *M. lendigera* and *M. marsupianthes*). Sori usually partly to completely covered by the recurved segment margins, the sporangia clustered at vein tips. Sporangia 64-spored (in sexual species) or 32-spored (in apomicts). Spores globose-tetrahedral, tan to brown, cristate to rugulate. Chromosome numbers $n = 29, 30, 58, 60$ (sexual species); $n = 2n = 87, 90$ (apomictic triploids); $n = 2n = 120$ (apomictic tetraploids).

**Distribution.** Species of *Myriopteris* range from southern Canada through the Caribbean and Central America to southern Chile, with one species (*M. rawsonii*) endemic to Namibia and South Africa. Mexico is the center of species diversity for the genus; 34 of the 44 species can be found in Mexico, and seven of these are endemic.

**New and resurrected combinations in Myriopteris**

1) *Myriopteris aemula* (Maxon) Grusz & Windham, **comb. nov.** *Cheilanthes aemula* Maxon, Contr. U.S. Natl. Herb. 10: 495. 1908. Type: Mexico. Tamaulipas: Victoria, in river canyon, under overhanging rocks, altitude about 320 meters, February 1 to April 9, 1907, Palmer 187 (holotype: US; isotype: US). urn:lsid:ipni.org:names:77134841-1

2) *Myriopteris alabamensis* (Buckley) Grusz & Windham, **comb. nov.** *Pteris alabamensis* Buckley, Amer. J. Sci. Arts 45: 177. 1843. *Cheilanthes alabamensis* (Buckley) Kunze, Linnaea 20: 4. 1847. Type: USA. Alabama: Growing in tufts on limestone rocks that form the banks of the Tennessee River, at the foot of Muscle Shoals, Buckley s.n. (holotype: PH; isotypes: MO, NY). urn:lsid:ipni.org:names:77134842-1

3) *Myriopteris allosuroides* (Mett.) Grusz & Windham, **comb. nov.** *Cheilanthes allosuroides* Mett., Abh. Senckenberg. Naturf. Ges. 3: 78. 1859. *Pellaea allosuroides* (Mett.) Hieron., Hedwigia 62: 18. 1920. Type: Mexico, Schmitz s.n. (holotype: location unknown). urn:lsid:ipni.org:names:77134843-1

4) *Myriopteris aurea* (Poir.) Grusz & Windham, **comb. nov.** *Pteris aurea* Poir. Encyclopédie Méthodique, Botanique 5: 710. 1804. Type: Peru. Elle a été recueillie au Pérou par Joseph de Jussieu s.n. (sheet 1333 in hb. Jussieu; holotype: P). urn:lsid:ipni.org:names:77134844-1
Acrostichum bonariense Willd., Sp. Pl., ed. 4, 5(1): 114. 1810. Notholaena bonariensis (Willd.) C. Chr., Index Filic. 459. 1906. Cheilanthes bonariensis (Willd.) Proctor, Bull. Inst. Jamaica, Sci. Ser. 5: 15. 1953.

In Cheilanthes, this has been called C. bonariensis (Willd.) Proctor because use of the oldest applicable epithet (based on Pteris aurea Poir.) was blocked by the earlier publication of Cheilanthes aurea Baker (Proctor 1953). With the transfer of this species to Myriopteris we revert to the older epithet and thus avoid the typification difficulties associated with the basionym Acrostichum bonariense Willd. (Ponce and Zimmer 2011).

5) Myriopteris chipinquensis (Knobloch & Lellinger) Grusz & Windham, comb. nov. Cheilanthes chipinquensis Knobloch & Lellinger, Amer. Fern J. 59: 8. 1969. Type: Mexico. Nuevo Leon: Chipinque Mesa, outside Monterey, Knobloch 1996B (holotype: MSC; isotypes: F, GH, MEXU, MICH, UC, US). urn:lsid:ipni.org:names:77134845-1

6) Myriopteris cinnamomea (Baker) Grusz & Windham, comb. nov. Notholaena cinnamomea Baker in Hook. & Baker, Syn. Fil. ed. 2. 515. 1874. Cheilanthes cinnamomea (Baker) Domin., Biblioth. Bot. 20: 153. 1913. hom. illeg. non Cheilanthes cinnamomea D. C. Eaton, Proc. Amer. Acad. Arts 18: 186. 1883. Type: Guatemala. Mo[n]tagua, 1862, Salvin & Goodman s.n. (holotype: K; isotype: BM). urn:lsid:ipni.org:names:77134870-1

Cheilanthes tryonii T. Reeves, Brittonia 32: 504. 1980.

In Cheilanthes, this species has been called C. tryonii T. Reeves because use of the oldest applicable epithet (based on Notholaena cinnamomea Baker) was blocked by the earlier publication of Cheilanthes cinnamomea D. C. Eaton (Reeves 1980). With the transfer of this species to Myriopteris, we revert to the older epithet.

7) Myriopteris clevelandii (D. C. Eaton) Grusz & Windham, comb. nov. Cheilanthes clevelandii D. C. Eaton, Bull. Torrey Bot. Club 6: 33. 1875. Type: USA. California: Growing on a mountain about forty miles from San Diego at an elevation of about 2500 feet, Cleveland s.n. (holotype: YU; isotypes: GH, P, US). urn:lsid:ipni.org:names:77134846-1

8) Myriopteris cooperae (D. C. Eaton) Grusz & Windham, comb. nov. Cheilanthes cooperae D. C. Eaton, Bull. Torrey Bot. Club 6: 33. 1875. Type: USA. California: near Santa Barbara, Mrs. Ellwood Cooper (syntype: YU); Sierra Valley, Lemmon s.n. (syntype: YU). urn:lsid:ipni.org:names:77134847-1

9) Myriopteris covillei (Maxon) Á. Löve & D. Löve, Taxon 26: 325. 1977. Cheilanthes covillei Maxon, Proc. Biol. Soc. Wash. 31: 147. 1918. Type: USA. California: Surprise Canyon, Panamint Mountains, 13 April 1891, 1550 meters, Coville & Funston 593 (holotype: US). urn:lsid:ipni.org:names:77134848-1

10) Myriopteris cucullans (Fée) Grusz & Windham, comb. nov. Cheilanthes cucullans Fée, Mém. Fam. Foug. 7: 39, t. 25, f. 4. 1857. Type: Mexico, ad vallem Mexicanum, Schaffner 82 [holotype: RB; isotypes: K, US (fragment)]. urn:lsid:ipni.org:names:77134873-1
11) Myriopteris fendleri (Hook.) E. Fourn., Mex. Pl. 1: 125. 1872. Cheilanthes fendleri Hook., Sp. Fil. 2: 103, p. 107b. 1852. Type: USA. New Mexico, 1847, Fendler 1015 [holotype: K; isotypes: GH, MO, NY, US (fragment)].

12) Myriopteris × fibrillosa (Davenp.) Grusz & Windham, comb. nov. Cheilanthes lanuginosa var. fibrillosa Davenp., Bull. Torrey Bot. Club 12: 21. 1885. Cheilanthes fibrillosa (Davenp.) Davenp., Bull. Torrey Bot. Club 15: 225. 1888. Type: USA. California: San Jacinto Mountains, June 1882, Parish & Parish s.n. (holotype: GH). urn:lsid:ipni.org:names:77134880-1

13) Myriopteris fimбриata (A. R. Sm.) Grusz & Windham, comb. nov. Cheilanthes microphylla (Sw.) Sw. var. fimбриata A. R. Sm., Amer. Fern J. 70: 19, 21., f. 9–10. 1980. Type: Mexico. Chiapas: Frontera Comalapa, 6–8 km east of Frontera Comalapa, Breedlove 39018 (holotype: DS). urn:lsid:ipni.org:names:77134881-1

Cheilanthes fimбриata (A. R. Sm.) Mickel & Beitel, Mem. New York Bot. Gard. 46: 112. 1988. hom. illeg., non Cheilanthes fimбриata Vis., Fl. Dalmat. 1. 42 t. 1 f. 1. 1842.

14) Myriopteris gracilis Fée, Mém. Fam. Foug. 5: 150, t. 29, f. 6. 1852. Cheilanthes gracilis (Fée) Mett. ex Riehl, Abh. Senckenberg. Naturf. Ges. 80. 1859. hom. illeg., non Cheilanthes gracilis (Michx.) Kaulf. With the transfer of this species to Myriopteris, we revert to the original name published by Fée in 1852.

15) Myriopteris gracillima (D. C. Eaton) J. Sm., Hist. Fil. 280. 1875. Cheilanthes gracillima D. C. Eaton, Rep. U.S. Mex. Bound. Botany 2: 234. 1859. Type: USA. Oregon: Cascade Mountains, 7000 feet of altitude, latitude 44°, Bigelow s.n. (lectotype: YU).

16) Myriopteris intertexta (Maxon) Grusz & Windham, comb. nov. Cheilanthes covillei Maxon subsp. intertexta Maxon, Proc. Biol. Soc. Wash. 31: 149. 1918. Cheilanthes intertexta (Maxon) Maxon in Abrams, Ill. Fl. Pacific States 1: 28. 1923. Type: USA. California: Santa Clara County, Santa Cruz Mountains, collected at the top of Black Mountain, 6 July 1903, Dudley s.n. (holotype: DS). urn:lsid:ipni.org:names:77134849-1

17) Myriopteris jamaicensis (Maxon) Grusz & Windham, comb. nov. Cheilanthes jamaicensis Maxon, Contr. U.S. Natl. Herb. 24: 51. 1922. Type: Jamaica. Below Cinchona, 28 February 1919, Harris 12905 (holotype: US; isotypes: GH, MO, NY). urn:lsid:ipni.org:names:77134850-1

18) Myriopteris lanosa (Michx.) Grusz & Windham, comb. nov. Nephrodium lanosum Michx. Fl. Bor.-Amer. 2: 270. 1803. Cheilanthes lanosa (Michx.) D.
C. Eaton, Rep. U.S. Mex. Bound., Botany 2: 234. 1859. Type: USA. Tennessee (sic) et Carolinae septentrionalis (non designatus). urn:lsid:ipni.org:names:77134851-1

Myriopteris vestita (Sw.) J. Sm., Cul. Ferns 29. 1857. (fide C. Chr. 1906.) Adiantum vestitum Spreng., Anleit. Kenntn. Gew. 3: 122. 1804.

19) Myriopteris lendigera (Cav.) Fée, Mém. Fam. Foug. 5: 149. 1852 (as M. lenticigera). Pteris lendigera Cav., Descr. Pl. 268. 1801. Cheilanthes lendigera (Cav.) Sw., Syn. Fil. 128, 328. 1806. Type: Mexico. Hidalgo: Ixmiquilpan en la Nueva España, Nee s.n. [syntype: MA, US (fragment)]; Ecuador. Bolivar: junto á Guaranda en el Reyno de Quito, Nee s.n. (syntype: MA).

Cheilanthes minor Mart. & Gal. Mém. Act. Brux. 75, pl. 21, f. 1. 1842. Myriopteris minor (Mart. & Gal.) Fée, Mém. Fam. Foug. 5: 150. 1852.

Cheilanthes lanuginosa Mart. & Gal. Mém. Act. Brux. 75, pl. 20, f. 2. 1842. Myriopteris lanuginosa (Mart. & Gal.) E. Fourn. Mex. Pl. 1: 125. 1872.

Myriopteris villosa Fée, Mém. Fam. Foug. 5: 149. t. 28, f. 1. 1852.

Cheilanthes frigida Linden ex T. Moore, Gard. Chr. 772. 1857. Myriopteris frigida (Linden ex T. Moore) J. Sm. Cat. Cult. Ferns 28. 1857.

Myriopteris lendigera (Cav.) J. Sm., Cat. Cult. Ferns 28. 1857. hom. illeg.

Pomataphytum pocillatum M. E. Jones, Contributions to Western Botany 16: 12. 1930.

20) Myriopteris lindheimeri (Hook.) J. Sm., Bot. Voy. Herald. 340. 1856. Cheilanthes lindheimeri Hook., Sp. Fil. 2: 101, t. 107a. 1852. Type: USA. Western Texas, 1847, Lindheimer 744 [lectotype: K; isolecotypes: GH, P (2 sheets), SD, US, YU].

21) Myriopteris longipila (Baker) Grusz & Windham, comb. nov. Cheilanthes longipila Baker, Ann. Bot. (Oxford) 5: 211. 1891. Type: Mexico. San Luis Potosí, 22°N Lat., 6000–8000 ft., Parry & Palmer 989 [holotype: K; isotype: US (fragment)]. urn:lsid:ipni.org:names:77134852-1

22) Myriopteris longipila subsp. brevipila (Mickel) Grusz & Windham, comb. nov. Cheilanthes longipila var. brevipila Mickel, Mem. New York Bot. Gard. 88: 198–199, f. 84N–Q, 87J–M. 2004. Type: Mexico. Guerrero: 2 km al SE de Amatitlán, 1600 m, 13 August 1994, Soto 1052 (holotype: NY; isotype: FCME). urn:lsid:ipni.org:names:77134882-1

23) Myriopteris marsupianthes Fée, Mém. Fam. Foug. 5: 149, t. 12A, f. 1. 1852. Cheilanthes marsupianthes (Fée) T. Reeves ex Mickel & A. R. Sm. Mem. New York Bot. Gard. 88: 201, f. 83M–P. 2004. Type: Mexico. Veracruz: Pic d’Orizaba, Martens & Galeotti 6256 (holotype: P; isotype: BR).

24) Myriopteris maxoniana (Mickel) Grusz & Windham, comb. nov. Cheilanthes maxoniana Mickel, Mem. New York Bot. Gard. 88: 201, f. 87A–D. 2004. Type: Mexico. Tamaulipas: San Lucas, Viereck 76 (holotype: US). urn:lsid:ipni.org:names:77134853-1

25) Myriopteris mexicana (Davenp.) Grusz & Windham, comb. nov. Cheilanthes mexicana Davenp., Bull. Torrey Bot. Club 15: 227. 1888. Type: Mexico. Chi-
Toward a monophyletic *Cheilanthes*: The resurrection and recircumscription...

26) *Myriopteris michelii* (T. Reeves) Grusz & Windham, *comb. nov.* *Cheilanthes michelii* T. Reeves, Brittonia 32: 502, f. 1–5. 1980. Type: Mexico. Oaxaca: Distr. Yautepec, Mickel 4210 (holotype: NY; isotypes: MO, UC, US, YU). urn:lsid:ipni.org:names:77134854-1

27) *Myriopteris microphylla* (Sw.) Grusz & Windham, *comb. nov.* *Adiantum microphyllum* Sw., Prodr. 135. 1788. *Cheilanthes microphylla* (Sw.) Sw., Syn. Fil. 127. 1806. Type: Jamaica, Swartz s.n. (holotype: S). urn:lsid:ipni.org:names:77134856-1

28) *Myriopteris moritziana* (Kunze) Grusz & Windham, *comb. nov.* *Cheilanthes moritziana* Kunze, Linnaea 23: 307. 1850. Type: Venezuela. Caracas: La Guayra, Moritz 263 (lectotype: B; isolecotype: GH). urn:lsid:ipni.org:names:77134857-1

29) *Myriopteris myriophylla* (Desv.) J. Sm., Bot. Voy. Herald, 340. 1856. *Cheilanthes myriophylla* Desv., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 5: 328. 1811. Type: South America. Anon. s.n. (holotype: P). *Cheilanthes elegans* Desv. Ges. Naturf. Freunde Berlin Mag. 5: 328. 1811. *Myriopteris elegans* (Desv.) J. Sm., Cat. Cult. Ferns 29. 1857. *Cheilanthes paleacea* Mart. & Gal., Mém. Foug. Mexique 76, pl. 21, f. 2. 1842. *Myriopteris paleacea* (Mart. & Gal.) Fée, Mém. Fam. Foug. 5: 149, t. 29, f. 6. 1852. *Myriopteris intermedia* E. Fourn., Bull. Soc. Bot. Fr. 27: 328. 1880. *hom. illeg.*, non *Fée, Mém. Fam. Foug. 5: 149. 1852.

30) *Myriopteris newberryi* (D. C. Eaton) Grusz & Windham, *comb. nov.* *Notholaena newberryi* D. C. Eaton, Bull. Torrey Bot. Club 4: 12. 1873. *Cheilanthes newberryi* (D. C. Eaton) Domin, Biblioth. Bot. 20: 133. 1913. Types: USA. California: San Diego, 9 November 1857, Newberry 1352 (syntype: MO, YU); San Diego, 1866, Wood s.n. (syntype: YU); Southern California: S. W. corner of San Bernardino County, rocks in the Temescal range, 22 January 1861, W. H. Brewer s.n. (syntype: YU). urn:lsid:ipni.org:names:77134858-1

31) *Myriopteris notholaenoides* (Desv.) Grusz & Windham, *comb. nov.* *Pteris notholaenoides* Desv., Mém. Soc. Linn. Paris 6: 299. 1827. *Cheilanthes notholaenoides* (Desv.) Maxon ex Weath., Contr. Gray Herb. 114: 34. 1936. Type: Hispaniola, Anon. s.n. (holotype: P). urn:lsid:ipni.org:names:77134859-1

32) *Myriopteris × parishii* (Davenp.) Grusz & Windham, *comb. nov.* *Cheilanthes parishii* Davenp., Bull. Torrey Bot. Club 8: 59. 1881. Type: USA. California: San Diego County, W. J. Parish s.n. (holotype: GH; isotypes: GH, YU). urn:lsid:ipni.org:names:77134860-1

33) *Myriopteris parryi* (D. C. Eaton) Grusz & Windham, *comb. nov.* *Notholaena parryi* D. C. Eaton, Amer. Naturalist 9: 351. 1875. *Cheilanthes parryi* (D. C. Eaton) Domin, Biblioth. 85: 133. 1913. Type: USA. Utah: C. C. Parry 263 (holotype: YU; isotypes: US, YU). urn:lsid:ipni.org:names:77134861-1
34) *Myriopteris peninsularis* (Maxon) Grusz & Windham, **comb. nov.** *Cheilanthes peninsularis* Maxon, Contr. U.S. Natl. Herb. 10: 496. 1908. Type: Mexico. Baja California, T. S. Brandegee s.n. (holotype: US). urn:lsid:ipni.org:names:77134862-1

35) *Myriopteris peninsularis* subsp. *insularis* (Weath.) Grusz & Windham, **comb. nov.** *Cheilanthes peninsularis* (Maxon) var. *insularis* Weath., Amer. Fern J. 21: 25. 1931. Type: Mexico. Socorro Island, Mason 1616 (holotype: CAS). urn:lsid:ipni.org:names:77134884-1

36) *Myriopteris pringlei* (Davenp.) Grusz & Windham, **comb. nov.** *Cheilanthes pringlei* Davenp., Bull. Torrey Bot. Club 10: 61, t. 34. 1883. Type: USA. Arizona: C. G. Pringle s.n. (holotype: GH; isotypes: DS, MO, NY, US, YU). urn:lsid:ipni.org:names:77134863-1

37) *Myriopteris pringlei* subsp. *moncloviensis* (Baker) Grusz & Windham, **comb. nov.** *Cheilanthes pringlei* var. *moncloviensis* Baker, Ann. Bot. (Oxford) 5: 210. 1891. *Cheilanthes pringlei* var. *moncloviensis* (Baker) Mickel, Mem. New York Bot. Gard. 88: 207–208, f. 79J–M. 2004. Type: Mexico. Coahuila: Soledad, E. Palmer 1378 (holotype: K; isotypes: MO, NY, US). urn:lsid:ipni.org:names:77134864-1

38) *Myriopteris rawsonii* (Mett. ex. Kuhn) Grusz & Windham, **comb. nov.** *Cheilanthes rawsonii* Mett. ex. Kuhn, Filices Africanae 75. 1868. Type: Africa. Cape Province: Namaqualand, between Specktakel and Komaggas, Whitehead s.n. (holotype: BM; isotype: K). urn:lsid:ipni.org:names:77134878-1

39) *Myriopteris rufa* Fée, Mém. Fam. Foug. 8: 77. 1857. Type: Mexico. Veracruz: Volcan de Orizaba, Schaffner 83 (holotype: P; isotype: RB). *Cheilanthes eatonii* Baker in Hook. & Baker, Syn. Fil. 140. 1867. *Cheilanthes castanea* Maxon, Proc. Biol. Soc. Wash. 32: 111. 1919.

In *Cheilanthes*, this has been called *C. eatonii* Baker. Examination of putative type specimens of *Myriopteris rufa* housed at RB (digital image) and P indicates that the latter name very likely represents the same species as broadly defined by recent authors (e.g., Mickel and Smith 2004). Because *M. rufa* (published in 1857) has priority over *C. eatonii* (1867), we take up Fée’s original name for this taxon in *Myriopteris*.

40) *Myriopteris scabra* (C. Chr.) Grusz & Windham, **comb. nov.** *Pellaea scabra* C. Chr., Index Filic. 483. 1906. Type: USA. Texas: crevices of rock on hills, Turkey Creek, 25 June 1849, Wright 824 (holotype: K; isotypes: GH, NY, US). *Cheilanthes aspera* Hook., Sp. Fil. 2: 111, t. 108A. 1852. *hom. illeg.*, non *Cheilanthes aspera* Kaulf., Linnaea 6(1): 186. 1831. urn:lsid:ipni.org:names:77134865-1

In *Cheilanthes*, this has been called *C. aspera* Kaulf. (Maxon 1918). With the transfer of this species to *Myriopteris*, we revert to the older, exceedingly appropriate epithet.

41) *Myriopteris tomentosa* (Link) Fée, Mém. Fam. Foug. 5: 149. 1852. *Cheilanthes tomentosa* Link, Hort. Berol. 2: 42. 1833. Type: Mexico. Anon. s.n. [holotype: B; isotypes: PH, US (fragment)].
**Cheilanthes bradburii** Hook., Sp. Fil. 2: 97, t. 109b. 1852. *Myriopteris bradburii* (Hook.) J. Sm. Hist. Fil. 280. 1875.

42) *Myriopteris viscida* (Davenp.) Grusz & Windham, **comb. nov.** *Cheilanthes viscida* Davenp., Bull. Torrey Bot. Club 6: 191. 1877. Types: USA. California: Eastern slope of the Sierra Nevada near San Gogorio Pass, April 1876, Parry & Lemmon 427 (syntype: NY); California/Nevada: Downieville Buttes and bluffs of White Water River on the Colorado Desert, April–May, Lemmon s.n. (syntype: NY). urn:lsid:ipni.org:names:77134866-1

43) *Myriopteris windhamii* Grusz, Amer. Fern J. 103: 113. 2013. Type: USA. Arizona: Huachuca Mountains, Windham 4165 (holotype: DUKE; isotypes: ARIZ, ASC, ASU, GH, MO, NMC, NY, TEX/LL, UNM, US, UT).

---

**Cheilanthes villosa** Davenp. *ex* Maxon, Proc. Biol. Soc. Wash. 31: 142. 1918. In *Cheilanthes*, this has been called *C. villosa* Davenp. *ex* Maxon. Because transfer of the epithet *villosa* to *Myriopteris* is blocked by the earlier publication of *M. villosa* Fée (= *M. lendigera* fide Reeves 1979), we use the replacement name for this distinctive taxon published by Grusz (2013).

44) *Myriopteris wootonii* (Maxon) Grusz & Windham, **comb. nov.** *Cheilanthes wootonii* Maxon, Proc. Biol. Soc. Wash. 3: 146. 1918. Type: USA. Arizona: Santa Rita Mountains, Wooton s.n. (holotype: US). urn:lsid:ipni.org:names:77134867-1

45) *Myriopteris wrightii* (Hook.) Grusz & Windham, **comb. nov.** *Cheilanthes wrightii* Hook., Sp. Fil. 2: 87, t. 110A. 1858. Type: USA. Texas–New Mexico: Wright 823 (holotype: K; isotypes: GH, NY, US). urn:lsid:ipni.org:names:77134868-1

46) *Myriopteris yatskievychiana* (Mickel) Grusz & Windham, **comb. nov.** *Cheilanthes yatskievychiana* Mickel, Mem. New York Bot. Gard. 88: 212–213, f. 74F–K. 2004. Type: Mexico. Sonora: Sierra del Aliso, A. Búrquez M. 96-302 (holotype: MO). urn:lsid:ipni.org:names:77134869-1

47) *Myriopteris yavapensis* (T. Reeves *ex* Windham) Grusz & Windham, **comb. nov.** *Cheilanthes yavapensis* T. Reeves *ex* Windham, Contr. Univ. Michigan Herb. 19: 32. 1993. Type: USA. Arizona: Yavapai County, Windham 202 (holotype: UT; isotypes: ASC, ASU, US). urn:lsid:ipni.org:names:77134879-1

---

**Name of uncertain application**

*Myriopteris cheiloglyphis* Fée, Mém. Fam. Foug. 8: 77. 1857.

---

**Excluded names**

*Myriopteris contracta* (Kunze) Fée, Mém. Fam. Foug. 5: 149. 1852. = *Cheilanthes contracta* (Kunze) Mett. *ex* Kuhn

*Myriopteris hirta* (Sw.) J. Sm., Ferns Brit. and For. 174. 1866. = *Cheilanthes hirta* Sw.

*Myriopteris induta* (Kunze) Fée, Mém. Fam. Foug. 5: 149. 1852. = *Cheilanthes induta* Kunze
Myriopteris intermedia (Kunze) Fée, Mém. Fam. Foug. 5: 149. 1852. = Cheilanthes hirta Sw. fide Christensen (1906)

Myriopteris macleanii J. Sm., Hist. Fil. 280. 1875. = Cheilanthes pilosa Goldm. fide Christensen (1906)

Myriopteris scariosa (Sw.) Fée, Mém. Fam. Foug. 5: 149, t. 29, f. 6. 1852. = Cheilanthes scariosa Sw.

Myriopteris szovitzii (Fisch. & Meyer) J. Sm., Hist. Fil. 281. 1875. = Cheilanthes persica (Bory) Mett. ex Kuhn fide Christensen (1906)

Acknowledgements

The authors thank A. R. Smith, R. Moran, K. N. Gandhi, and L. J. Dorr for assistance interpreting and/or obtaining obscure taxonomic literature. We also extend our appreciation to K. M. Pryer, G. J. Gastony, G. Yatskievych, L. Huiet, E. M. Sigel, F.-W. Li, and C. J. Rothfels for helpful comments on the manuscript. This study was completed in partial fulfillment of a doctoral dissertation in Biology at Duke University by the first author. Research support to A. L. G. was provided by a Society for Systematic Biologists Graduate Student Research Award, the American Society of Plant Taxonomists Shirley and Alan Graham Graduate Student Research Grant, as well as an NSF Doctoral Dissertation Improvement Grant (NSF-DDIG 1110767). Additional funding for this project was provided by NSF-DEB 0717398 awarded to M.D.W.

References

Beck JB, Windham MD, Yatskievich G, Pryer KM (2010) A diploids-first approach to species delimitation and interpreting polyploid evolution in the fern genus Astrolepis (Pteridaceae). Systematic Botany 35: 223–234. doi: 10.1600/036364410791638388

Ching RC (1941) The studies of Chinese ferns—XXXI. Hong Kong Naturalist 10: 194–204.

Christensen CFA (1906) Index Filicum. H. Hagerup, 1–744.

Copeland EB (1947) Genera Filicum. Chronica Botanica Co., 1–247.

Domin K (1913) Beiträge zur Flora und Pflanzengeographie Australiens. 1. Abt. Pteridophyta. Bibliotheca Botanica 85: 1–240.

Eiserhardt WL, Rohwer JG, Russell SJ, Yesilyurt JC, Schneider H (2011) Evidence for radiations of cheilanthoid ferns in the Greater Cape Floristic Region. Taxon 26: 1–15.

Fée ALA (1852) Genera filicum. Exposition des genres de las famille des Polypodiacées (Classe des fougères)...(Cinquième mémoire sur la famille des fougères) [Mém. Fam. Foug. 5]. Victor Masson and Veuve Berger-Levrault et fils, [I]–387, [388, cont.], t. I–30, 27bis, 27ter.

Gastony GJ, Rollo DR (1998) Cheilanthoid ferns (Pteridaceae: Cheilantheoideae) in the southwestern United States and adjacent Mexico: a molecular phylogenetic reassessment of generic lines. Aliso 17: 131–144. doi: 10.2307/1547814
Toward a monophyletic *Cheilanthes*: The resurrection and recircumscription...

Grusz, AL (2013) *Myriopteris windhamii* sp. nov., a new name for *Cheilanthes villosa* (Pteridaceae). American Fern Journal 103: 112–117. doi: 10.1640/0002-8444-103.2.112

Grusz AL, Windham MD, Yatskievych G, Huiet L, Gastony GJ, Pryer KM (in review) Patterns of diversification in the xeric-adapted fern genus *Myriopteris* (Pteridaceae). Systematic Botany.

Hevly RH (1963) Adapations of cheilanthoid ferns to desert environments. Journal of the Arizona Academy of Science 2: 164–175. doi: 10.2307/40026172

Hooker WJ (1852) *Species Filicium*. 2. London, 1–250.

Jones ME (1930) Botanizing in Arizona. Contributions to Western Botany 16: 1–31.

Kirkpatrick REB (2007) Investigating the monophyly of *Pellaea* (Pteridaceae) in the context of a phylogenetic analysis of cheilanthoid ferns. Systematic Botany 32: 504–518. doi: 10.1600/036364407782250616

Kramer KU, Tryon RM, Tryon AF (1990) *Cheilanthes*. In: The families and genera of vascular plants: volume 1. Pteridophytes and gymnosperms, Eds. Kramer, K.U. and P.S. Green. Springer-Verlag, 240–241.

Lellinger DB (1965) A quantitative study of generic delimitation in the adiantoid ferns. PhD Thesis, University of Michigan, USA.

Li F-W, Pryer KM, Windham MD (2012) *Gaga*, a new fern genus segregated from *Cheilanthes* (Pteridaceae). Systematic Botany 37: 845–860. doi: 10.1600/036364412X656626

Link-Perez MA, Watson LE, Hickey RJ (2011) Redefinition of *Adiantopsis* Fée (Pteridaceae): systematics, diversification, and biogeography. Taxon 60: 1255–1268.

Löve A, Löve D (1977) New combinations in ferns. Taxon 26: 324–326. doi: 10.2307/1220575

Mickel, JR (1979) The fern genus *Cheilanthes* in the continental United States. Phytologia 41: 431–437.

Mickel JR, Smith AR (2004) The Pteridophytes of Mexico. New York Botanical Garden Press, 1–1054.

Nardi E, Reichstein T (1985) Nomenclatural notes on *Cheilanthes pteridioides* (Reichard) C. Chr. (Sinopteridaceae). Webbia 39: 135–139. doi: 10.1080/00837792.1985.10670363

Pichi-Sermolli REG (1953) The nomenclature of some fern genera. Webbia 9: 387–454. doi: 10.1080/00837792.1954.10669618

Pichi-Sermolli REG (1977) Tentamen Pteridophytorum genera in taxonomicum ordinem redigendi. Webbia 31: 313–512. doi: 10.1080/00837792.1977.10670077

Ponce MM, Zimmer B (2011) Nomenclature and revised typification of *Cheilanthes bonariensis* (Cheilantheae, Pteridaceae). Taxon 60: 866–867.

Prado J, Rodriguez CDN, Salatino A, Salatino MLF (2007) Phylogenetic relationships among Pteridaceae, including Brazilian species, inferred from *rbcL* sequences. Taxon 56: 355–368.

Proctor GR (1953) A preliminary checklist of Jamaican pteridophytes. Bulletin of the Institute of Jamaica, Science Series 5: 1–89.

Pryer KM, Schuettpelz E, Huiet L, Grusz AL, Rothfels CJ, Avent T, Schwartz D, Windham MD (2010) DNA barcoding exposes a case of mistaken identity in the fern horticultural trade. Molecular Ecology Resources 10: 979–985. doi: 10.1111/j.1755-0998.2010.02858.x

Reeves T (1980) *Cheilanthes mickelii* (Adiantaceae), a new species from southern Mexico. Brittonia 32: 502–504. doi: 10.2307/2806158
Rothfels CJ, Gaya E, Pokorny L, Rothfels Paul, Rothfels Peter, Feulner G (2012) Significant fern, lichen, and bryophyte collections from the UAE and northern Oman, including five new records for the Arabian Peninsula. Tribulus 20: 4–20.

Rothfels CJ, Windham MD, Grusz AL, Gastony GJ, Pryer KM (2008) Toward a monophyletic Notholaena (Pteridaceae): resolving patterns of evolutionary convergence in xeric-adapted ferns. Taxon 57: 712–724.

Schuettpelz E, Schneider H, Huiet L, Windham MD, Pryer KM (2007) A molecular phylogeny of the fern family Pteridaceae: assessing overall relationships and the affinities of previously unsampled genera. Molecular Phylogenetics and Evolution 44: 1172–1185. doi: 10.1016/j.ympev.2007.04.011

Sigel EM, Windham MD, Huiet L, Yatskievych G, Pryer KM (2011) Species relationships and farina evolution in the cheilanthoid fern genus Argyrochosma (Pteridaceae). Systematic Botany 36: 554–564. doi: 10.1600/036364411X583547

Smith J (1875) Historia Filicum. Macmillan and Co., 1–429.

Stafleu FA, Lanjouw J, Baehni C, Robyns W, Ross R, Rousseau J, Schopf JM, Schulze GM, Smith AC, DeVilmorin R (1961) International Code of Botanical Nomenclature. Adopted by the Ninth International Botanical Congress, Montreal, August 1959. Utrecht: Kemink en Zoon [Regnum Veg. vol. 23].

Swartz O (1806) Synopsis Filicum 5. Iveson, Blakeman, & Taylor, 1–445.

Trevisan V (1877) Cheilosoria, nuovo genere di Polipodiacee Platilomee. Atti del Reale Istituto Veneto di Scienze, Lettere ed Arti 3: 575–592.

Tryon A, Lugardon B (1991) Spores of the Pteridophyta. Springer-Verlag, 1–648.

Tryon RM, Tryon AF (1973) Geography, spores, and evolutionary relations in the cheilanthoid ferns. In: Jermy AC, Crabbe JA, Thomas BA (Eds) The phylogeny and classification of ferns. Botanical Journal of the Linnaean Society 67 (Suppl. 1), Academic Press, New York, 145–153.

Tryon RM, Tryon AF (1982) Ferns and allied plants, with special reference to tropical America. Springer-Verlag, 1–857.

Windham MD (1987) Argyrochosma, a new genus of cheilanthoid ferns. American Fern Journal 77: 37–41. doi: 10.2307/1547438

Windham MD, Huiet L, Schuettpelz E, Grusz AL, Beck JB, Yatskievych G, Pryer KM (2009) Using plastid and nuclear DNA sequences to redraw generic boundaries and demystify species complexes in cheilanthoid ferns. American Fern Journal 99: 128–132.

Yesilyurt J (2004) Systematic revision of the genus Doryopteris J. Sm. (Pteridaceae-Cheilanthoideae). PhD Thesis, University of Reading, United Kingdom.

Zhang ZC, Liu H, Yang W (2007) First insights in the phylogeny of Asian cheilanthoid ferns based on sequences of two chloroplast markers. Taxon 56: 369–378.