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

Michael D. Windham,[1,3] Kathryn T. Picard,[2] and Kathleen M. Pryer[1]

[1]Department of Biology, Duke University, Durham, North Carolina 27708, USA; mdw26@duke.edu; pryer@duke.edu
[2]Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia 20560, USA; PicardK@si.edu
[3]Author for correspondence

Communicating Editor: Alejandra Vasco

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 glassy, needle-like apices and compact conical bodies that are partially embedded in the leaf surface to form swollen, pustulate 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 northeastern 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*, cheilanthoid ferns, chromosomes, *Pellaea*, ploidy, 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 cheilanthoid 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. polyphyletic). Every major clade of cheilanthoid 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 Schuettpelz 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 cheilanthoids (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 cheilanthoid 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; Soltis 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; Schuettpelz 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 cytogenetic 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 glassy, 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 acetocarmine; the cells were then squashed in a 1:1 mixture of acetocarmine 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 MT5310L 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 cytogenetic 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 trilete 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 *rnaturalearth* (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 binomial 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
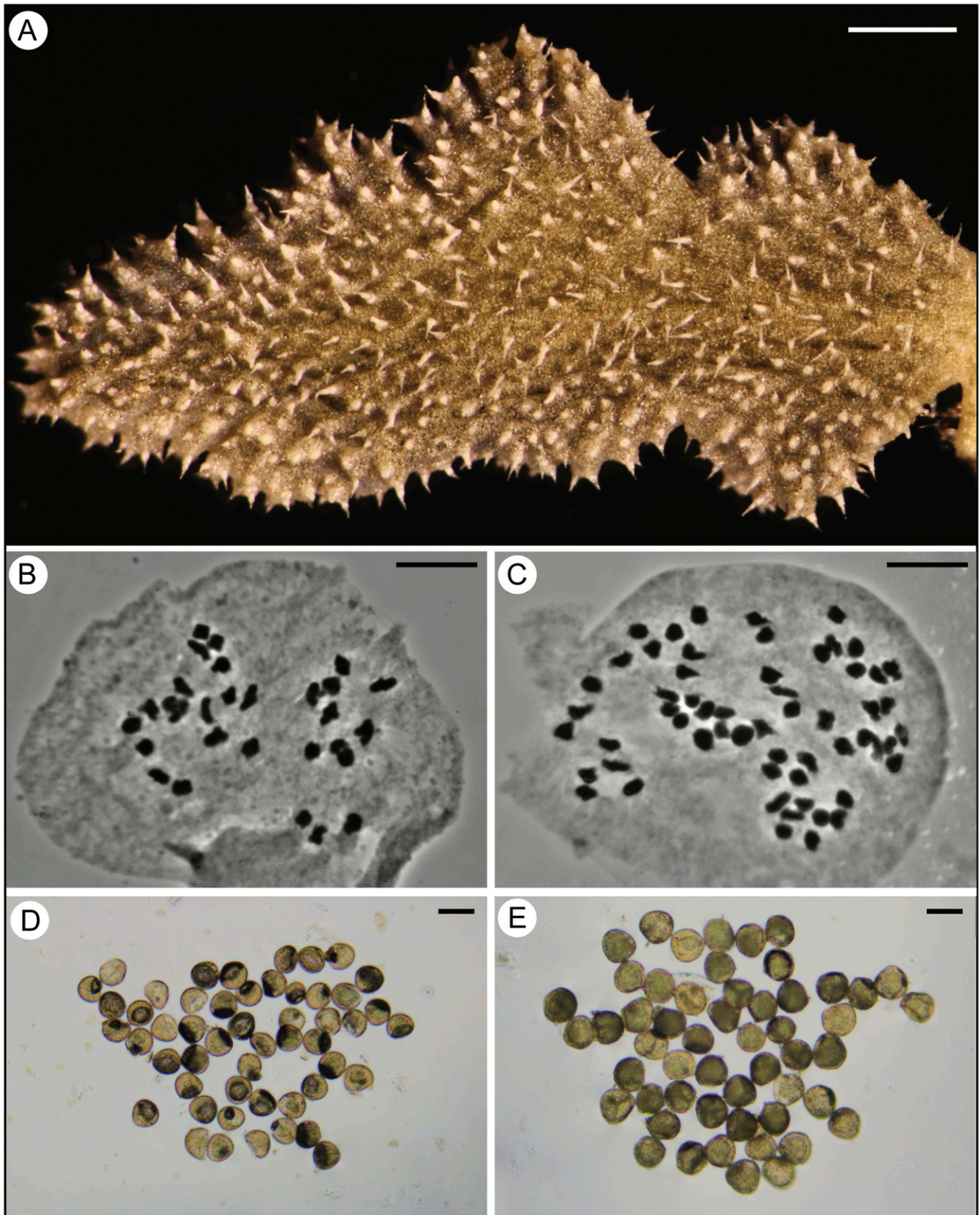
Fig. 1.   A. Close-up of ultimate segment of *Myriopteris scabra* from *Windham 3495* showing distinctive scabrous trichomes; scale bar = 0.5 mm. B–C. Meiotic chromosome preparations at diakinesis; scale bars = 20 μm. B. *M. scabra* with 29 bivalents from *Windham 3495*. C. *M. grusziae* showing 58 bivalents 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. grusziae* with mean spore length = 52.3 μm from *Windham et al. 4436*.
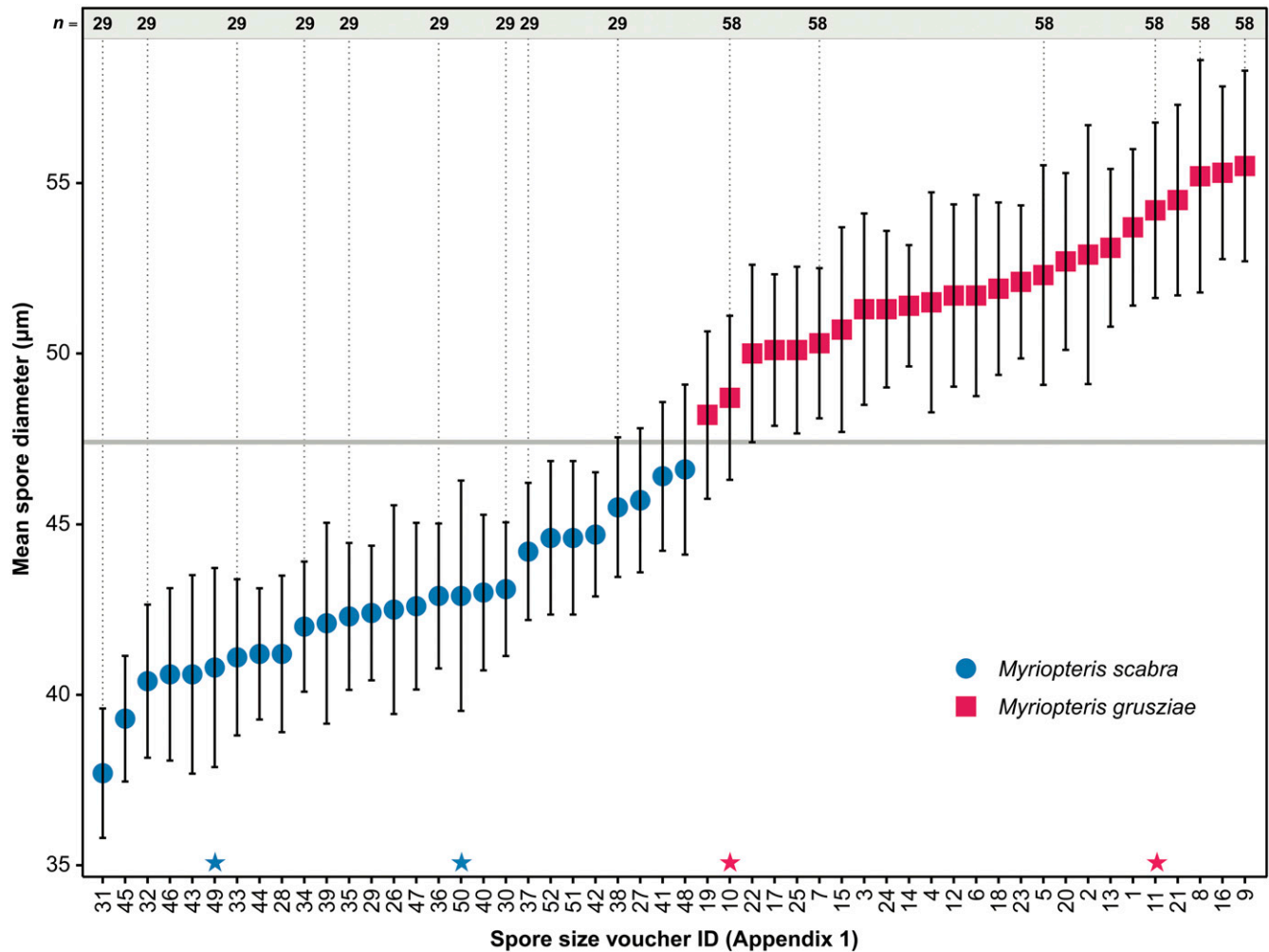
Fig. 2. Average spore lengths (in μm) for specimens of *Myriopteris scabra* (blue circles) and *M. grusziae* (red squares); error bars indicate one standard deviation. Number below each sample is a unique identifier linked to voucher data in Appendix 1; stars above numbers on x-axis indicate samples 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*.

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 four 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 mm^2 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 mm^2 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.
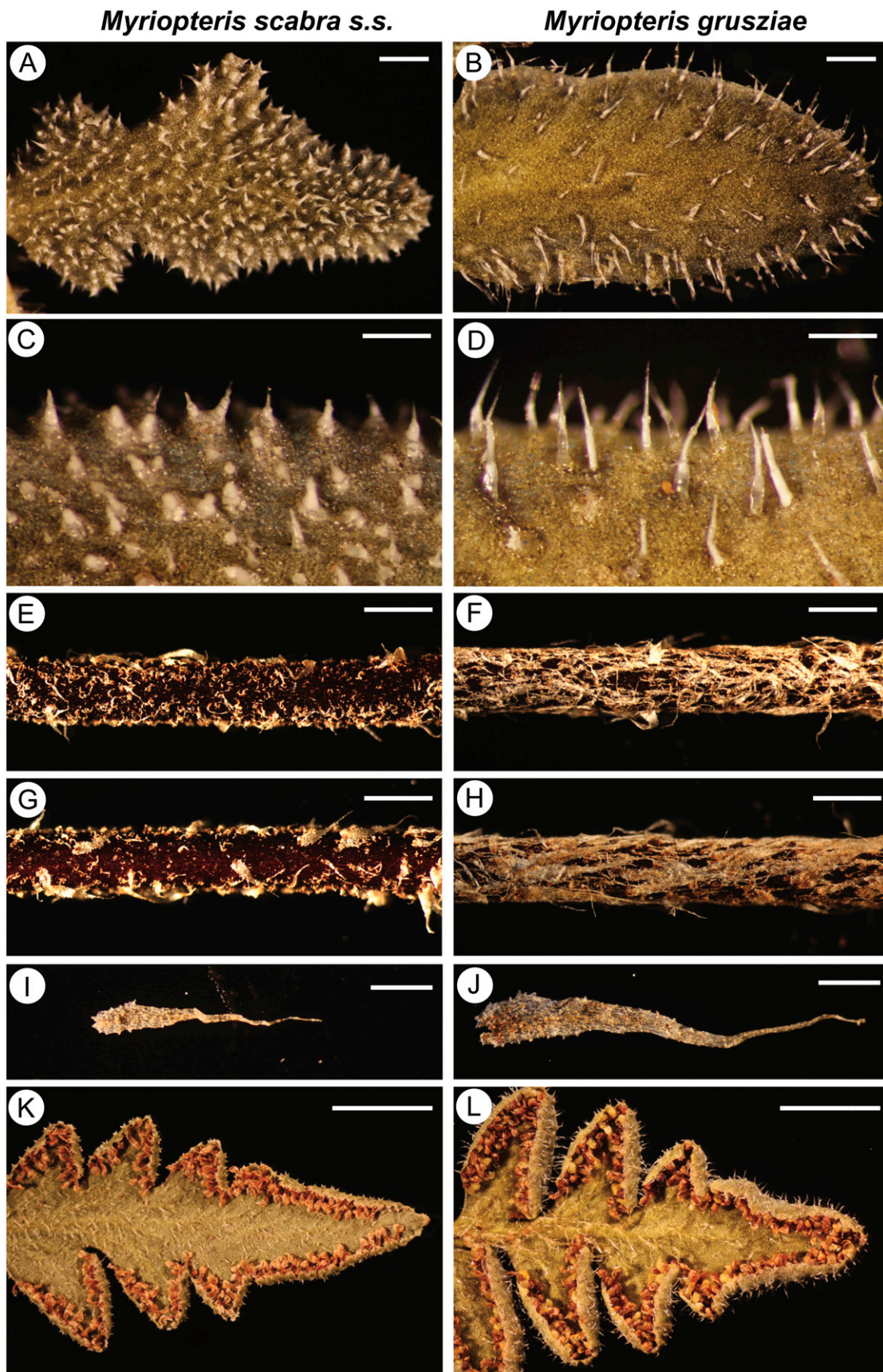
Myriopteris scabra s.s.   Myriopteris grusziae

FIG. 3.   Morphological features distinguishing *M. scabra* (left column; all from *Windham 3495*) and *M. grusziae* (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.

Myriopteris 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
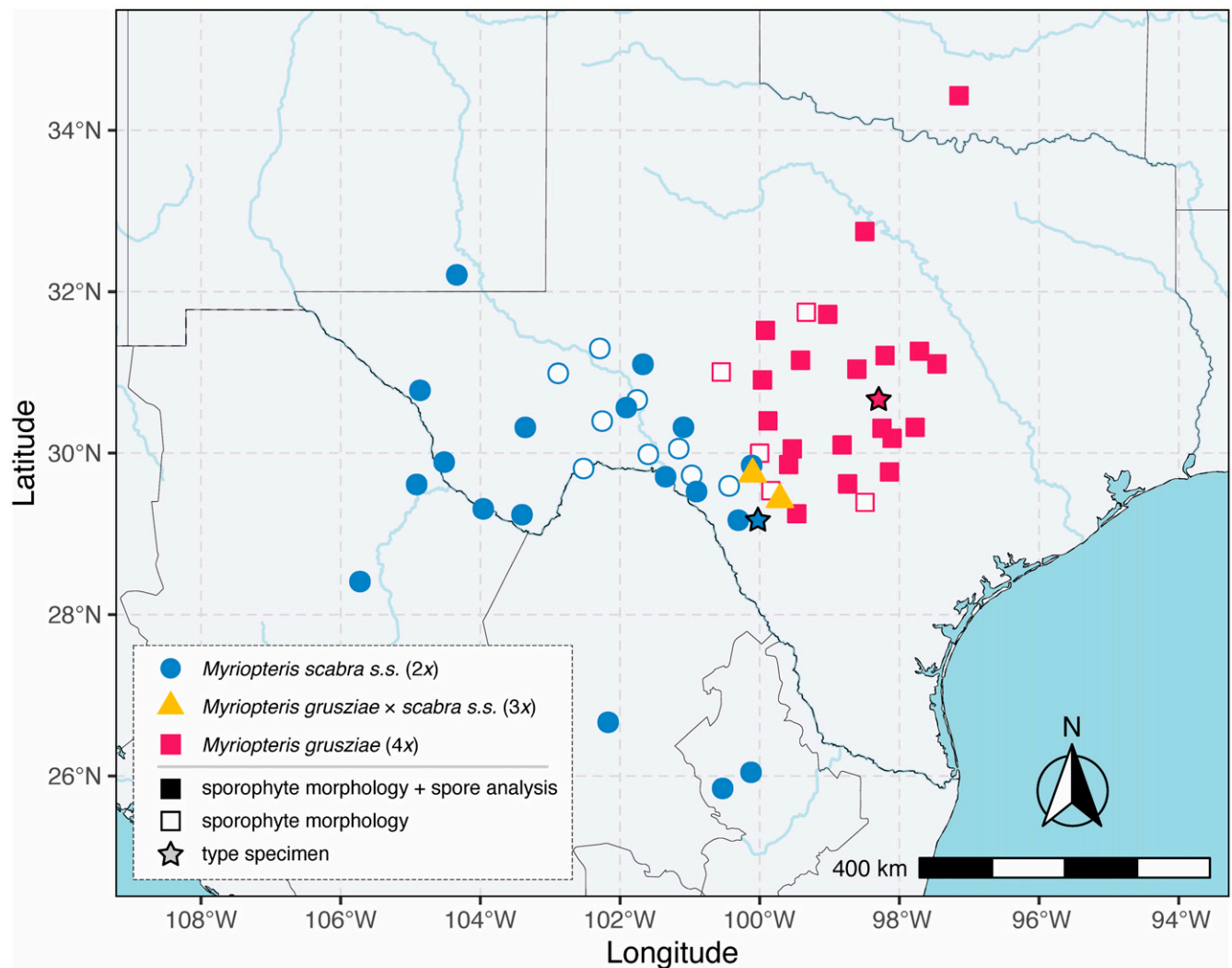

Fig. 4. Geographic distributions of *Myriopteris scabra* (blue circles), *M. grusziae* (red squares), and probable triploid hybrids characterized by an abundance of malformed spores (yellow triangles). Type specimens of the two fertile taxa are identified by colored stars. Filled symbols indicate samples with spore data (see Fig. 2); open symbols represent collections identified solely using sporophyte morphology (see Appendix 1).

diploid species grows primarily on limestone (or rarely volcanic) 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. grusziae* based on cytogenetic and/or spore data (solid red squares) are scattered from south-central Texas to south-central Oklahoma (Fig. 4). Specimens 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 grusziae* 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 Timbers 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. grusziae* 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 encountered 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 characterize this distinctive species. Instead, we propose to recognize the tetraploid "cytotype" of *M. scabra* as a separate species under the following name:

Myriopteris grusziae 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*, *Berberis*, *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 superficial (vs. embedded-pustulate); 2) scales on proximal portion of rachises abundant 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 pseudoindusia; 4) larger spores (averaging > 47 vs. < 47 μm); 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 slightly contorted with long attenuate apices ending in an eglandular, acicular tip, appressed, persistent, strongly bicolored 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

tips; **leaves** with non-circinate (hooked) vernation, clustered, ± 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 often largely obscured by multiseriate scales intermixed with scattered hair-like trichomes; multiseriate scales linear-lanceolate, to 6 × 0.4 mm, straight to slightly contorted with long attenuate apices ending in an eglandular, acicular tip, loosely appressed, often belatedly deciduous, concolored or somewhat darker centrally and proximally at petiole bases, mostly light brown, thin, chartaceous, with denticulate to entire margins; hair-like trichomes to 0.7 mm long, multicellular with cells strongly flattened, appressed, more prevalent on adaxial surfaces, fully intergrading with smallest scales; **fertile blades** narrowly oblong-lanceolate, 2-pinnate-pinnatifid proximally, 10–20 cm long and 3–6 cm wide at broadest point near middle of blade; **rachises** dark reddish brown gradually transitioning to green near blade apex, terete, indument similar to petioles but with multiseriate scales becoming smaller and hair-like trichomes more prevalent distally; **pinnae** usually 24–40 per fertile leaf, alternate to subopposite, not articulate, dark color of rachises continuing into costae proximally, the lowermost pinnae with dark reddish brown stalks 1–3 mm; basal pinnae usually slightly smaller than adjacent pinnae, equilateral, triangular-ovate, 10–20 × 8–15 mm, appearing sparsely hispid adaxially and sparsely pubescent/scaly abaxially; **costae** adaxial surfaces greenish except at base, with scattered hair-like trichomes; abaxial surfaces usually dark reddish brown on proximal half of pinna, with hair-like trichomes resembling those of petioles and rachises and scattered multiseriate scales smaller than those of petioles (to 3 × 0.4 mm) but otherwise similar; **fertile ultimate segments** narrowly elliptic to elongate-deltate, mostly 3–6 × 1.5–3 mm, usually broadly attached to subtending costae (rarely short stalked), entire or shallowly lobed, the edges slightly recurved, with poorly-differentiated marginal pseudoindusium; adaxial segment surfaces somewhat hispid, trichomes arising individually from non-pustulate basal cells, the largest 0.2–0.4 mm long with acicular tips, < 25 per mm^2, 2–5 celled, the largest cells > 0.1 mm long; abaxial segment surfaces with flattened, hair-like trichomes and a few multiseriate scales < 2 mm long, trichome density mostly < 10 per mm^2; **veins** obscure, not anastomosing, terminating before reaching segment margins; **sori** consisting of 3–8 sporangia attached to slightly enlarged vein tips in close proximity (ca. 0.2 mm) to pseudoindusium, closely spaced and becoming confluent with age, ± continuous around segment margins; **pseudoindusia** 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—*Myriopteris grusziae* is confined to seasonally xeric (summer monsoon) 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). Populations 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 Diggs

Fig. 5.   Holotype of *Myriopteris grusziae* 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 gruszae* 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. gruszae* 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 gruszae*, 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. gruszae* 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. gruszae* ($n = 58$; 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. gruszae* is as well.

The morphology of trichomes occurring on adaxial blade surfaces of *M. gruszae* (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. gruszae* 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.

Acknowledgments

Author Contributions

Literature Cited

Anderson, L. E. 1954. Hoyer's solution as a rapid permanent mounting medium for bryophytes. *Bryologist* 57: 242–244

Barrington, D. S., C. A. Paris, and T. A. Ranker. 1986. Systematic inferences from spore and stomate size in the ferns. *American Fern Journal* 76: 149–159.

Barrington, D. S., N. R. Patel, and M. W. Southgate. 2020. Inferring the impacts of evolutionary history and ecological constraints on spore size and shape in the ferns. *Applications in Plant Sciences* 8: e11339.

Beck, J. B., M. D. Windham, G. A. Yatskievych, and K. M. Pryer. 2010. A diploids-first approach to species delimitation and interpreting polyploid evolution in the fern genus *Astrolepis* (Pteridaceae). *Systematic Botany* 35: 223–234.

Ching, R. C. 1941. The studies of Chinese ferns—XXXI. *Hong Kong Naturalist* 10: 194–204.

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

Diggs, G. M. Jr. and B. L. Lipscomb. 2014. *The Ferns and Lycophytes of Texas*. Fort Worth: Botanical Research Institute of Texas Press.

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

Eiserhardt, W. L., J. G. Rohwer, S. J. Russell, J. C. Yesilyurt, and H. Schneider. 2011. Evidence for radiations of cheilanthoid ferns in the Greater Cape Floristic Region. *Taxon* 26: 1–15.

Fée, A. L. A. 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, G. J. and D. R. Rollo. 1998. Cheilanthoid ferns (Pteridaceae: Cheilanthoideae) in the southwestern United States and adjacent Mexico: A molecular phylogenetic reassessment of generic lines. *Aliso* 17: 131–144.

Google Earth Pro version 7.3. 2017. https://www.google.com/earth/versions (accessed Dec 2021).

Grusz, A. L. 2013. *Myriopteris windhamii* sp. nov., a new name for *Cheilanthes villosa* (Pteridaceae). *American Fern Journal* 103: 112–117.

Grusz, A. L. and K. M. Pryer. 2015. Development of microsatellite markers for the apomictic triploid fern, *Myriopteris lindheimeri* (Pteridaceae). *Applications in Plant Sciences* 3: e1500061.

Grusz, A. L. and M. D. Windham. 2013. Toward a monophyletic *Cheilanthes*: The resurrection and recircumscription of *Myriopteris* (Pteridaceae). *PhytoKeys* 32: 49–64.

Grusz, A. L., M. D. Windham, and K. M. Pryer. 2009. Deciphering the origins of apomictic polyploids in the *Cheilanthes yavapensis* complex (Pteridaceae). *American Journal of Botany* 96: 1636–1645.

Grusz, A. L., M. D. Windham, G. Yatskievych, L. Huiet, G. J. Gastony, and K. M. Pryer. 2014. Patterns of diversification in the xeric-adapted fern genus *Myriopteris* (Pteridaceae). *Systematic Botany* 39: 698–714.

Hevly, R. H. 1963. Adaptations of cheilanthoid ferns to desert environments. *Journal of the Arizona Academy of Science* 2: 164–175.

Hooker, W. J. 1852. *Species Filicum* 2. London: William Pamplin.

Hooker, W. J. and J. G. Baker. 1867. *Synopsis Filicum* 148. London.

Kao, T.-T., C. J. Rothfels, A. Melgoza-Castillo, K. M. Pryer, and M. D. Windham. 2020. Infraspecific diversification of the star cloak fern (*Notholaena standleyi*) in the deserts of the United States and Mexico. *American Journal of Botany* 107: 658–675.

Li, F.-W., K. M. Pryer, and M. D. Windham. 2012. *Gaga*, a new fern genus segregated from *Cheilanthes* (Pteridaceae). *Systematic Botany* 37: 845–860.

Maxon, W. R. 1918. Further notes on *Pellaea*. *American Fern Journal* 8: 89–94.

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

Mickel, J. T. and A. R. Smith. 2004. *The Pteridophytes of Mexico.* New York: The New York Botanical Garden Press.

Nobel, P. S. 1978. Microhabitat, water relations, and photosynthesis of a desert fern, *Notholaena parryi*. *Oecologia* 31: 293–309.

Ponce, M. M. and M. A. Scataglini. 2021. Phylogenetic position of South American *Cheilanthes* (Cheilanthoideae, Pteridaceae): Advances in the generic circumscription and segregation of the new genus *Mineirella*. *Journal of Systematics and Evolution* 60: 266–280.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Schuettpelz, E., H. Schneider, L. Huiet, M. D. Windham, and K. M. Pryer. 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.

Schuettpelz, E., K. M. Pryer, and M. D. Windham. 2015. A unified approach to taxonomic delimitation in the fern genus *Pentagramma* (Pteridaceae). *Systematic Botany* 40: 629–644.

Sigel, E. M., M. D. Windham, L. Huiet, G. Yatskievych, and K. M. Pryer. 2011. Species relationships and farina evolution in the cheilanthoid fern genus *Argyrochosma* (Pteridaceae). *Systematic Botany* 36: 554–564.

Smith, J. 1875. *Historia Filicum.* London: Macmillan and Co.

Soltis, D. E., P. S. Soltis, D. W. Schemske, J. F. Hancock, J. N. Thompson, B. C. Husband, and W. S. Judd. 2007. Autopolyploidy in angiosperms: Have we grossly underestimated the number of species? *Taxon* 56: 13–30.

South, A. 2017. rnaturalearth: World map data from Natural Earth. R package version 0.1.0. https://CRAN.R-project.org/package=rnaturalearth.

Swartz, O. 1806. *Synopsis Filicum* 5. Iveson, Blakeman, & Taylor.

Topozone. 1999. TopoZone, the Web's topographic map. Available through the Library of Congress, lccn.loc.gov/2002628501 (accessed Dec 2021).

Tryon, R. M. and A. F. Tryon. 1973. Geography, spores, and evolutionary relations in the cheilanthoid ferns. Pp. 145–153 in *The Phylogeny and Classification of Ferns.* eds. A. C. Jermy, J. A. Crabbe, and B. A. Thomas. *Botanical Journal of the Linnaean Society* 67 (Suppl. 1).

Tryon, R. M. and A. F. Tryon. 1982. *Ferns and Allied Plants with Special Reference to Tropical America.* New York: Springer-Verlag.

Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis.* New York: Springer-Verlag.

Windham, M. D. and E. W. Rabe. 1993. *Cheilanthes*. Pp. 152–169 in *Flora of North America North of Mexico*, vol. 2, eds. Flora of North America Editorial Committee. New York: Oxford University Press.

Windham, M. D. and G. Yatskievych. 2003. Chromosome studies of cheilanthoid ferns (Pteridaceae, Cheilanthoideae) from the western United States and Mexico. *American Journal of Botany* 90: 1788–1800.

Windham, M. D., L. Huiet, J. S. Metzgar, T. A. Ranker, G. Yatskievych, C. H. Haufler, and K. M. Pryer. 2022. Once more unto the breach, dear friends: Resolving the identity, origin, and relationships of *Pellaea wrightiana*. *American Journal of Botany* 109: 821–850.

APPENDIX 1. List of specimens included in Figs. 2 and 4. **Taxon:** descriptive locality, georeferenced coordinates, *collector's data* (voucher location), chromosome number, mean spore diameter (s.d.; **sample number** in Fig. 2).

Myriopteris grusziae: USA. **Oklahoma**, Murray Co., Turner Falls Park, 34.4281N 97.1471W, *Beck 1436* (DUKE), —, 53.7 µm (2.29; **1**). **Texas**, Bandera Co., head of Sabinal Canyon, 29.8576N 99.5858W, *Correll & Correll 12831* (LL), —, 52.9 µm (3.79; **2**); Bell Co., Miller Springs Park, 31.1056N 97.4616W, *Carr & Robbins 11160* (TEX), —, 51.3 µm (2.80; **3**); Bexar Co., 14 mi E of intersection of Mico and Park Road 37, 29.6192N 98.7419W, *Seigler et al. 1987* (TEX), —, 51.5 µm (3.23; **4**); Mission Concepción, San Antonio Missions NHP, 29.3908N 98.4915W, *Carr & Benesh 19811* (TEX), —, — (—; —); Blanco Co., side canyon of Pedernales River above Twin Falls, 30.3081N 98.2495W, *Windham et al. 4436* (DUKE), n = 58, 52.3 µm (3.22; **5**); Brown Co., 2 mi W of Brownwood, 31.7185N 99.0268W, *Stanford 1659* (OKLA), —, 51.7 µm (2.95; **6**); Burnet Co., Longhorn Cavern State Park, 30.6971N 98.3798W, *Windham & Yatskievych 732* (DUKE), n = 58, 50.3 µm (2.20; **7**), 55.2 µm (3.41; **8**), 55.5 µm (2.80; **9**); NW of Marble Falls (isotypes of *Myriopteris grusziae*),

30.6963N 98.3769W, *Windham et al. 4427* (TEX), n = 58, 48.7 µm (2.40; **10**), (NY), n = 58, 54.2 µm (2.57; **11**); Coleman Co., Santa Anna, 31.7457N 99.3322W, *Correll & Correll 12930* (LL), —, — (—; —); Comal Co., Huaco Camp, 29.7660N 98.1417W, *Soxman 493* (TEX), —, 51.7 µm (2.67; **12**); Concho Co., Paint Rock, 31.5199N 99.9180W, *Correll & Correll 12924* (SMU), —, 53.1 µm (2.31; **13**); Coryell Co., Fort Hood, Rambo Point, 31.2616N 97.7132W, *Hansen 6564* (TEX), —, 51.4 µm (1.78; **14**); Edwards Co., 2 mi NE of Kalentine Hole along Hackberry Creek, 29.9985N 100.0002W, *Smith & Butterwick 261* (LL), —, — (—; —); Hays Co., Dripping Springs, 30.1825N 98.1039W, *Correll 13404* (LL), —, 50.7 µm (3.00; **15**); Kendall Co., Old Tunnel Wildlife Management Area, 30.1008N 98.8201W, *Hansen 6090* (TEX), —, 55.3 µm (2.53; **16**); Kerr Co., N Fork of Guadalupe River, 14 mi above Hunt, 30.0528N 99.5339W, *Correll & Correll 12788* (LL), —, 50.1 µm (2.22; **17**); Kimble Co., along S Llano River 10 mi S of Junction, 30.3997N 99.8816W, *Correll & Correll 12838* (LL), —, 51.9 µm (2.53; **18**); Lampasas Co., NW portion of Big Dog Ranch, 31.2091N 98.2055W, *Hansen 6233* (TEX), —, 48.2 µm (2.45; **19**); McCulloch Co., N side of Brady Lake, 31.1499N 99.4152W, *Whisenant 557* (SAT), —, 52.7 µm (2.59; **20**); Menard Co., 12 mi W of Menard, headwaters of Clear Creek of the San Saba River, 30.9070N 99.9604W, *Blassingame 800* (SAT), —, 54.5 µm (2.80; **21**); Palo Pinto Co., ca. 4 mi W of Metcalf Gap, 32.7452N 98.4952W, *Correll & Correll 12342* (LL), —, 50.0 µm (2.60; **22**); San Saba Co., 5 mi W of Chappel, 31.0404N 98.6088W, *Correll & Correll 12685* (LL), —, 52.1 µm (2.25; **23**); Schleicher Co., N of Eldorado, 31.0044N 100.5506W, *Hansen 8046* (TEX), —, — (—; —); Travis Co., Mount Bonnell near Austin, 30.3206N 97.7735W, *Warnock et al. 46454* (TEX), —, 51.3 µm (2.30; **24**); Uvalde Co., ca. 6 mi S of Sabinal, 29.2497N 99.4697W, *Powell & Powell 6498* (SRSC), —, 50.1 µm (2.45; **25**); Reagan Wells, 29.5352N 99.8401W, *Soxman 37* (TEX) —, — (—; —). *Myriopteris grusziae* × *M. scabra:* USA. **Texas**, Edwards Co., W side of Powers Mountain, 29.7398N 100.1020W, *Carr & Moring 28804* (TEX), —, — (—; —); Uvalde Co., ca. 3 mi WSW of R.M. 2690 bridge over Frio River, 29.4387N 99.7055W, *Carr 16763* (TEX), —, — (—; —). *Myriopteris scabra:* Mexico. **Chihuahua**, N end of Sierra del Cuchillo Parado, 29.6116N 104.9116W, *Wendt et al. 9801A* (LL), —, 42.5 µm (3.06; **26**); Bachimba Canyon S of Cd. Chihuahua, 28.4083N 105.7235W, *Knobloch 625* (LL), —, 45.7 µm (2.11; **27**); **Coahuila**, N side of Canon de la Fragua, 26.6643N 102.1702W, *Van Devender et al. 84–612* (TEX), —, 41.2 µm (2.30; **28**); **Nuevo Leon**, 7 mi N of Ciénega de Flores, 26.0461N 100.1248W, *Correll & Johnston 19766* (LL), —, 42.4 µm (1.97; **29**); along State Highway 16 in the Sierra El Fraile, 25.8462N 100.5308W, *Windham et al. 470* (UT), n = 29, 43.1 µm (1.96; **30**). USA. **New Mexico**, NE of Whites City, 32.2077N 104.3375W, *Windham 3495* (DUKE), n = 29, 37.7 µm (1.90; **31**), 40.4 µm (2.25; **32**), 41.1 µm (2.29; **33**), 42.0 µm (1.91; **34**), 42.3 µm (2.16; **35**), 42.9 µm (2.13 **36**), 44.2 µm (2.01; **37**), 45.5 µm (2.05; **38**). **Texas**, Brewster Co., ca. 28 mi E of Alpine, 30.3188N 103.3565W, *Correll 14077* (LL), —, 42.1 µm (2.95; **39**); S side of Burro Mesa, 29.2373N 103.4034W, *Correll 33853–A* (LL), —, 43.0 µm (2.28; **40**); near Tank 19 on Bullis Gap Ranch, 29.8086N 102.5220W, *Butterwick & Lott 3523* (TEX), —, — (—; —); Crockett Co., 15 mi N of Juno, 30.3201N 101.0916W, *Warnock & McBryde 15189* (LL), —, 46.4 µm (2.17; **41**); E of Pecos River on US 290, 30.6596N 101.7544W, *Seigler et al. 2396a* (TEX), —, — (—; —); Culberson Co., ca. 7 mi WSW of Lobo, 30.7781N 104.8640W, *Turner 24–556* (TEX), —, 44.7 µm (1.81; **42**); Edwards Co., 14 mi S of Rock Springs, 29.8471N 100.1153W, *Douglas 495* (BRIT), —, 40.6 µm (2.91; **43**); Kinney Co., W side of Anacacho Mts., 29.1693N 100.3064W, *Correll & Correll 30762* (LL), —, 41.2 µm (1.93; **44**); Kickapoo Cavern State Park, 29.5939N 100.4383W, *Carr 10444* (TEX), —, — (—; —); Pecos Co., 6 mi N of Ft. Stockton, 30.9887N 102.8855W, *Warnock 20919* (TEX), —, — (—; —); Presidio Co., Chinati Mtns. State Natural Area, 29.8878N 104.5186W, *Lott et al. 5522* (SRSC), —, 39.3 µm (1.84; **45**); NE of Willow Campground along Rio Grande River, 29.3101N 103.9590W, *Butterwick & Strong B–1052* (TEX), —, 40.6 µm (2.53; **46**); Reagan Co., 5.5 mi S & 13.5 mi W of Big Lake, 31.1004N 101.6720W, *Rowell 15207* (SAT), —, 42.6 µm (2.45; **47**); Terrell Co., 13 mi S of Sheffield, 30.5641N 101.9090W, *Webster 139* (TEX), —, 46.6 µm (2.49; **48**); Big Canyon off Sanderson-Sheffield highway, 30.3967N 102.2553W, *Correll & Johnston 24603* (LL), —, — (—; —); Upton Co., ca. 10 mi N of McCamey, 31.2954N 102.2896W, *Correll 13566* (LL), —, — (—; —); Uvalde Co., Turkey Creek (isotypes of *Myriopteris scabra*), 29.1825N 100.0312W, *Wright 824* (US), —, 40.8 µm (2.92; **49**), 42.9 µm (3.37; **50**); Val Verde Co., 10–12 mi N of Del Rio toward Alta, 29.5238N 100.9050W, *Warnock & McBryde 15021* (LL), —, 44.6 µm (2.17; **51**); US 90 Pecos River Bridge, 29.7067N 101.3480W, *Beck et al. 1036* (DUKE), —, 44.6 µm (2.25; **52**); 12.7 mi N of Langtry, 29.9843N 101.5948W, *Seigler & Renold 955* (TEX),

—, — (—; —); 9 mi S of Juno on Route 163, 30.0549N 101.1595W, *Seigler & Renold 959* (TEX), —, — (—; —); Little Satan Canyon, 29.7238N 100.9738W, *Carr 30651* (TEX), —, — (—; —).

APPENDIX 2.   Additional specimens examined not included in Fig. 2 or 4. *Taxon*: descriptive locality, georeferenced coordinates, *collector's data* (voucher location).

Myriopteris grusziae: USA. **Oklahoma**, Camp Classen on Brush Creek, 34.4410N 97.1702W, *Magrath 15871* (OKL). **Texas**, Bandera Co., Medina Lake, 29.5753N 98.9512W, *Soxman 84* (TEX); Plum Creek, 29.5703N 98.9625W, *Soxman 97* (TEX); Bell Co., Fort Hood, Seven Mile Mountain, 31.0601N 97.8633W, *Hansen 5538* (TEX); Bexar Co., 2 mi W of Helotes, 29.5762N 98.7230W, *Soxman 134* (TEX); Government Canyon tract (RTC), 29.5597N 98.7449W, *Carr & Turner 12387* (TEX); Brown Co., SE side of Brownwood, Camp Bowie, 31.6373N 98.9222W, *Carr & Pinto-Torres 30950* (TEX); Muse Wildlife Management Area, 31.8845N 98.8575W, *Hansen 7030* (TEX); Burnet Co., Mormon Hole near Mormon Mills, 30.6365N 98.2356W, *Correll & Correll 12718* (LL); N Fork of Morgan Creek, 30.8737N 98.3204W, *Correll & Correll 12743* (LL); Comal Co., W of New Braunfels, 29.7727N 98.2741W, *Soxman 502* (TEX); Kerr Co., Kerr Wildlife Management Area, 30.0611N 99.5018W, *Hansen 6998* (TEX); Kimble Co., Walter Buck Wildlife Management Area in Hunt Area 5, 30.4290N 99.7992W, *Hansen 5916* (TEX); McCulloch Co., SE of Brady along Hwy 71, 31.0426N 99.2436W, *Hansen 7606* (TEX); Palo Pinto Co., Lovers Retreat, 32.7557N 98.3413W, *Gill & Gill 185* (TEX); Real Co., Prade Ranch, Frio Canyon, 29.9159N 99.7848W, *Correll & Correll 12855* (LL); NW corner of county, 29.9736N 99.9588W, *Correll 13428* (LL); Travis Co., near head of Bull Creek, 30.4133N 97.8319W, *Palmer s.n.* (TEX); ca. 6 mi NW of Beecaves, 30.3357N 98.3447W, *Correll 13413* (LL); Barton Creek E of Loop 360 bridge, 30.2453N 97.8019W, *Carr 10913* (TEX); Uvalde Co., Concan, 29.4979N 99.7098W, *Soxman 141–4* (TEX); ca. 3 mi WSW of R.M. 2690 bridge over Frio River, 29.4387N 99.7055W, *Carr 16763* (TEX); John Garner State Park, 29.5792N 99.7393W, *Correll & Correll 12874* (LL); valley of Hackberry Creek ca. 1000 ft. E of Co. Rd. 336, 29.4686N 99.6237W, *Carr 25933* (TEX). *Myriopteris scabra*: 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 13462* (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 104.4443W, *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 1957* (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, 29.5406N 100.9809W, *Correll 14920* (LL); E end of bridge on Pecos River on US 90, 29.7066N 101.3481W, *Seigler & Renold 946* (TEX); Devils River State Natural Area Southern Unit, 29.7186N 100.9517W, *Carr 30288* (TEX).