Myriopteris grusziae: A New Species from Texas and Oklahoma Segregated from the Chihuahuan Desert Taxon M. scabra (Pteridaceae)

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Abstract—Myriopteris scabra (until recently called Cheilanthes horridula) is a xeric-adapted fern species, endemic to the southwestern United States and northern Mexico. It is one of the most recognizable ferns in North America due to the unusual nature of the indument present on its adaxial leaf surfaces. This consists of rigid, multicellular trichomes with glasy, needle-like apices and compact conical bases that are partially embedded in the leaf surface to form swollen, pubescent bases. Despite the seemingly distinctive nature of M. scabra, published chromosome counts indicate that collections assigned to this taxon encompass both diploids (n = 29) and tetraploids (n = 58). Here we investigate this case of cryptic diversity by integrating data from cytogenetic and spore analyses, observations of sporophyte morphology, and geographic distributions. Myriopteris scabra s.l. is shown to comprise two genetically disparate, morphologically recognizable taxa that exhibit little or no geographic overlap. The tetraploid taxon is described as a new species, M. grusziae, which completely supplants diploid M. scabra in the north-eastern portion of its range (central Texas and south-central Oklahoma). This presumed allotetraploid is most like M. scabra but differs in having ultimate segments with adaxial trichomes that are longer, more flexible, mostly linear, and superficially attached. In addition, tetraploid M. grusziae has larger, more abundant scales that largely conceal the dark, sclerified leaf rachises, and it produces consistently larger spores than diploid M. scabra. We hypothesize that M. grusziae is an allotetraploid hybrid that acquired half of its chromosomes from M. scabra. However, the identity of the other diploid parent has yet to be resolved.

Keywords—Cheilanthes, cheilanthisoid ferns, chromosomes, Pellaea, ploid, spores, sporophyte morphology, trichomes.

The fern species herein called Myriopteris scabra (C. Chr.) Grusz & Windham will undoubtedly be unfamiliar to most readers. In part, this is due to its restricted distribution in and around the Chihuahuan Desert of Mexico and the southwestern United States. However, the situation is further complicated by nomenclatural changes spanning 170 yr and three different epithets. This taxon was originally called Cheilanthes aspera Hook. (Hooker 1852) and typified based on specimens collected near Turkey Creek, Texas by C. Wright in 1849. Fifteen years later, Hooker and Baker (1867) transferred the species to Pellaea under the name P. aspera (Hook.) Baker. Unknown to either of these authors, the name Cheilanthes aspera had been validly published by Kaulfuss in 1831 for a different species, rendering both Hooker’s and Baker’s names illegitimate. To rectify this situation, Christensen (1906) published a replacement name, Pellaea scabra C. Chr., based on the type collection of C. aspera Hook. However, Christensen’s placement of this taxon in Pellaea was challenged by Maxon (1918), who was convinced that the species was more appropriately included in Cheilanthes. Aware that the name C. scabra was preoccupied (by C. scabra H. Karst. published in 1854), Maxon proposed the replacement name C. horridula Maxon, based on the same collection used to typify C. aspera Hook. and P. scabra C. Chr.

For the past 100 yr, the accepted name for this taxon has been Cheilanthes horridula, and that was the name applied to it in both the Flora of North America (Windham and Rabe 1993) and The Pteridophytes of Mexico (Mickel and Smith 2004). However, it is important to note that Cheilanthes has long been used as a “dumping ground” for any species not easily accommodated in one of the better-defined cheilanthisoid genera. Grusz and Windham (2013) summarized the situation as follows: “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.”

Molecular phylogenetic studies published over the past 25 yr have confirmed earlier suspicions that Cheilanthes was “unnatural” (i.e. polyphylectic). Every major clade of cheilanthisoid ferns included one or more species matching the traditional morphological definition of Cheilanthes (Gastony and Rollo 1998; Eiserhardt et al. 2011; Ponce and Scataglini 2021). Thus, before accepting that a certain species is appropriately assigned to Cheilanthes, we must assess its relationship to the type species of that genus (C. micropteris Sw.). The first molecular analysis to include both C. micropteris and a specimen identified as C. horridula was published by Schuettpeitz et al. (2007). Their well-supported phylogenetic tree revealed such deep divergence between these taxa that they could not be accommodated in the same genus unless nearly all other cheilanthisoids (ca. 500 species) were included as well. Subsequent research by Grusz et al. (2014) revealed that the plants previously assigned to C. horridula belong to a well-supported clade that includes the type species of Myriopteris (M. marsupianthes Fée). Based on these results, Grusz and Windham (2013) transferred C. horridula to Myriopteris, taking up the oldest legitimate epithet to create the name M. scabra.

Some of the most useful features separating genera and species of cheilanthisoid ferns relate to the diversity of trichomes found on the leaves. These perform a variety of functions depending on their color, form, and density. Some trichomes prevent overheating by reflecting excess light, others reduce evaporative water loss by forming an
insulating layer over the stomata, and some presumably present a physical barrier to herbivores (Hevly 1963; Nobel 1978; Diggs and Lipscomb 2014). The peculiar nature of the adaxial leaf trichomes in *Myriopteris scabra* make it one of the most easily recognized ferns in North America. These trichomes consist of a sharp, nearly transparent apical cell inserted on a compact, whitish, multicellular, conical body that is partially embedded in the leaf surface, often forming a swollen, pustulate base (Fig. 1A). All three epithets previously applied to the species represent different ways to say “rough” in Latin, directly referencing these characteristic prickly trichomes. Despite the seemingly distinctive nature of *Myriopteris scabra*, research conducted over the past two decades has revealed unexpected diversity within the taxon. The first hint of this emerged from cytogenetic studies done by Windham and Yatskievych (2003). Up to that time, no chromosome counts had been published for the taxon then known as *Cheilanthes horridula*. The two counts reported by Windham and Yatskievych (2003) came from widely-separated populations, one of which was diploid (*n* = 29) while the other was composed of fertile sexual tetraploids (*n* = 58).

Differences in ploidy like those reported for *Myriopteris scabra* can be of great biological significance, regardless of whether the polyploids arose through interspecific hybridization (allopolyploidy) or evolutionary processes occurring within a single, recognized species (autopolyploidy; Solits et al. 2007). Though crucial to understanding biodiversity, studies of such “ploidy-diverse species” can be difficult to pursue if chromosome counts are in short supply. However, a little cytogenetics can go a long way in ferns, where average spore size often shows a strong positive correlation with ploidy (Barrington et al. 1986, 2020). This correlation has been used to good effect in studying a diversity of cheilanthoid ferns (Beck et al. 2010; Sigel et al. 2011; Li et al. 2012; Schuett-pestel et al. 2015; Kao et al. 2020; Windham et al. 2022) and was employed here as a possible pathway to resolving the taxonomy of *Myriopteris scabra*. Here we integrate chromosome counts (both new and previously published), ploidy-calibrated spore measurements, morphological observations of sporophytes, and correlated geographic distributions to explore the cytotypic diversity attributed to *M. scabra* and circumscribe a new species we herein call *Myriopteris grusziae* Windham & Pryer.

**Materials and Methods**

**Taxon Sampling**—Collections made by the lead author during fieldwork in 1983, 1986, 2007, and 2016 provided the core dataset presented herein, and were the source of all cytogenetic analyses. Additional spore measurements, morphological observations, and geographical data were derived from herbarium specimens curated at BRIT, DUKE, LL, OKL, OKLA, SRSC, TEX, and UTEP. In all, nearly 100 collections spanning the known geographic range of *Myriopteris scabra* s.l. were examined for this study, including two isotypes housed at United States National Herbarium (US). Relevant data for each of these is provided in Appendices 1 and 2.

**Cytogenetic Analyses**—Young leaves at the peak of meiosis (i.e. with an abundance of glossy, nearly transparent sporangia lacking an evident annulus) were collected during fieldwork in 2007 and 2016. These were immediately fixed in a mixture of absolute ethanol and glacial acetic acid (3:1). After 24 hr, they were removed from the fixative and stored (up to five years) in 70% ethanol at -20°C. Slides were prepared by macerating 25–50 sporangia in a drop of 1% iron acetoacarmine; the cells were then squashed in a 1:1 mixture of acetoacarmine and Hoyer’s Medium (Anderson 1954). All meiotic chromosome counts were derived from sporocytes at diakinesis. Representative cells were photographed using a Canon EOS Rebel T3i digital camera mounted on a Meiji MT510L phase contrast microscope.

**Spore Studies**—Spores were obtained from mature, unopened sporangia that were individually transferred to drops of glycerol and ruptured with the tip of a dissecting needle. Spore number was estimated for each sporangium, and only those containing approximately 64 spores were included in subsequent analyses to ensure strict cytotypic comparability across the dataset. Spore sizes of representative sporangia were documented using the same photographic setup described above. Twenty-five normally developed spores from each sporangium were randomly selected and measured using an ocular micrometer mounted on the microscope used for cytogenetic analyses. Maximum diameter of the tri-lete spores was determined by spanning the exospore, visible as a dark ring just below the rugulate spore surface. Sample means and standard deviations were calculated and visualized in R version 4.0.4 (R Core Team 2021). The largely malformed spores of putative hybrids were not measured due to the inability to determine the ploidy of spores produced by irregular meiotic events.

**Sporophyte Morphology**—Diploid and tetraploid populations identified by cytogenetic and spore analyses were compared based on more than 100 qualitative and quantitative morphological characters of the sporophytes. A complete list of these characters is provided in the species description of *Myriopteris grusziae* presented in the Taxonomic Treatment section. Morphological features that consistently distinguished diploids from tetraploids were documented photographically using a Canon EOS Rebel XSi digital camera mounted on a Leica MZ12.5 dissecting microscope.

**Geographic Distributions**—All collections included in our analyses were georeferenced based on a consensus of relevant data (descriptive location, elevation, habitat) provided on the specimen labels. Latitude and longitude were estimated using Google Earth Pro version 7.3 (2017) in conjunction with USGS topographic maps accessed via Topozone (1999). Species distributions were mapped in R using the packages rnaturlaerth (South 2017) and ggplot2 (Wickham 2016).

**Results**

Windham and Yatskievych (2003) reported that plants identified as *Cheilanthes horridula* (now *Myriopteris scabra*) from Nuevo Leon, Mexico were diploid (*n* = 29) whereas those from the Edwards Plateau in Texas were tetraploid (*n* = 58). Because the data presented below show that these “cytotypes” are morphologically divergent and show minimal geographic overlap, we assign each a binominal name (validated in the Taxonomic Treatment). To simplify presentation of our results and link these data to a formal nomenclatural construct, we use these names from this point forward. Spores collected from two isotypes of *M. scabra* housed at the US National Herbarium showed average diameters of 40.8 and 42.9 μm, respectively (Appendix 1). These measurements fall well within the range of confirmed diploid collections (Fig. 2), and the morphological characteristics of the type specimens match those of known diploids in all respects. Therefore, we associate Christensen’s epithet *scabra* with the diploid taxon and apply the name *Myriopteris grusziae* to the tetraploid.

**Cytogenetic Analyses**—Three new chromosome counts were obtained during this study. A population of *Myriopteris scabra* from Eddy Co., NM (Windham 3495; Appendix 1) was found to be diploid, exhibiting 29 pairs of chromosomes at diakinesis (Fig. 1B). Two Texas populations of *M. grusziae*, one from Blanco Co. (Windham et al. 4436) and the other from Burnet Co. (Windham et al. 4427), were tetraploid with 58 bivalents at diakinesis (Fig. 1C).

**Spore Studies**—Microscopic examination of spores from chromosome vouchers of *Myriopteris scabra* s.l. revealed consistent size differences between the two known ploidy levels. The spores of *M. scabra* s.s. were relatively small (Fig. 1D) compared to those of *M. grusziae* (Fig. 1E). This raised the
FIG. 1. A. Close-up of ultimate segment of *Myriopteris scabra* from Windham 3495 showing distinctive scabrous trichomes; scale bar = 0.5 mm. B–C. Meiotic chromosome preparations at diakinesis; scale bars = 20 μm. B. *M. scabra* with 29 bivalents from Windham 3495. C. *M. gruszczak* showing 58 bivalents from Windham *et al.* 4427. D–E. Spore contents of individual sporangia; scale bars = 50 μm. D. *M. scabra* with mean spore length = 42.9 μm from Windham 3495. E. *M. gruszczak* with mean spore length = 52.3 μm from Windham *et al.* 4436.
possibility that spore measurements could be used to infer the ploidy of fertile collections that lack cytogenetic data. Figure 2 presents spore size data for 52 samples representing 42 populations of *M. scabra* s.l. The means of spore samples gathered from confirmed diploid plants of *M. scabra* ranged from 37.7 to 45.5 µm, whereas mean spore sizes of known tetraploid plants of *M. grusziae* ranged from 48.7 to 55.5 µm.

Among sporulating plants without chromosome data, 15 samples exhibited mean spore sizes intercalated within the established diploid range of *M. scabra*, and another 19 samples fell within the established tetraploid range of *M. grusziae* (Fig. 2). Four samples exhibited mean spore sizes falling within the 3.2 µm gap between confirmed diploids and tetraploids. Based on newly-recognized morphological features that consistently distinguish *M. scabra* and *M. grusziae* (see Sporophyte Morphology section below), the three samples producing smaller spores (averaging 45.7, 46.4, and 46.6 µm, respectively) were identified as *M. scabra* (Fig. 2). The sample with the largest mean spore size (48.2 µm) was identified as *M. grusziae*. Although these three samples narrow the spore size gap between *M. scabra* and *M. grusziae* to just 1.6 µm, they do not close it. Based on current sampling, mean spore sizes < 47 µm are diagnostic of *M. scabra* whereas means > 47 µm are indicative of *M. grusziae* (Fig. 2). Two sporulating collections with predominantly malformed spores were identified as possible triploid hybrids between *M. scabra* and *M. grusziae*.

**Sporophyte Morphology**—Plants identified as *Myriopteris scabra* and *M. grusziae* via cytogenetic and spore analyses were compared based on more than 100 qualitative and quantitative morphological characters. The most useful distinguishing features are associated with the indument of the leaf blades. Even at relatively low magnification, the trichomes on the adaxial surfaces of ultimate segments show clear differences in size and density (Fig. 3A, B). Those of *M. scabra* are all relatively short (< 0.2 mm) and more abundant (mostly 36–64 per mm² close to segment margins). In *M. grusziae*, the largest adaxial trichomes on the ultimate segments are > 0.2 mm long and less dense (mostly 9–25 per mm² close to segment margins). A closer examination of these adaxial trichomes reveals major differences in their form and structure (Fig. 3C, D). In *M. scabra*, these trichomes arise from whitish, pustulate bases embedded in the leaf surface, with each base supporting 1–3 trichomes; the trichomes themselves are stiff, conical and composed of cells about as wide as long except for the sharply pointed, easily broken terminal cell.

![Fig. 2. Average spore lengths (in µm) for specimens of *Myriopteris scabra* (blue circles) and *M. grusziae* (red squares); error bars indicate one standard deviation. Number below each sample is a unique identifier linked to voucher data in Appendix 1; stars above numbers on x-axis indicate samples taken from type specimens. Numbers in bar across top indicate samples derived from chromosome vouchers; 29 = diploid, 58 = tetraploid. Horizontal gray line represents estimated spore size threshold between *M. scabra* and *M. grusziae*.](image-url)
FIG. 3. Morphological features distinguishing *M. scabra* (left column; all from Windham 3495) and *M. gruzsiae* (right column; all from Windham et al. 4427). A–B. Adaxial views of representative ultimate segments showing differences in trichome size and density; scale bars = 0.5 mm. C–D. Adaxial views of recurved segment margins illustrating differences in trichome shape and structure; scale bars = 0.2 mm. E–F. Adaxial views of proximal portion of rachises showing differences in the preponderance of hairs and scales; scale bars = 1 mm. G–H. Abaxial views of proximal portion of rachises illustrating differences in scale density; scale bars = 1 mm. I–J. Largest rachis scales showing differences in size; scale bars = 0.5 mm. K–L. Abaxial views of distal portion of pinnae illustrating differences in indument and pseudoindusia; scale bars = 2 mm.
By contrast, the adaxial trichomes of *M. grusziae* usually lack whitish swollen bases, arising individually from non-pustulate epidermal cells; these trichomes are flexible, linear, and composed of cells that are longer than wide, including the long (often > 0.1 mm) acicular, usually persistent terminal cell.

*M. scabra* and *M. grusziae* can also be distinguished based on the types of indument present on non-abraded portions of the rachises. In *M. scabra*, adaxial rachis surfaces exhibit scattered multicellular hairs and few, if any, linear-lanceolate scales (Fig. 3E), whereas abaxial surfaces show scattered, subappressed scales and very few hairs (Fig. 3G). By contrast, *M. grusziae* has rachis surfaces largely obscured by appressed, linear-lanceolate scales (Fig. 3F, H). The largest rachis scales of *M. scabra* are mostly 1–2 mm long (Fig. 3I), while those of *M. grusziae* are typically 3–4 mm long (Fig. 3J). Additional characters useful for separating *M. scabra* and *M. grusziae* can be seen on the abaxial surfaces of pinnae (Fig. 3K, L). In *M. scabra*, the linear-lanceolate scales occurring on the costae are usually restricted to the sclerified (dark brown) proximal portion, whereas those of *M. grusziae* extend onto the green midveins of ultimate segments. Thus, the abaxial pinna surfaces of *M. grusziae* appear “scalier” than those of *M. scabra*. Although difficult to quantify, the two taxa also exhibit subtle differences in their recurved leaf margins (Fig. 3K, L). The margins of *M. scabra* tend to be narrower and less continuous, with very inconspicuous pseudoindusia usually < 0.1 mm wide. In *M. grusziae*, the recurved margins tend to be broader and more continuous, with slightly more conspicuous pseudoindusia 0.1–0.2 mm wide.

**Geographic Distributions**—Specimens identified using a combination of cytogenetic analyses, spore measurements, and sporophyte morphology were georeferenced and used to plot the distributions of *Myriopteris scabra*, *M. grusziae*, and two putative triploid hybrid individuals (Fig. 4). Collections assigned to *M. scabra* based on cytogenetic and/or spore data (blue dots) are scattered from southern New Mexico, USA to Nuevo Leon, Mexico. We have not confirmed published reports of “Cheilanthes horridula” occurring further south in Mexico (Mickel and Smith 2004), but our distribution data suggest that most of these collections likely represent *M. scabra*. Specimens identified as *M. scabra* based solely on sporophyte morphology (open blue circles in Fig. 4) lie entirely within the range established by cytogenetic/spore data. This

![Fig. 4. Geographic distributions of *Myriopteris scabra* (blue circles), *M. grusziae* (red squares), and probable triploid hybrids characterized by an abundance of malformed spores (yellow triangles). Type specimens of the two fertile taxa are identified by colored stars. Filled symbols indicate samples with spore data (see Fig. 2); open symbols represent collections identified solely using sporophyte morphology (see Appendix 1).](image-url)
diploid species grows primarily on limestone (or rarely volca-
nic) rocks at elevations between 900 and 5600 ft (274 and
1700 m), and it is largely endemic to the Chihuahuan Desert.

Collections assigned to M. grusiae based on cytogenetic
and/or spore data (solid red squares) are scattered from
south-central Texas to south-central Oklahoma (Fig. 4). Spec-
imens identified based solely on sporophyte morphology
(open red squares) extend the documented range slightly to
the west, nearly closing the geographic gap between the two
taxa. Myriopteris grusiae grows on or about calcareous rocks
at elevations between 550 and 2300 ft (167 and 700 m), and
the species is common on the extensive limestone outcrops of the
Edwards Plateau, with outlying occurrences in the Cross Tim-
bers and Prairies region of north-central Texas and the
Arbuckle Mountains of south-central Oklahoma. Although
we have not observed mixed populations or mixed herbarium
sheets of M. grusiae and M. scabra, the two species have been
collected within 20 km of one another on the western slope of
the Edwards Plateau. There is likely some geographic overlap
in this region, and it is the only area in which we have encoun-
tered plants with predominantly malformed spores that may
represent triploid hybrids (yellow triangles in Fig. 4).

**Taxonomic Treatment**

Although the parentage of our presumed allotetraploid is
currently unresolved, we are convinced that it should not be
treated as conspecific with M. scabra. To do so would require
the inclusion of the missing diploid parent as well, which
would obviate all the morphological features that character-
ize this distinctive species. Instead, we propose to recognize
the tetraploid “cytotype” of M. scabra as a separate species
under the following name:

*Myriopteris grusiae* Windham & Pryer, sp. nov. **Type**: USA.
Texas: Burnet Co., NW of Marble Falls on ridge overlooking
Hoovers Valley along Park Road 4S ca. 0.5 road miles
SE of its junction with County Road 2342, 30.6963N
98.3769W (WGS84 Datum); 1135 ft (346 m); ledges of
S-facing limestone outcrops with Opuntia, Quercus, Ber-
beris, Rhus & Juniperus, Windham et al. 4427 (holotype:
DUKE; isotypes: ASU, BRIT, MO, NMC, NY, OKL, TEX,
UC, UNM, US, UT).

Most similar to *Myriopteris scabra* but differing in having: 1)
ultimate segments with adaxial trichomes longer (the largest
> 0.2 vs. < 0.2 mm), more flexible (vs. stiff, scabrous, and easily
broken), mostly linear with cells longer than wide (vs.
mostly conical with many cells wider than long), and superfi-
cial (vs. embedded-pustulate); 2) scales on proximal portion
of rachis obtuse and often overlapping (vs. scattered) with
the largest > 3 mm long (vs. all < 3 mm); 3) abaxial segment
surfaces with scattered scales proximally and more prominent
pseudoidindusia; 4) larger spores (averaging > 47 vs. < 47 mm);
and 5) a chromosome number of n = 58 (vs. n = 29).

**Plants** rupestral; **rhizomes** horizontal, short-creeping to
compact, 5–10 mm in diam including persistent petiole bases;
**rhizome scales** linear-lanceolate, to 5 × 0.3 mm, straight
to shortly constricted with long attenuate apices ending in an
eglandular, acicular tip, appressed, persistent, strongly bicol-
ored proximally, with broad, thickened, dark brown central
stripe and narrow, thin, light brown entire margins, with
tufted concolorous scales like those of petioles at growing

**leaves** with non-circinate (hooked) vernation, cluster-
ed, ± monomorphic, the small, sterile leaves of immature
plants eventually completely replaced by fertile leaves
10–35 cm long; **petioles** ca. 1/3 of leaf length, with 1 vascular
bundle proximally, dark reddish brown, terete, non-abraded
surfaces in contact with age, ± continuous around segment margins; **sori** consisting of 3–8 sporangia
attached to slightly enlarged vein tips in close proximity (ca.
0.2 mm) to pseudoidindusium, closely spaced and becoming
confluent with age, ± continuous around segment margins;
**pseudoidindusia** pale, chartaceous, to 0.2 mm wide, not
concealing mature sori, sparsely ciliate with trichomes similar to
those of adaxial segment surfaces; **sporangia** containing 64
spores, stalks < 0.1 mm, annulus 16–19-celled; **spores** trilete,
averaging 48–56 μm in diam; **chromosome number** n = 58
(Fig. 1C). Figure 5.

**Distribution, Habitat, and Conservation Status—** *Myriop-
teris grusiae* is confined to seasonally xeric (summer mon-
soon) habitats in the south-central United States. Data
obtained from herbarium specimens listed in Appendices 1
and 2 indicate that it grows on or about calcareous rocks at
elevations between 550 and 2300 ft (167 and 700 m). Popula-
tions are concentrated on the Edwards Plateau region of
south-central Texas, with additional occurrences in the Cross
Timbers and Prairies region (north-central Texas; see Digg
Fig. 5. Holotype of *Myriopteris grusiae* in the Duke University Herbarium; scale bar = 2 cm.
and Lipscomb (2014) for map of the vegetational areas of Texas) and the Arbuckle Mountains (south-central Oklahoma). *Myriopteris grusziae* occupies about 25% of the global range formerly attributed to *M. scabra*, and it comprises hundreds of documented (and many more undocumented) populations widely dispersed over the central Texas landscape. Neither *M. grusziae* nor *M. scabra* are of conservation concern at this time.

**Etymology**—This species is named for former graduate student Dr. Amanda L. Grusz in recognition of her contributions toward understanding cryptic patterns of biodiversity in ferns, especially through her dissertation research on *Myriopteris* (Grusz et al. 2009, 2014; Grusz 2013; Grusz and Pryer 2015; Grusz and Windham 2013).

**DISCUSSION**

By integrating data from a variety of sources, we have shown that *Myriopteris scabra* s.l. comprises two genetically disparate (Fig. 1B, C), morphologically recognizable (Fig. 3) taxa with little or no geographic overlap (Fig. 4). Spore measurements (Fig. 2) and morphological studies of two *M. scabra* isotypes at the US National Herbarium indicate that all previously published names are associated with the diploid taxon. *Myriopteris grusziae*, on the other hand, has remained unnamed and apparently unrecognized despite having been collected by scores of botanists over the past 170 yr. Given that *M. grusziae* is clearly related to but easily distinguished from *M. scabra* (Fig. 3), we hypothesize that it is an allotetraploid hybrid that acquired half (i.e. 29) of its chromosomes from *M. scabra*. Based on the chromosome number of *M. grusziae* (*n* = 58, Fig. 1C), the other parent should also have 29 gametic chromosomes. Within *Myriopteris*, the base number *x* = 29 is restricted to the *M. alabamensis* clade (Grusz et al. 2014); *M. scabra* is a member of this clade and, apparently, the other parent of *M. grusziae* is as well.

The morphology of trichomes occurring on adaxial blade surfaces of *M. grusziae* (Fig. 3B, D) broadly supports the hypothesis proposed above. These are more or less intermediate between the distinctive rigid, sharp-tipped, short-celled, embedded-pustulate trichomes of *M. scabra* (Fig. 3A, C) and the flexible, blunt, long-celled, superficial trichomes characteristic of most other species in the *M. alabamensis* clade. The most distinctive features of *M. grusziae* attributable to the unidentified parent are those of the rachis and pinna scales. In known and inferred tetraploid plants, these scales are larger, more abundant, and more broadly distributed than those found in *M. scabra* (see Fig. 3E-L). Assuming that the putative allotetraploid is more or less intermediate between its parents, the unidentified parent should be even more extreme in this regard. To date, we have not found a diploid *M. alabamensis* clade taxon possessing scales like those predicted for the missing diploid parent. However, we have a lot of ground (both poorly explored territory and unstudied herbarium specimens) still to cover.

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**AUTHOR CONTRIBUTIONS**

This study was conceived of and organized by MDW, with project development by KMP. Samples were gathered by MDW and KMP. Data collection and analyses were conducted by MDW and KTP. MDW was the primary author of the new species description. All authors discussed the results and contributed to the final manuscript.

**LITERATURE CITED**


Christensen, C. F. A. 1906. *Index Filicum. H. Hagenrup*.


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APPENDIX 2. Additional specimens examined not included in Fig. 2 or 4. 

**Taxon: M. grusziae**


USA. Texas, Brewster Co., along Smoky Creek, 29.0863N 103.4218W, Warnock & Wallmo 13228 (LL); W mouth of Boquillas Canyon, 29.2019N 102.9318W, Correll & Warnock 14977 (LL); Edwards Co., 13 mi. S of Rocksprings, 29.8589N 100.1096W, Soxman 336 (TEX); Kinney Co., Chilipotin Canyon, Anacacho Mts., 29.1803N 100.1600W, Correll 13426 (LL); ca. 5 mi SSW of Kickapoo Cavern, 29.5514N 100.4768W, Carr 22115 (TEX); Presidio Co., W side of the Chinati Mts, 29.8728N 104.4433W, Warnock 329 (SRSC); Val Verde Co., Langtry, 29.8091N 101.5624W, Correll & Correll 12901 (LL); 15.6 mi N of Comstock, 29.8945N 101.1530W, Seigler & Payne 1557 (TEX); Del Rio, Pecos River, 29.5652N 101.0663W, Whitehouse s.n. (TEX); NW of Amistad Dam along Rio Grande River, 29.5691N 101.2303W, Mears & Mears 2587 (TEX); Seminole Canyon State Historical Park, 29.6831N 101.3110W, Labus 49 (TEX); E side of Walk Lake, Devil’s River, 29.5408N 100.9809W, Correll 14820 (LL); E end of bridge on Pecos River on US 90, 29.7066N 101.3481W, Seigler & Renold 566 (TEX); Devils River State Natural Area Southern Unit, 29.7186N 100.9517W, Carr 30288 (TEX).