RESEARCH ARTICLE

Ynesmexia: A novel genus uniting morphologically disparate cheilanthoid ferns (Pteridaceae)

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Abstract Here we focus on the "*skinneri* clade" of cheilanthoid ferns (Pteridaceae), revising its taxonomy based on a new set of molecular, cytogenetic, and morphological analyses. Though previously assigned to disparate genera, the five taxa formally recognized in this clade form a strongly supported monophyletic group when analyzed with both plastid (*rbcL*, *atpA*, *trnG-R*) and nuclear (*gapCp*) datasets. This novel lineage is recognized here as *Ynesmexia* gen. nov. in honor of Ynés Mexía, a pioneering Mexican-American botanist. Our molecular analyses indicate that *Ynesmexia* comprises two monophyletic groups, referred to here as the "*subcordata*" and "*seemannii*" subclades. The "*subcordata*" subclade encompasses plants previously treated as *Cheilanthes skinneri*, ×*Hemionanthes gryphus* and *Hemionitis subcordata*. Our data indicate that the first taxon comprises two species: a diploid treated here as *Ynesmexia fournieri* (comb. nov.) and a tetraploid corresponding to *Y. skinneri* (comb. nov.) s.str. Amplifying the differences in ploidy, these two taxa are distinguished by several aspects of sporophyte morphology, non-overlapping spore sizes, and allopatric geographic distributions. Our analyses also highlight the role of hybridization and polyploidy in the evolution of the group, indicating that: (1) *Y.* ×*gryphus* (comb. nov.) is a largely fertile homoploid hybrid between *Y. subcordata* (comb. nov.) and *Y. fournieri*, and (2) *Y. skinneri* s.str. is an allotetraploid between members of the "*subcordata*" and "*seemannii*" subclades. Although the latter subclade is morphologically (and likely cytogenetically) diverse, current data are insufficient to propose formal subdivision of the only recognized species, *Y. seemannii* (comb. nov.). The findings presented here challenge earlier taxonomic frameworks and offer new insights into the evolutionary history of this xeric-adapted fern lineage, underscoring the importance of using multi-faceted approaches to resolve complex taxonomic issues in plant biology.

Keywords *Cheilanthes*; cytogenetics; *Hemionitis*; Mexico; *Pellaea*; phylogeny; spore studies

■ INTRODUCTION

Among ferns, the ca. 500 species of the cheilanthoid clade (Cheilanthoideae; Pteridaceae) are especially notable for having adapted to, and diversified within, xeric habitats across the globe (Tryon & Tryon, 1982; Schuettpelz & Pryer, 2007; Windham & al., 2009; Schuettpelz & al., 2025). Convergent evolution of morphological adaptations to arid environments (e.g., highly divided leaves with leathery ultimate segments, an abundance of hairs, scales or farina deposits that reflect light and reduce transpiration) is rampant in cheilanthoid ferns. As a result, generic boundaries have been poorly defined and unstable in what has been called "the most contentious group of ferns with respect to a practical and natural generic classification" (Tryon & Tryon, 1982: 248). Building on the seminal cheilanthoid molecular phylogenetic analyses of Gastony & Rollo (1995, 1998), the last 25 years have seen phenomenal progress in the recognition of robust monophyletic groups. This has led to the re-circumscription of some broadly accepted cheilanthoid genera (e.g., *Notholaena* R.Br., Rothfels & al., 2008; Kao & al., 2019; *Adiantopsis* Fée, Link-Pérez & al., 2011; *Doryopteris* J.Sm., Yesilyurt & al., 2015; Yesilyurt, 2023), the resurrection of several abandoned generic names (e.g., *Myriopteris* Fée, Grusz & Windham, 2013; *Ormopteris* J.Sm., Yesilyurt & al., 2015), and the recognition of a significant number of novel genera, including *Calciphilopteris* Yesilyurt & Schneider (Yesilyurt & Schneider, 2010), *Gaga* Pryer, F.-W. Li, & Windham (Li & al., 2012), *Baja* Windham & L.O.George (George & al., 2019), and *Mineirella* Ponce & Scataglini (Ponce & Scataglini, 2022).

Previous molecular work has shown that cheilanthoid ferns comprise seven major lineages (Fig. 1) (Windham & al., 2009). Calciphilopterids (previously referred to as the "*ludens* clade") and the bommeriids are successively sister to a clade containing all other species. The pellaeids are sister to myriopterids and together these are sister to the "*skinneri* clade". These three clades are, in turn, sister to notholaenids and the large hemionitid clade, which accounts for nearly 70% of cheilanthoid diversity (Windham & al., 2009; Schuettpelz & al., 2025). Six of these seven major lineages include at least one accepted, non-hybrid generic name typified on a known member of that clade (Fig. 1). The sole exception is the "*skinneri* clade" wherein representatives have been assigned to genera scattered across the fern phylogeny (Fig. 2). One nothogeneric name (×*Hemionanthes* Mickel)

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was typified on a potential member of this clade (×*H. gryphus* (Mickel) Mickel); however, its association with the "*skinneri* clade" requires confirmation (see below).

Despite being one of the smallest lineages of cheilanthoid ferns (estimated to include 4–5 species by Windham & al., 2009), members of the "*skinneri* clade" have had tortuous nomenclatural histories (Fig. 2). The best-known and most widely distributed member of the clade was initially described as *Pellaea skinneri* by Hooker (1858) (Fig. 2A). This species was transferred to *Cheilanthes* by Moore (1861), a generic assignment subsequently accepted by most taxonomists. Nevertheless, it has also been placed in *Allosorus* (Kuntze, 1891) and *Doryopteris* (Christensen, 1905). It was returned to *Cheilanthes* by Tryon & Tryon (1981) (as a nom. illeg. superfl.; Turland & al., 2018) and most recently, Christenhusz (in Christenhusz & al., 2018) moved the species to *Hemionitis*, enlarging this historically small, relatively well-defined genus to encompass all 500+ species of cheilanthoid ferns. Based on leaf and rhizome similarities, it has been hypothesized (e.g., Mickel, 1987; Mickel & Smith, 2004) that the closest relative of *Cheilanthes skinneri* is *C. lozanoi* (Maxon) R.M.Tryon & A.F.Tryon, whose nomenclatural history closely parallels that of *C. skinneri* (i.e., originally named in *Pellaea* and later transferred into *Cheilanthes*). Unpublished molecular data cited by Windham & al. (2009) indicated that these two taxa form a well-supported lineage (the "*skinneri* clade"), phylogenetically distant from the hemionitid clade that contains the type species of both *Cheilanthes* and *Hemionitis* (Fig. 1).

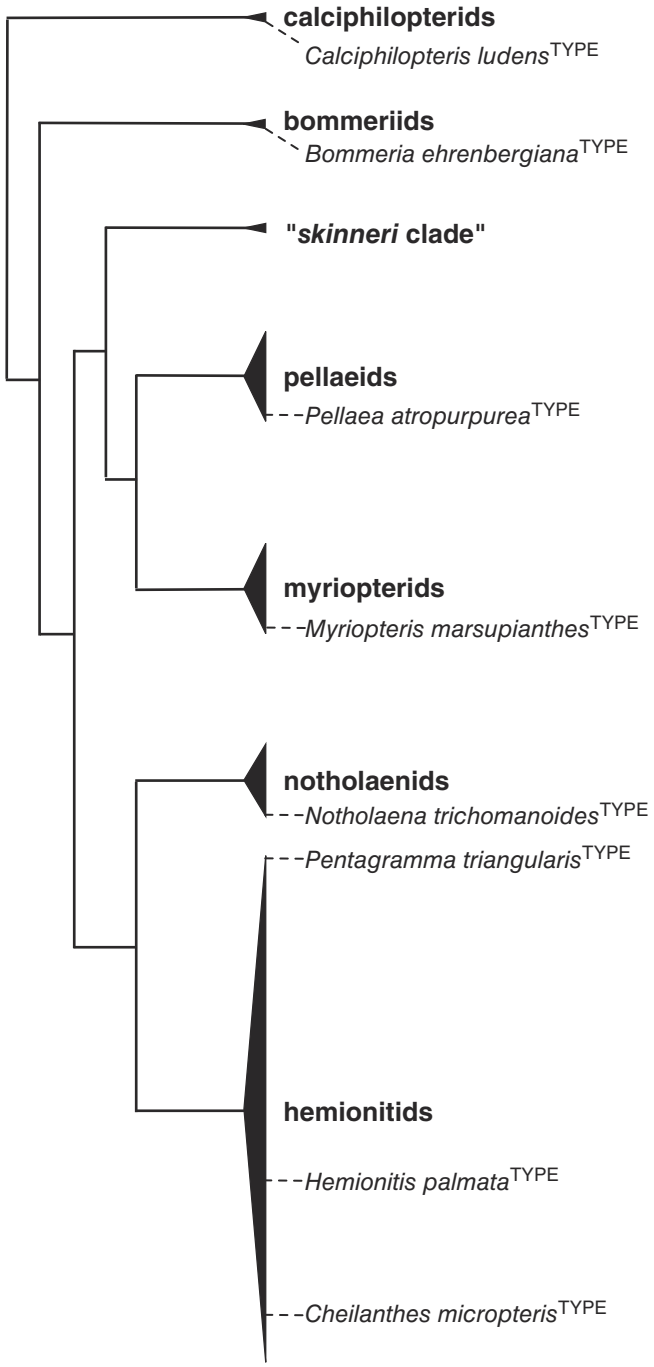


Fig. 1. Diversity and relationships of major cheilanthoid fern clades (adapted from Windham & al., 2009). Phylogenetic positions of relevant generitypes are indicated for each clade. Triangles at clade tips are roughly proportional in size to species diversity.

Morphology-focused studies by Mickel (1987, 1992) identified another possible member of the "*skinneri* clade", the taxon commonly known as *Hemionitis subcordata* (D.C. Eaton ex Davenp.) Mickel. Strikingly distinct from *Cheilanthes skinneri* (Fig. 3), this species has an equally complex nomenclatural history involving a divergent set of generic names (Fig. 2B). Originally named *Gymnogramma subcordata* by Davenport (1897), the species was transferred to *Gymnopteris* by Underwood (1902), then to *Coniogramme* by Maxon (1913). More recently, Mickel (in Giannasi & Mickel, 1979) assigned this species to *Hemionitis* but then later transferred it to *Cheilanthes* (Mickel, 1987). This taxonomic change followed Mickel's discovery of a taxon that he hypothesized to be a hybrid between the species commonly known as *Hemionitis subcordata* and *Cheilanthes skinneri*. This putative hybrid was strikingly intermediate in leaf dissection, sorus distribution, and pseudoindusium development between the proposed parental taxa (Fig. 3), both of which were present at the type locality. Based solely on these morphological intermediacies and co-occurrences, Mickel (1992) went on to describe this plant as an intergeneric hybrid between *Hemionitis* and *Cheilanthes* and proposed the nothogeneric condensed formula ×*Hemionanthes* to accommodate the only known species: ×*H. gryphus*.

In sum, preliminary data suggest that the "*skinneri* clade" comprises *Cheilanthes skinneri* (sensu Mickel, 1987), *C. lozanoi* (two varieties sensu Mickel & Smith, 2004), *Hemionitis subcordata*, and the monospecific putative "intergeneric" hybrid ×*Hemionanthes*. These unexpected connections among taxa previously placed in separate genera (Fig. 2), and even in different families (Pichi Sermolli, 1977), was the main justification used by Christenhusz & al. (2018) to ignore 250+ years of taxonomic research on cheilanthoid ferns and transfer all ca. 500 species into a single genus, *Hemionitis*. According to Christenhusz & al. (2018: 7), cheilanthoid ferns

"consisted of several genera that were found not to be monophyletic […]. As numerous hybrids are known, a number of intergeneric hybrids would additionally need to be coined. As this has been destabalising [*sic*] the nomenclature of genera like *Cheilanthes* Sw., *Doryopteris* J. Sm., and *Pellaea* Link., it seems reasonable to treat the entire subfamily as a single genus, stabalising [*sic*] this genus in future taxonomic study […]." The existence of intergeneric hybrids in this group has never been supported by any comprehensive phylogenetic study and, to date, remains purely speculative. Despite this, Christenhusz & al. (2018) cited the presumed occurrence of such hybrids as justification for merging all cheilanthoid ferns into a single genus, *Hemionitis*, to "stabilize" the taxonomy.

Here we specifically address the question of intergeneric hybridization among cheilanthoid ferns, focusing on the case of ×*Hemionanthes*, which has been considered the preeminent example of broad hybridization in the subfamily (Mickel, 1992; Mickel & Smith, 2004). We use three plastid (*rbcL*, *atpA*, *trnG-R*) and one nuclear marker (*gapCp*) to shed light on the phylogenetic relationships among members of the "*skinneri* clade" and the type species of other genera with which its members have been aligned in the past. We also integrate data from cytogenetics, ploidy estimates derived from spore measurements, sporophyte morphology, and geography to provide a framework for species delineation in the group.

■ MATERIALS AND METHODS

Taxon sampling. — Collections representing all potential members of the "*skinneri* clade" were obtained on loan from the following herbaria: ASU, DUKE, IND, MEXU, MO, P, and UC. These specimens were the data source for all analyses presented herein (Appendix 1). Outgroup taxa for the plastid phylogenetic analysis included the type species from each of the genera most often associated with members of this clade (*Cheilanthes micropteris*, *Hemionitis palmata*, and *Pellaea atropurpurea*; see Fig. 1) as well as representatives from every major cheilanthoid clade (sensu Windham & al., 2009), except for the more distantly related calciphilopterids (Fig. 1). For the nuclear phylogenetic analysis, *Pellaea atropurpurea* was selected as our outgroup because it is a member of the apparent sister group to the "*skinneri* clade" (sensu Windham & al., 2009). Vouchers, spore measurement data, and GenBank accession numbers are provided in Appendix 1.

Plastid loci: sequence alignment, datasets, and phylogenetic analysis. — The plastid loci examined here are the protein-coding genes *rbcL* and *atpA*, as well as the intergenic spacer *trnG-R*. Plastid markers from the "*skinneri* clade" taxa were extracted from draft plastome assemblies using Geneious v.2022.0.2 (Kearse & al., 2012). These plastomes were assembled from 150 bp paired-end Illumina reads using NOVOPlasty v.4.3.3 (Dierckxsens & al., 2016) with the *rbcL* sequence of *Hemionitis subcordata* (GenBank Accession

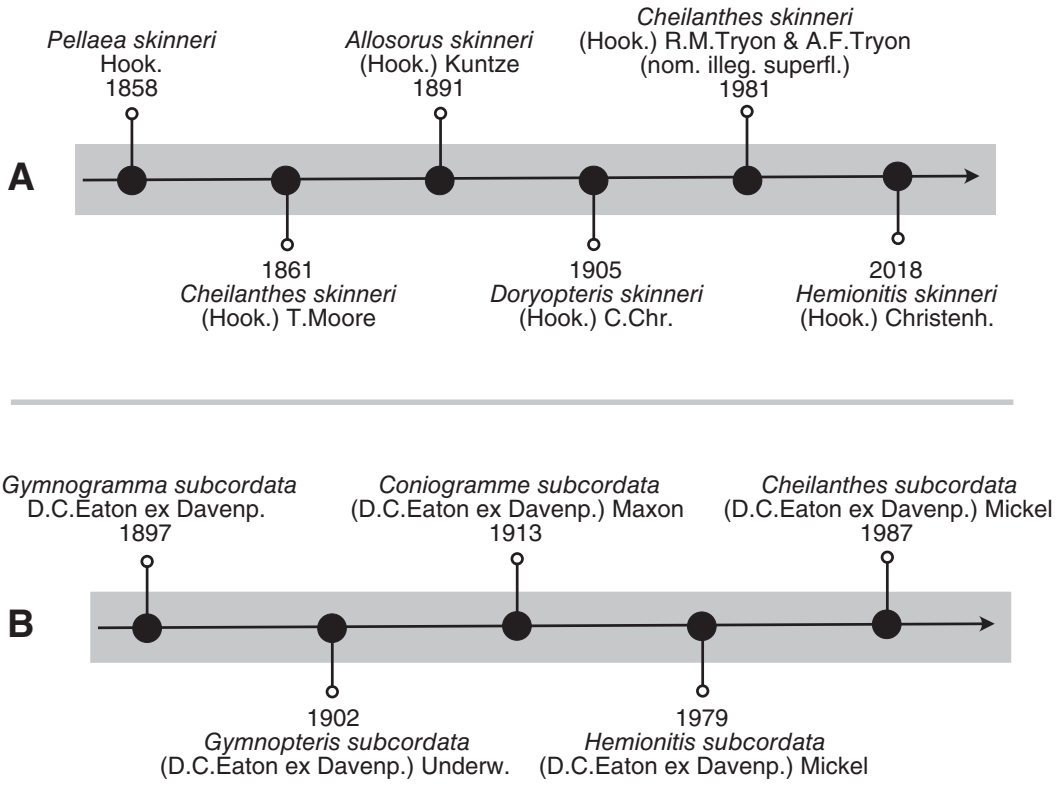


Fig. 2. Schematic timeline illustrating the complex nomenclatural history for two members of the "*skinneri* clade". **A**, *Cheilanthes skinneri*; **B**, *Hemionitis subcordata*.

no. MH173072.1) used as the seed sequence. Plastomes were annotated using the BLAST (Altschul & al., 1990) plugin in Geneious with the gene sequences of *H. subcordata* as reference. Plastid markers from outgroup taxa were obtained from GenBank (see Appendix 1 for accession numbers). Some accessions from GenBank, which were generated via PCR and Sanger sequencing and can vary in length and completeness, were first aligned to closely related reference plastomes in Geneious and then manually trimmed to include regions with low amounts of missing data. Each individual plastid locus was aligned using MAFFT v.7.505 (Katoh & Standley, 2013) with the following parameters: --maxiterate 1000 and --genafpair. Alignments are available at https://github.com/bfauskee/Ynesmexia-alignments-Taxon2025.git. Alignments for each locus were then manually trimmed again in Geneious, and then concatenated using AMAS (Boroweic, 2016) and partitioned by gene. Phylogenetic tree estimation was then conducted using both maximum likelihood and Bayesian inference. The maximum likelihood tree estimation was conducted in IQ-TREE2 v.2.2.2.7 (Minh & al., 2020). Substitution-model selection was carried out on each gene partition independently using the MFP+MERGE option. The best model for each gene partition was selected based on the Bayesian information criterion (BIC). Bayesian phylogenetic tree estimation was carried out in RevBayes v.1.2.3 (Höhna & al., 2016) using a general time-reversible (GTR) substitution model with a proportion of invariant sites (+I) and gamma-distributed rate heterogeneity across four rate classes. Two independent Markov chain Monte Carlo (MCMC) runs were performed for 1,000,000 generations, sampling every 100 generations, with the first 10% of samples being discarded as burn-in. Convergence between runs and sufficient parameter estimation were assessed manually in Tracer v.1.7.2 (Rambaut & al., 2018), ensuring that parameters had effective sampling sizes (ESS) ≥ 200. The resulting trees were then rooted with *Bommeria hispida* (bommeriid clade, Fig. 1) using the pxrr program in the Phyx package v.1.3 (Brown & al., 2017) and visualized in R using the ggtree v.3.20 package (Yu & al., 2017).

Nuclear locus: sequence alignment and phylogenetic analysis. — One nuclear locus (*gapCp*) was obtained for each member of the "*skinneri* clade" and one outgroup taxon (*Pellaea atropurpurea*) by first extracting DNA from silica-dried leaf tissue using a modified CTAB protocol (Doyle & Dickson, 1987; Beck & al., 2010). *gapCp* was amplified using the gapCpSh primers described in Rothfels & al. (2017) and the resulting amplicons were sequenced on a single SMRT cell on the PacBio RSII sequencer using P4-C2

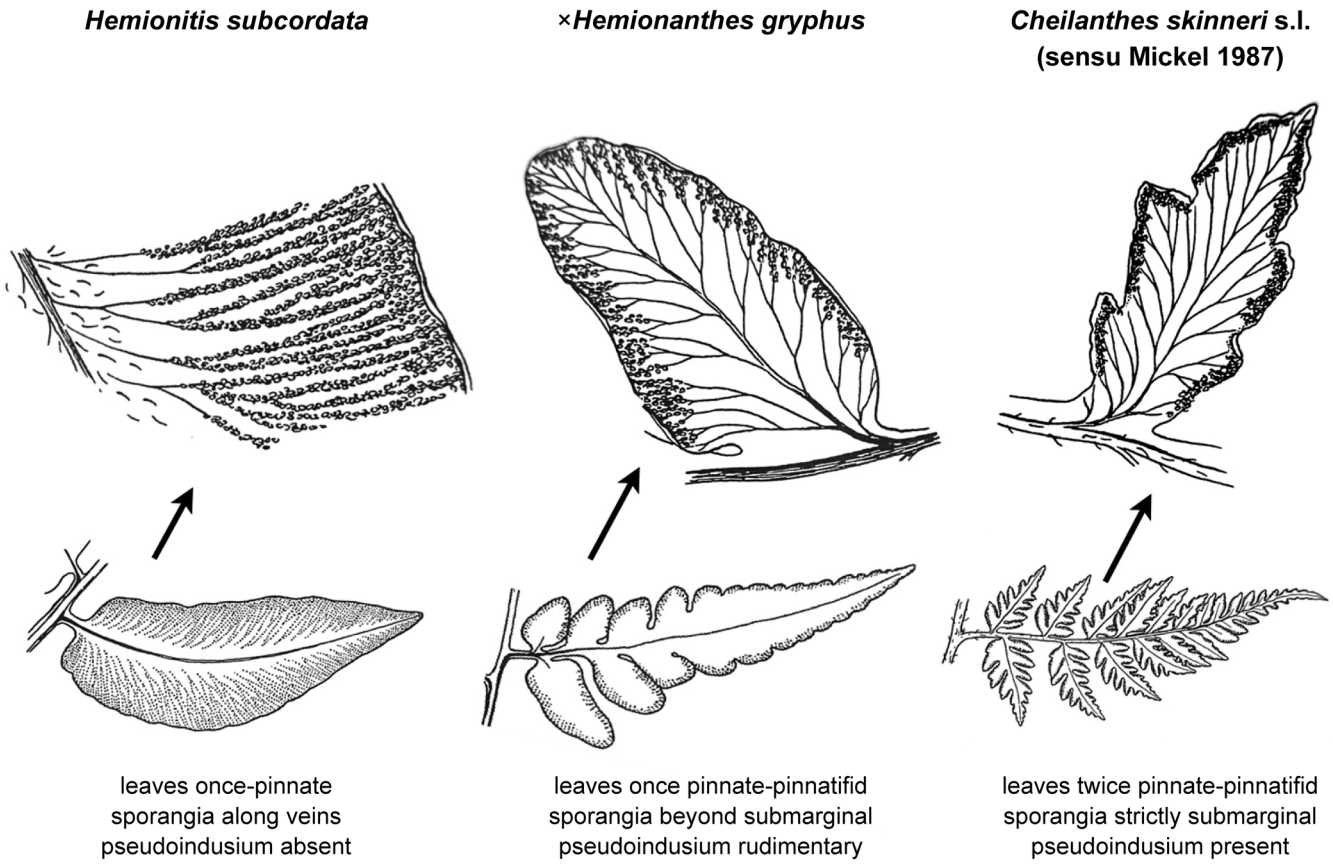


Fig. 3. Morphological intermediacy of putative "intergeneric" hybrid between *Hemionitis subcordata* and *Cheilanthes skinneri* s.l. described by Mickel (1992) as ×*Hemionanthes gryphus* (Mickel) Mickel. Drawings modified from Mickel (1987).

chemistry and a 3-h movie length. Sequence data were then analyzed using CCS SMRT ANALYSIS v.2.2.0 and four filtering passes. Library preparation and sequencing were performed at the Sequencing and Genomic Technologies Core Facility of the Duke University Center for Genomic and Computational Biology. Raw PacBio CCS fastq files were cleaned using the fastq filter in USEARCH (Edgar, 2010), set to remove all reads less than 400 bp or that had more than 10 expected errors. Reads were then demultiplexed using PURC v.1 (Rothfels & al., 2017) using three clustering rounds and a 95% similarity threshold. *gapCp* sequences were aligned with MAFFT v.7.505 (Katoh & Standley, 2013), with the following parameters: --maxiterate 1000 and --genafpair. The *gapCp* alignment is available at https://github.com/bfauskee/Ynesmexia-alignments-Taxon2025.git. Substitution model selection was carried out in IQ-TREE2 v.2.2.2.7 using the MFP option (Minh & al., 2020), with the HKY model being selected as the best fitting substitution model according to BIC. A maximum-likelihood phylogenetic tree with 1000 bootstrap replicates was then generated in IQ-TREE2 (Minh & al., 2020). Similarly, a Bayesian phylogenetic estimation was carried out in RevBayes v.1.2.3 (Höhna & al., 2016) using a HKY substitution model. Two independent MCMC runs were performed for 1,000,000 generations, sampling every 100 generations, with the first 10% of samples being discarded as burn-in. Convergence between runs and sufficient parameter estimation were assessed manually in Tracer v.1.7.2 (Rambaut & al., 2018), ensuring that parameters had effective sampling sizes (ESS) ≥ 200. The consensus (or maximum clade credibility for Bayesian inference) nuclear trees were then rooted with *Pellaea atropurpurea* (pellaeid clade, Fig. 1) using the pxrr program in the Phyx package v.1.3 (Brown & al., 2017) and visualized in R using the ggtree v.3.20 package (Yu & al., 2017).

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 by collaborators Carl Rothfels (Utah State Univ.) and James Beck (Wichita State Univ.). The leaves were immediately fixed in a mixture of absolute ethanol and glacial acetic acid (3:1). After 24 hours, they were removed from the fixative and stored (up to 10 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 per sporangium and average spore sizes were documented using the same microscopic equipment used for chromosome studies (see above). Twenty-five normally developed spores from each sporangium were randomly selected and measured using an ocular micrometer. Maximum diameter of the trilete spores was determined by spanning the exospore, visible as a dark ring just below the cristate spore surface. Sample means and standard deviations were calculated and visualized in R version 4.0.4 (R Core Team, 2021).

Distribution and morphology of cytotypes within "*skinneri* s.l." — The cytogenetic and spore analyses discussed above revealed the existence of diploid and tetraploid cytotypes among samples commonly identified as *Ynesmexia skinneri*. All chromosome and spore vouchers attributed to this species in the past 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 (2017) in conjunction with USGS topographic maps accessed via TopoZone (1999). Species distributions were mapped in R using the packages rnaturalearth v.1.0.1 (South, 2017), sf v.1.9-19 (Pebesma, 2018), and ggplot2 v.3.5.1 (Wickham, 2016). The same herbarium specimens used to map cytotype distributions were carefully examined to identify any morphological features consistently distinguishing diploids from tetraploids. These were documented photographically using a Canon EOS Rebel XSi digital camera mounted on a Leica MZ12.5 dissecting microscope.

■ RESULTS

Synopsis of nomenclatural changes required. — Our phylogenetic results (Fig. 4) confirm the monophyly of the "*skinneri* clade" with two robust subclades ("*subcordata*", "*seemannii*") and provide new insights into its members and their relationships. Nomenclatural changes necessitated by this study (detailed below in the Taxonomic Treatment) are summarized here to facilitate the presentation and discussion of our findings.

The "*skinneri* clade" is shown to be only distantly related to the type species of the genera to which its members are currently assigned (*Cheilanthes* and *Hemionitis*, see Fig. 1) (Windham & al., 2009), thus we have chosen to circumscribe the clade as a novel genus, herein and henceforth named *Ynesmexia* gen. nov. (see Taxonomic Treatment). The only potential competing name for this genus is ×*Hemionanthes*, which Mickel (1992) created to accommodate the "gryphon fern" (formerly *Cheilanthes gryphus*) on the presumption that the species was an intergeneric hybrid between *Hemionitis subcordata* and *Cheilanthes skinneri*. Given our results show that it is not an intergeneric hybrid, we cannot simply call this clade *Hemionanthes* (without the ×), because ×*Hemionanthes* is a condensed formula (Art. H.6 and H.8, Turland & al., 2018), and it can be used only for hybrids between *Hemionitis* and *Cheilanthes*.

Additional changes are necessary at the species level. Our data indicate that specimens traditionally identified as *Cheilanthes skinneri* represent two species: a diploid here

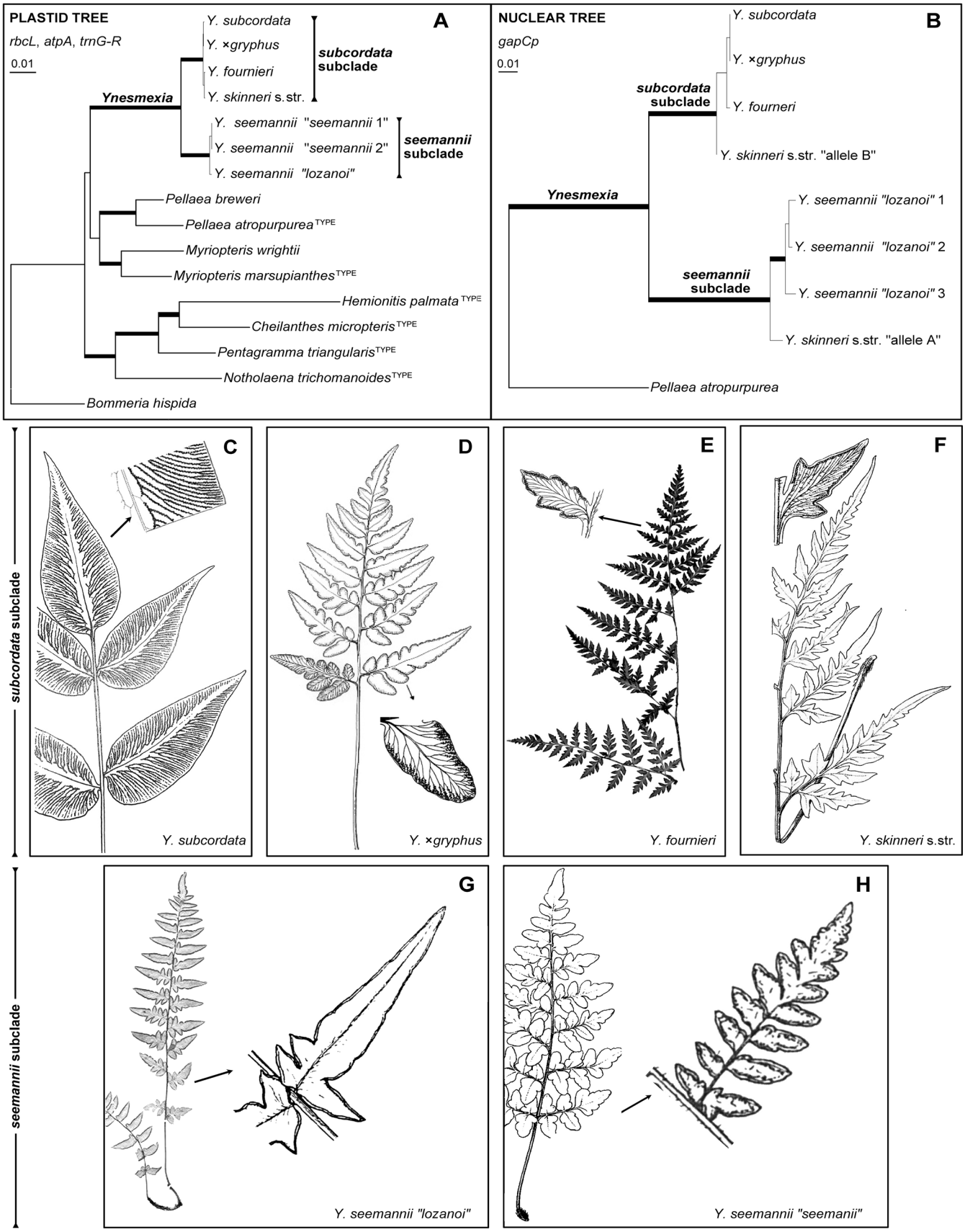


Fig. 4. Caption on opposite page.

referred to *Ynesmexia fournieri* (for the new combinations made in *Ynesmexia*, see Taxonomic Treatment) and an allotetraploid recognized as *Y. skinneri* s.str. Use of the new genus *Ynesmexia* also requires substitution of the epithet *seemannii* for what has been called *Cheilanthes lozanoi*. The first species to be recognized in this subclade was *Pellaea seemannii* Hook. (Hooker, 1858) (see Taxonomic Treatment). Maxon (1908) recognized a second species within this clade that he called *Pellaea lozanoi*, but most subsequent authors have considered these two taxa to be conspecific. When Tryon & Tryon (1981) moved this lineage to *Cheilanthes*, transfer of the older epithet *seemannii* was blocked by *Cheilanthes seemannii* Hook. (the basionym for *Adiantopsis seemannii* (Hook.) Maxon). With the transfer of the lineage to the new genus *Ynesmexia*, we resurrect the older epithet "*seemannii*" to represent this species.

Molecular phylogenetic analyses. — Our three-gene plastid phylogenetic analysis (Fig. 4A) recovered a robustly supported *Ynesmexia* (formerly "*skinneri*") clade weakly resolved as sister to members of the pellaeid and myriopterid lineages (69% bootstrap support). Both the maximum likelihood and Bayesian inference phylogenies were congruent in the relationships they resolved. *Ynesmexia* comprises two well-supported species groups, here referred to as the "*subcordata*" and "*seemannii*" subclades. The former includes plants of *Y. subcordata* (Fig. 4C), *Y.* ×*gryphus* (Fig. 4D), and two samples representing the morphological extremes observed within "*skinneri* s.l." (here labelled *Y. fournieri* [Fig. 4E] and *Y. skinneri* s.str. [Fig. 4F]). Our sampling of the "*seemannii* subclade" similarly encompassed the diversity of morphologies commonly treated as varieties of *Cheilanthes lozanoi*, here informally recognized as *Y. seemannii* "*lozanoi*" (Fig. 4G) and *Y. seemannii* "*seemannii*" (Fig. 4H). The "*subcordata* subclade" in particular exhibited very low levels of nucleotide divergence among its members, with a single parsimony-informative substitution across the 4147 bp present in the entire plastid dataset. Our nuclear *gapCp* trees (both maximum likelihood and Bayesian inference trees were completely congruent) (Fig. 4B) resolved the same two subclades within *Ynesmexia*, with one interesting twist. The sample morphologically most like the type specimen of *Y. skinneri* s.str. contained two divergent *gapCp* alleles. One of these (*Y. skinneri* s.str. "allele B") clustered with strong support with *Y. subcordata*, *Y.* ×*gryphus*, and *Y. fournieri* in the "*subcordata* subclade"; the other allele (*Y. skinneri* s.str. "allele A") was strongly supported as sister to *Y. seemannii* s.l. (Fig. 4B), suggesting a possible hybrid origin for *Y. skinneri* s.str.

Cytogenetic analyses. — Although the sampling is quite limited, we now have chromosome counts for all five taxa of *Ynesmexia* formally recognized herein (Fig. 5; Appendix 1). Four of these exhibited 30 pairs of chromosomes at diakinesis and were thus diploid. However, the only available sample of *Y. skinneri* s.str. formed 60 bivalents at diakinesis (Fig. 5D), making it tetraploid. Notably, cytogenetic preparations for *Y.* ×*gryphus* consistently showed normal chromosome pairing (Fig. 5B), despite substantial evidence that it represents a hybrid between two species previously assigned to disparate genera. Within the species here recognized as *Y. seemannii*, one of the informally recognized morphs ("*seemannii*" s.str.) included plants that are known diploids (Fig. 5E; Appendix 1). Chromosome numbers have not yet been determined for the "*lozanoi*" morph.

Spore studies. — The discovery that *Ynesmexia* included both diploids and polyploids prompted analyses of mature spores to determine whether the positive correlation between spore size and ploidy level commonly observed in ferns might prove useful for predicting ploidy and mapping cytotypes in the group. Casual observations of spores produced by our cytogenetic vouchers (i.e., the actual plants from which the chromosome counts were obtained) suggested the presence of such a correlation, with the documented tetraploid taxon (*Y. skinneri* s.str.; Fig. 5D) producing larger spores than any of the confirmed diploids (Fig. 5A–C,E). Violin plot analyses comparing the contents of individual sporangia from cytogenetic vouchers (white dots in Fig. 6) to those of morphologically similar herbarium specimens of each taxon (black dots) showed a clear pattern. Confirmed diploid individuals of three taxa (*Y. subcordata*, *Y. fournieri*, *Y. seemannii* "*seemannii*") showed average spore lengths (ASL) ranging from 29.9 to 38.4 µm whereas the ASL of the known tetraploid *Y. skinneri* s.str. ranged from 40.2 to 43.7 µm. Thus, in this

Fig. 4. Molecular phylogenetic analyses for *Ynesmexia* gen. nov. (formerly "*skinneri* clade"; **A** & **B**) and leaf silhouette depictions (**C**–**H**) for each taxon studied here (with image sources indicated). **A**, Three-locus plastid topology (*rbcL*, *atpA*, *trnG-R*); bolded branches with bootstrap support ≥90%; numbers following taxon names identify different individuals of the same taxon (see Appendix 1). Vouchers for the plastid tree are: *Y. fournieri* (*Breedlove 36706*: MEXU); *Y.* ×*gryphus* (*Beck 1171*: DUKE); *Y. seemannii* "*lozanoi*" (*Matuda 31543*: MEXU); *Y. seemannii* "*seemannii*" 1 (*R. Ramirez 3431*: MEXU); *Y. seemannii* "*seemannii*" 2 (*Rojas-Martínez 189*: MEXU); *Y. skinneri* (*F. Ventura A. 18905*: MEXU); *Y. subcordata* (*Ranker 727*: UC). **B**, Nuclear *gapCp* phylogeny; bolded branches with bootstrap support of at least 90%; numbers following taxon names indicate different individuals of the same taxon (see Appendix 1). Vouchers for the nuclear tree are: *Y. fournieri* (*Beck 1170*: DUKE); *Y.* ×*gryphus* (*Beck 1173*: DUKE); *Y. skinneri* [alleles A and B] (*C.J. Rothfels 2645*: DUKE); *Y. seemannii* "*lozanoi*" 1 (*C.J. Rothfels 3202*: DUKE); *Y. seemannii* "*lozanoi*" 2 (*C.J. Rothfels 3121*: DUKE); *Y. seemannii* "*lozanoi*" 3 (*Dyer 37*: DUKE); *Y. subcordata* (*Beck 1176*: DUKE). **C**, *Y. subcordata* (Mickel & Smith, 2004: fig. 1C, D). **D**, *Y.* ×*gryphus* (Mickel, 1987: figs. A, C; see also Mickel & Smith, 2004: fig. 149A, C). **E**, *Y. fournieri* (silhouette taken of *Roe & al. 1638*, LL00188648; inset from Mickel, 1987: fig. E). **F**, *Y. skinneri* (Hooker, 1858: 141, t. CXVIII. B, figs. 1, 2). **G**, *Y. seemannii "lozanoi"* (silhouette taken from *C.G. Pringle 13947*: VT001586, isotype of *Pellaea lozanoi* Maxon; inset modified from Mickel & Smith, 2004; fig. 81G). **H**, *Y. seemannii "seemannii"* (Hooker, 1858: 141, t. CXVII. B, fig. 1; inset modified from Mickel & Smith, 2004: fig. 81H).

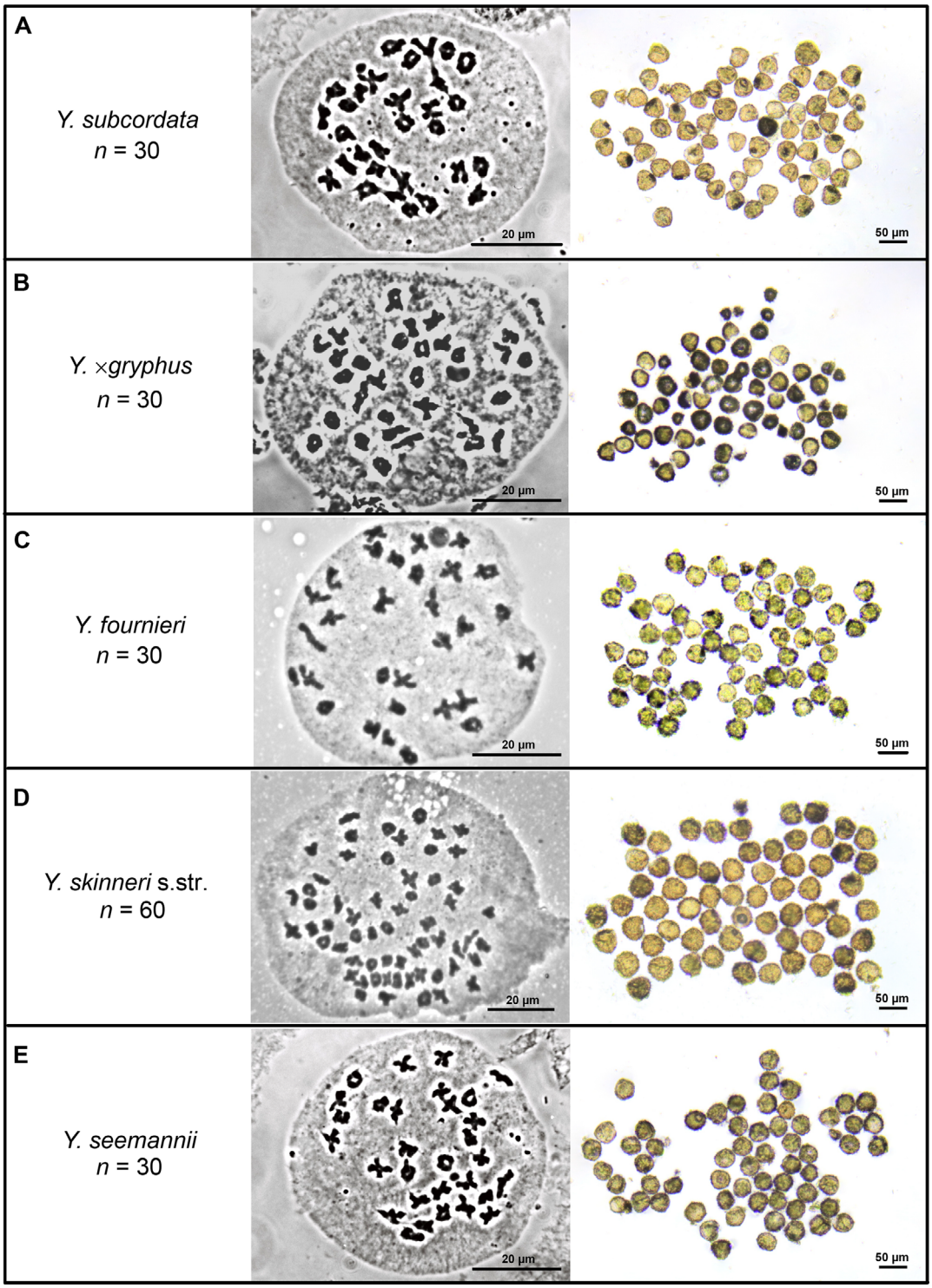


Fig. 5. Meiotic chromosomes at diakinesis and spore contents of individual sporangia for each of the five species recognized here in *Ynesmexia*. **A**, *Y. subcordata* with 30 bivalents from *Ranker & al. 729* (UC); 64 spores/sporangium with average spore length (from 6 individual sporangia) ranging from 36.1 to 38.2 µm from *Ranker & al. 729* (UC); see Appendix 1 (#96–101). **B**, *Y. ×gryphus* with 30 bivalents from *Ranker & Yatskievych 799* (KANU); 64 spores/sporangium with average spore length (from 2 individual sporangia) ranging from 35.5 to 35.9 µm from *Beck & al. 1171* (DUKE); see Appendix 1 (#27–28). **C**, *Y. fournieri* with 30 bivalents from *Rothfels & al. 3108* (DUKE, MEXU); 64 spores/sporangium with average spore length (from 5 individual sporangia) ranging from 29.9 to 35.4 µm from *Rothfels & al. 3108* (DUKE, MEXU); see Appendix 1 (#8–12). **D**, *Y. skinneri* s.str. with 60 bivalents from *Rothfels & al. 2645* (DUKE); 64 spores/sporangium with average spore length (from 4 individual sporangia) ranging from 40.2 to 43.7 µm from *Rothfels & al. 2645* (DUKE); see Appendix 1 (#71–74). **E**, *Y. seemannii* with 30 bivalents from *Yatskievych 89-259 & Gastony* (IND); 64 spores/sporangium with average spore length (from 1 sporangium) of 37.4 µm from *Yatskievych 89-259 & Gastony* (IND); see Appendix 1 (#59).

dataset, there was no overlap between the ASL of confirmed diploids and tetraploids. In fact, there was a gap of 1.8 µm, potentially making this a very useful character for estimating ploidy in *Ynesmexia*.

Expanding our spore analyses beyond the cytovouchers, we were able to develop a broader picture of each taxon. Additional sampling of *Ynesmexia subcordata* (black dots in Fig. 6) identified several collections with ASL slightly smaller than the chromosome vouchers (as low as 29.9 µm; Appendix 1), but the upper limit (38.2 µm) was unchanged, suggesting that the species (at least as sampled here) was uniformly diploid. Although unable to obtain spore data from the cytovouchers of *Y.* ×*gryphus* (all sporangia were too immature), we did sample nearly every fertile herbarium collection of this very rare taxon. With ASL ranging from 27.1 to 35.9 µm (Fig. 6; Appendix 1), all samples of *Y.* ×*gryphus* were inferred to be diploid. The proportion of small, malformed, and presumably inviable spores was often noticeably higher in these samples (Fig. 5B), likely reflecting some incompatibility between the parental genomes not apparent in their impeccable chromosome pairing.

A five-fold increase in spore sampling covering the geographic range of *Ynesmexia fournieri* yielded ASL ranging from 28.6 to 38.2 µm (Fig. 6; Appendix 1). Thus, this taxon, like *Y. subcordata* and *Y.* ×*gryphus*, was consistently diploid within the context of our sampling. A four-fold increase in geographic representation of *Y. skinneri* s.str. barely altered the range of ASL (40.1–43.8 µm), indicating that our sampling of this species was likely uniformly tetraploid. Based on the available data, we have drawn the ASL dividing line between diploid and tetraploid plants at 39.3 µm, midway across the small gap between the cytotypes (vertical gray line in Fig. 6). This provided a potential clue regarding the still unresolved taxonomy of *Y. seemannii*. The few chromosome counts available for *Y. seemannii* "*seemannii*" were diploid, and the ASL for the voucher specimens fell within the

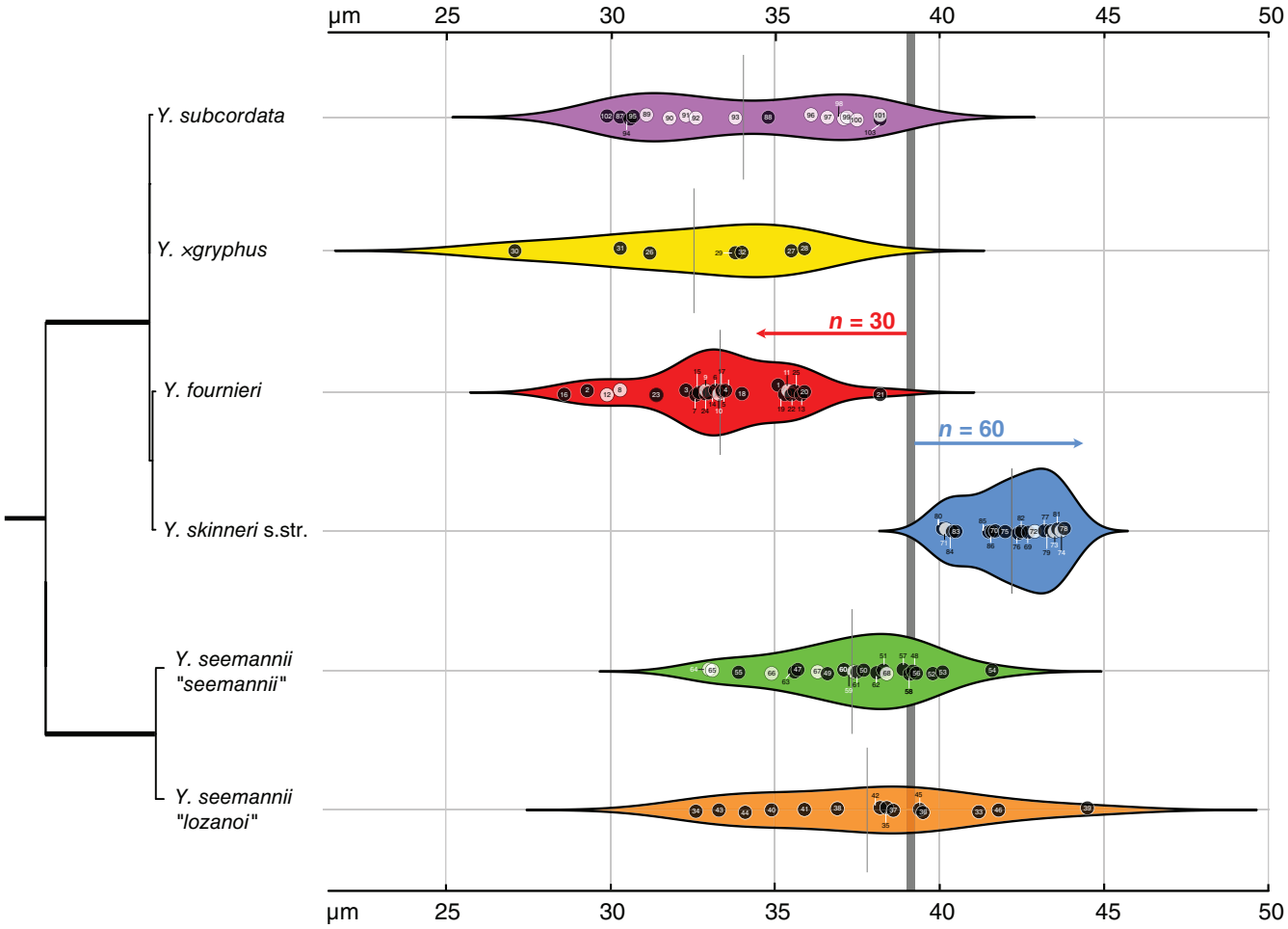


Fig. 6. Violin plots documenting the range of average spore lengths from individual sporangia for each taxon examined in this study. Skeleton phylogenetic tree to the left of the figure provides phylogenetic context. White dots represent average spore lengths from individual sporangia for cytogenetic vouchers; black dots represent average spore lengths from a single sporangium for morphologically similar herbarium specimens; each dot is numbered according to its unique identifier number linked to spore voucher data in Appendix 1. Average spore length for each taxon is shown as a thin vertical line drawn through each violin plot. A thickened vertical gray line centered at 39.3 µm across all plots represents estimated spore size threshold between diploid and tetraploid *Ynesmexia* (based on horizontal gray line in Fig. 7A).

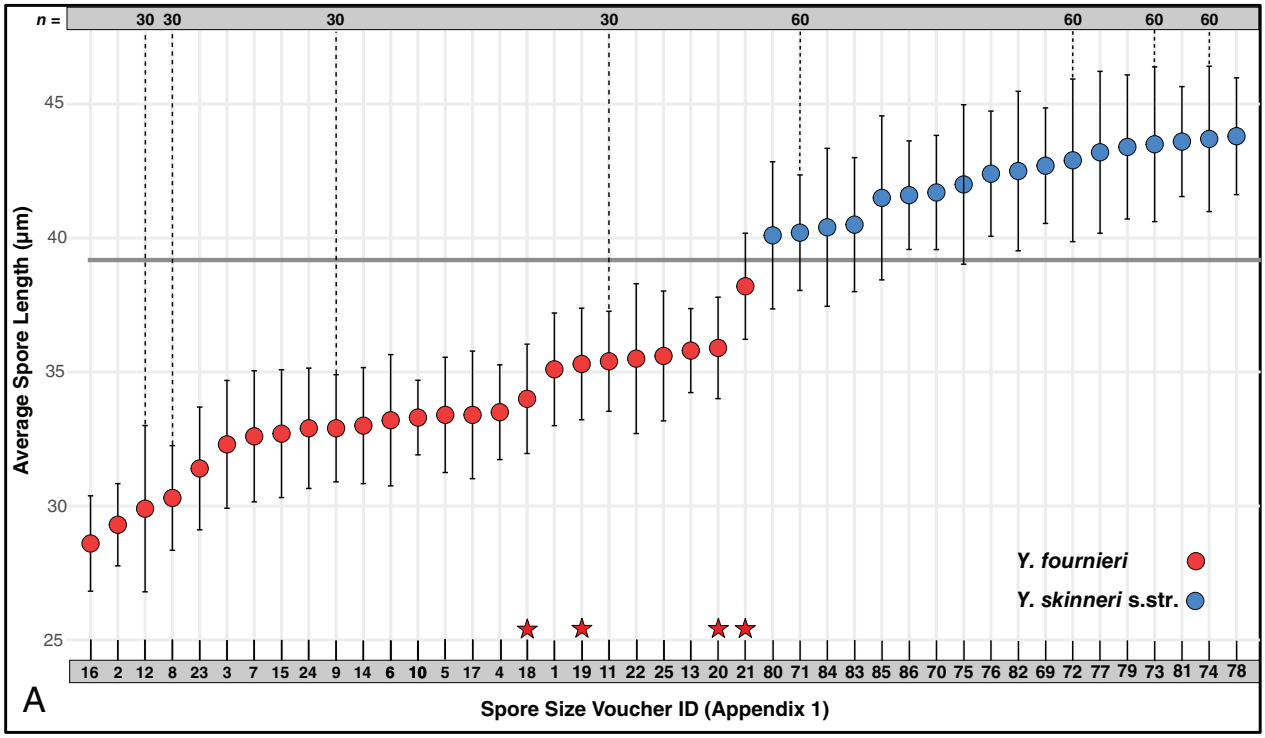
expected size range (33.0–38.4 µm; Fig. 6). However, the expanded geographic sampling of *Y. seemannii* "*seemannii*" encompassed several collections that breached the proposed diploid/tetraploid boundary, including one with an ASL of 41.6 µm. This might be dismissed as an unusually large-spored diploid given that it encroaches on the established range of tetraploids by just 0.4 µm, but the situation observed in the *Y. seemannii* "*lozanoi*" morph suggested another possibility. Although no chromosome counts were obtained for this taxon, it showed a very broad array of ASL (Fig. 6; Appendix 1) ranging from 32.6 µm (clearly diploid) to 44.5 µm (exceeding the ASL of the largest-spored tetraploid so far documented in *Ynesmexia*). Based on these data, we hypothesize that both morphs of *Y. seemannii* may be chromosomally variable, comprising diploid and tetraploid cytotypes. A complex set of hybridizations between the morphs of *Y. seemannii* and their constituent cytotypes might explain both the common observation of malformed spores in the group as well as our continuing inability to identify discrete taxa.

Spore studies provided the first broadly applicable character (ASL) useful for distinguishing *Ynesmexia fournieri* (diploid) from *Y. skinneri* s.str. (tetraploid). Spore data were also critical to constructing a list of correlated characters, determining the correct names for the taxa involved, and documenting geographic distributions. Using ASL as a basis for sorting herbarium specimens into diploid and tetraploid bins, we were able to substantially increase sample sizes for morphological analyses, improving both the quantity and quality of the characters studied. A variety of diagnostic features were identified (see below), somewhat surprising given that the two taxa have consistently been treated as a single, readily identifiable species.

The name originally applied to what we here recognize as a heteroploid species complex was *Pellaea skinneri* (Fig. 2A), published by Hooker (1858) based on a specimen collected by G. Skinner in Guatemala. Fourteen years later, E. Fournier (1872) published the name *P. flavescens* for a superficially similar plant collected by Bourgeau near Cuernavaca, Mexico. This was soon discovered to be a later homonym of *P. flavescens* Fée (1869), and the taxon was renamed *P. fournieri* Baker in 1874 (Hooker & Baker, 1874: 476), again based on Bourgeau's type collection. Baker's name never found broad acceptance in the botanical community and, for the past 150 years, *P. fournieri* has been considered a heterotypic synonym of *P. skinneri*, regardless of its generic assignment. To investigate the association between these names and the newly documented diploid and tetraploid cytotypes, we borrowed the holotype of *P. fournieri* from the Paris Herbarium (P01278110) with permission to remove several sporangia to determine ASL. Figure 7A provides a summary of spore size and chromosome number for the two cytotypes, with data derived from the holotype of *P. fournieri* marked by red stars. ASL for these four samples ranged from 34.0 to 38.4 µm, overlapping spore measurements from one of the diploid chromosome vouchers (Fig. 7A; voucher 11), and clearly positioned on the diploid side of the proposed boundary between diploid and tetraploid cytotypes (39.3 µm; Figs. 6, 7). Although we have not had a similar opportunity to measure spores from the holotype of *P. skinneri*, geography and ecology suggest that it represents the tetraploid cytotype.

Distribution and morphology of cytotypes within "*skinneri* s.l." — The geographic distribution of all "*skinneri* s.l." collections for which spore measurements are available is shown in Fig. 7B, with the populations color-coded by inferred ploidy and the type localities of the two validly published names indicated by stars. Based on the current dataset, there is no spatial overlap between the diploid and tetraploid cytotypes previously assigned to *Pellaea skinneri*. Diploids appear to be confined to the Pacific slope of Mexico, ranging from southern Sonora in the north to western Chiapas in the south. The type locality of *P. fournieri* falls within this range, supporting the hypothesis that this name applies to the diploid cytotype (Fig. 7B). By contrast, known and inferred tetraploids are primarily Central American, extending north to Veracruz, Mexico and south to Colombia. Unlike the diploids, putative tetraploids occur on both sides of the Continental Divide, with populations in Veracruz occupying the Caribbean lowlands. Considering both location and habitat, it appears likely that the name *P. skinneri* (based on a collection from the Caribbean slope of Guatemala) applies to the tetraploid cytotype (Fig. 7B).

Differences in average spore length coupled with the apparent geographic separation of the diploid and tetraploid cytotypes of "*skinneri* s.l." provided a solid basis for identifying additional morphological traits that distinguish these taxa. Although there was significant overlap in the degree of leaf dissection, this character was diagnostic for nearly half the specimens examined, with the tetraploids less divided (2-pinnate-pinnatifid to 3-pinnate; Fig. 4F) and the diploids more so (mostly 3–4-pinnate-pinnatifid; Fig. 4E). A partially correlated character involves the distribution of sporangia along the margins of fertile ultimate segments. In the tetraploid *Ynesmexia skinneri* s.str., the sporangia typically formed a wide, nearly continuous band paralleling the segment margins (Fig. 8A). About 20% of diploid *Y. fournieri* collections showed a very different pattern, with discrete sori forming an interrupted series encircling the segment margins (Fig. 8B). Although most diploids have sori partially to wholly confluent at maturity, these can still be distinguished from the truly continuous sori of the tetraploid by examining the pseudoindusia as viewed from the adaxial leaf surface. In the tetraploid, the pseudoindusia form smoothly integrated, entire or slightly crenate linear flaps arising from a ± continuous sporangial receptacle formed by laterally expanded (Y-shaped) vein tips (Fig. 8C). By contrast, even the diploids with fully confluent sori usually show evidence that they originated as distinct sporangial clusters. In nearly all diploid specimens examined, the pseudoindusia either appear as separate flaps (relatively rare) or form a partially fused, scalloped margin arising from discrete vein tips (Fig. 8D). This appears to be the single most useful



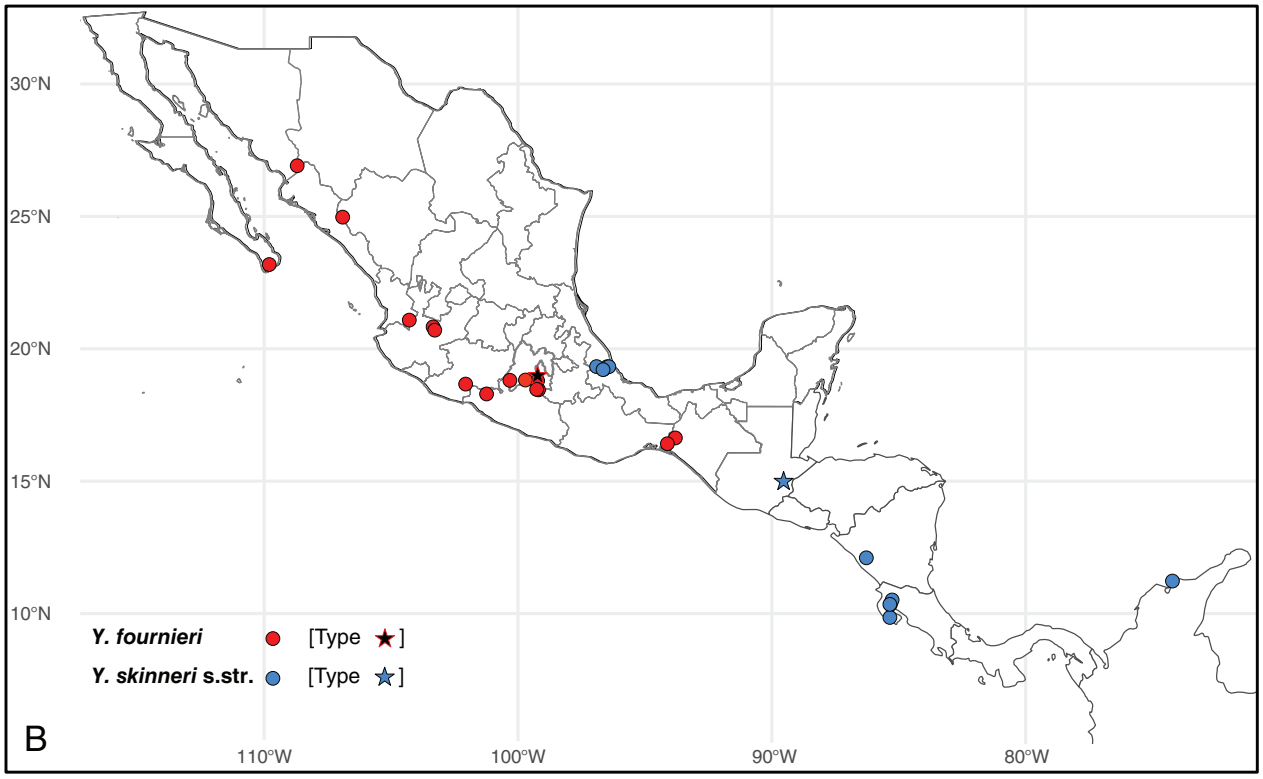


Fig. 7. Spore data and geographical distribution for *Ynesmexia fournieri* and *Y. skinneri* s.str. **A**, Average spore lengths (in µm) for specimens of *Y. fournieri* (red circles) and *Y. skinneri* s.str. (blue circles); error bars indicate one standard deviation. Number below each sample is a unique identifier linked to spore voucher data in Appendix 1; red stars above sample identifier on x-axis indicate samples taken from holotype specimen of *Y. fournieri* (*Bourgeau s.n*. (P); Appendix 1). Numbers in bar across top indicate samples derived from chromosome vouchers: 30 = diploid (*C.J. Rothfels 3108* (DUKE, MEXU)), 60 = tetraploid (*C.J. Rothfels 2645* (DUKE)). Horizontal gray line represents estimated spore size threshold between diploid *Y. fournieri* and tetraploid *Y. skinneri* s.str. **B**, Geographic distributions of *Y. fournieri* (red circles) and *Y. skinneri* s.str. (blue circles) in the Americas. Type localities for the two species are identified by colored stars.

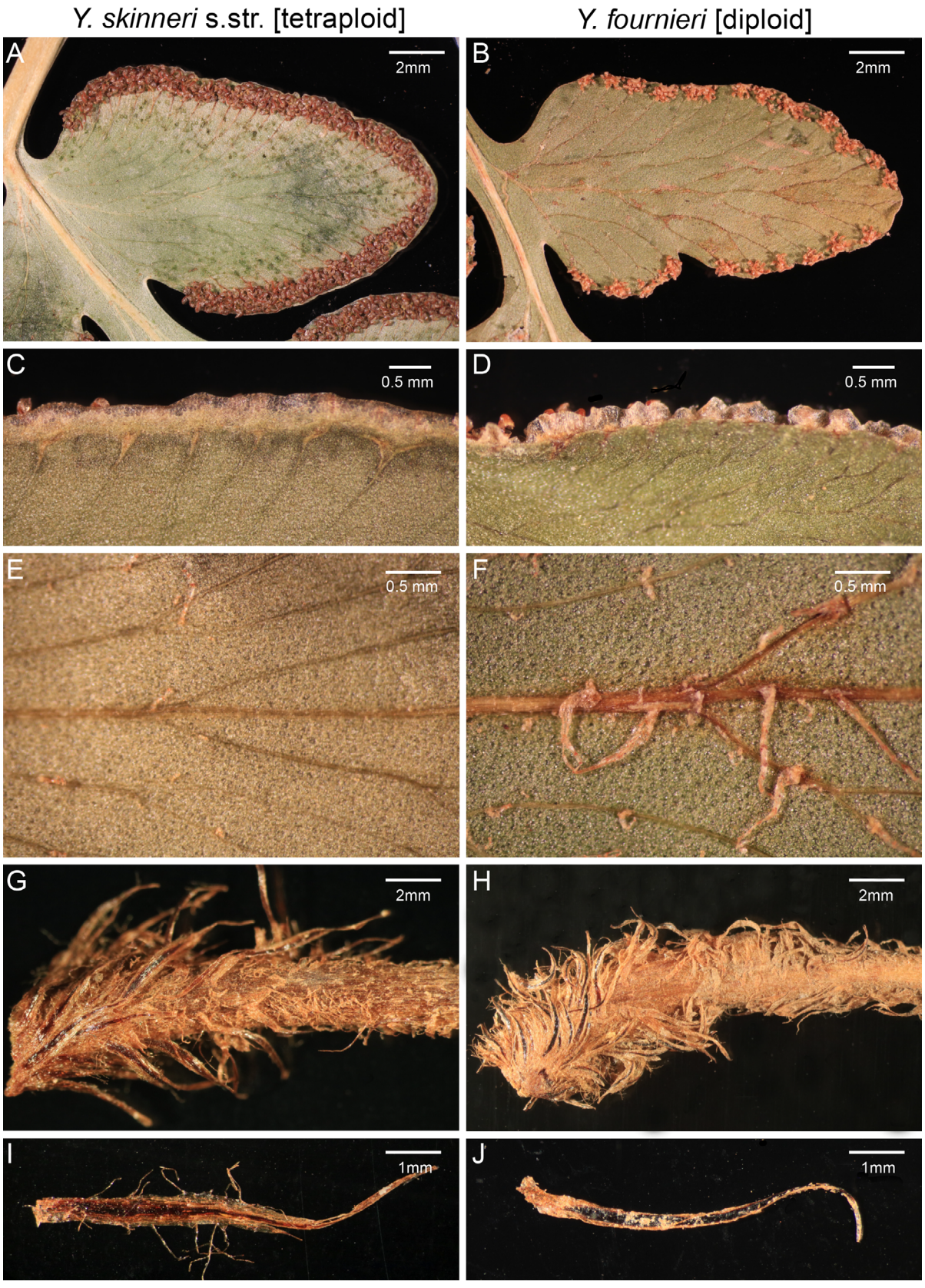


Fig. 8. Morphological comparison of *Ynesmexia skinneri* s.str. and *Y. fournieri*. **A** & **B**, Abaxial view of fertile ultimate segment; **C** & **D**, Adaxial view of marginal pseudoindusia; **E** & **F**, Abaxial view of distal portion of ultimate segment; **G** & **H**, Petiole base; **I** & **J**, Representative bicolored scale from petiole base.

morphological feature for distinguishing diploid *Y. fournieri* from tetraploid *Y. skinneri* s.str.

Distinctions drawn based on blade dissection, soral, pseudoindusial and spore traits are supported by a series of indument characters as well. Abaxial blade surfaces of the tetraploids are very sparsely hairy distally (Fig. 8E) and often somewhat glaucous (Fig. 8A). Diploids have a more conspicuous abaxial indument throughout, consisting of both hairs and linear scales (Fig. 8F) and are never glaucous. Petiole bases of both cytotypes exhibit a dense covering of scales (both bicolored and concolored) and hairs. However, the scales are usually completely supplanted by hairs within the first few centimeters in the tetraploid (Fig. 8G), whereas multiseriate scales three or more cells wide are common distally on the petioles (and rachises) of diploid plants (Fig. 8H). The bicolored petiole base scales provide additional distinguishing features. Among the tetraploids, the dark central stripe of these scales is poorly differentiated, grading into the broad, brown margins that are usually long-ciliate on the proximal half (Fig. 8I). By contrast, the bicolored petiole base scales of the diploids exhibit a sharp distinction between the blackish central stripe and the narrow, tan margins that are eciliate (Fig. 8J) or ciliate only near the point of attachment.

■ DISCUSSION

Taxonomic synopsis. — By integrating phylogenetic analyses of plastid and nuclear DNA sequences (Fig. 4A,B) with cytological and spore data (Figs. 5–7A), geographic distributions (Fig. 7B), and morphology (Fig. 8), we have made significant progress toward understanding what was formerly called the "*skinneri* clade" (herein the genus *Ynesmexia*). Our findings strongly support the robust monophyly of this group, which comprises two well-supported subclades ("*subcordata*", "*seemannii*"). The more diverse of the two lineages (the "*subcordata* subclade") comprises *Y. subcordata*, *Y.* ×*gryphus*, *Y. fournieri*, and *Y. skinneri* s.str. (Fig. 4C–F). The other subclade contains only *Y. seemannii*, but this taxon is quite diverse, encompassing two morphological extremes (and a confusing array of intermediates) that previous authors have treated as varieties of *Cheilanthes lozanoi* (Fig. 4G,H).

Molecular phylogenetic analyses. — The five species of *Ynesmexia* recognized here differ from one another so remarkably in their morphology (Fig. 4C–H) that they were previously recognized as belonging in separate genera (*Cheilanthes*, *Hemionitis*), and even in different families (Pichi Sermolli, 1977). At one morphological extreme, *Y. subcordata* (Fig. 4C, previously *Hemionitis subcordata*), displays once-pinnate leaves with sori that follow the veins nearly up to the midvein (Figs. 3A, 4C). At the other, *Y. fournieri* has leaves that can be up to 4-pinnate-pinnatifid and have sori restricted to the leaf margins (Figs. 3C, 4E). Given the remarkable morphological diversity encompassed by *Ynesmexia* (Fig. 4C–H), it was particularly surprising to us to recover such low phylogenetic signal in both our plastid and nuclear analyses. Using morphology to distinguish among fern species can be challenging because of the cryptic nature of many of the diagnostic characters. The availability of some molecular data (even just *rbcL*) often serves as an independent test of species delimitation hypotheses based solely on morphology (e.g., Smith & al., 2001). For example, *rbcL* sequence divergence values of 0.3%–0.5% (four to seven nucleotides) between two morphologically distinct varieties of *Onoclea sensibilis* L. prompted a new combination to accommodate their recognition at the species level (Gastony & Ungerer, 1997). Despite the diverse morphologies present within the "*subcordata* subclade" (Fig. 4C–F), their *rbcL*, *atpA*, and *trnG-R* sequences differ at only 8 of 4147 positions (0.2%), with only one of these differences representing a parsimony-informative site. On a per-gene basis, there is only one difference in their *rbcL* sequences, two in *atpA*, and five in *trnG-R*.

Our discovery of two divergent alleles in the nuclear *gapCp* phylogeny for *Ynesmexia skinneri* s.str. (Fig. 4B) from the same individual that was the voucher for our tetraploid chromosome count (*C.J. Rothfels 2645* (DUKE), Fig. 5; see Appendix 1) was unexpected. One allele (A) is sister to the *Y. seemannii* subclade with robust support and the other allele (B) clusters with *Y. fournieri* + *Y.* ×*gryphus* + *Y. subcordata* (Fig. 4B). From this, we hypothesize that *Y. skinneri* s.str. is an allotetraploid and that the newly recognized diploid *Y. fournieri* is likely its "*subcordata* subclade" parent. The leaf blades of tetraploid *Y. skinneri* s.str. (Fig. 4F) are less dissected than those of *Y. fournieri* (Fig. 4E), and one possible origin might have involved *Y. fournieri* and the "*lozanoi*" morph of *Y. seemannii* (Fig. 4G). This seems unlikely, however, in light of the abundance of trichomes on the ultimate segments of *Y. seemannii* and their very sparse occurrence in *Y. skinneri* s.str. (Fig. 8E). Another possibility is that *Y. skinneri* is an allotetraploid hybrid that formed prior to the diversification of the extant species of *Ynesmexia*. These scenarios are explored in further detail in an upcoming manuscript (Fauskee & al., in prep.).

The "*seemannii* subclade". — Although morphological variability within the "*seemannii* subclade" (Fig. 4G,H) has long been formally recognized the varietal level, Mickel & Smith (2004) suggested that the two varieties needed more careful study to determine if the variation seen throughout their Mexican distribution might instead represent 2–3 species with hybrid intermediates. In our study, we observed a rich continuum of morphologies transitional between the once-pinnate to pinnate-pinnatifid "var. *lozanoi*" (Fig. 4G) and the bipinnate to 2-pinnate-pinnatifid "var. *seemannii*" (Fig. 4H). In addition, quite a few collections had aborted spores, suggesting that hybridization may be widespread within the subclade. Our survey of mean spore size across specimens identified as either the "*lozanoi*" extreme or the "*seemannii*" extreme documented a very broad and completely overlapping range of spore sizes from 32.6–44.5 µm; see Fig. 6; Appendix 1). The range of ASL for both morphological extremes extend from the range of the known diploids (*Y. subcordata*,

Y. ×*gryphus*, *Y. fournieri*) into and even beyond the range of the tetraploid *Y. skinneri* s.str. (Fig. 6). This broad range of spore sizes suggests that there is cryptic diversity present, likely involving polyploidy and hybridization. Additional chromosome studies are needed to confirm whether multiple ploidy levels indeed exist within *Y. seemannii*. If so, additional nuclear molecular data either from target-enrichment or amplicon sequencing would be integral to determining whether potential polyploids are auto- or allopolyploids. Because of the lack of taxonomic resolution within the "*seemannii* subclade", we agree with Mickel & Smith (2004) that more analyses are necessary. For the time being we do not see sufficient evidence to formally recognize the two morphological extremes, treating them here simply as "morphs": *Y. seemannii* "*seemannii*" and *Y. seemannii* "*lozanoi*".

Concluding remarks on Mickel's "gryphon fern". — Mickel (1987) described a species displaying a phenotype intermediate between *Ynesmexia subcordata* (then *Hemionitis subcordata*) and *Y. fournieri* (then *Cheilanthes skinneri*) in nearly every morphological feature. This resulted in its description as a putative intergeneric hybrid ×*Hemionanthes gryphus*, with the specific epithet drawing from the word "gryphon" or "griffin", a mythological creature that is part lion and part eagle, hence "an archetype of the union of incompatibles". Our phylogenetic data here show that *Y.*× *gryphus* is not an intergeneric hybrid, but rather is nested firmly within the "*subcordata* subclade" of *Ynesmexia*. Although Mickel (1987, 1992) originally proposed *H. subcordata* and *C. skinneri* as the probable parents of this taxon, this hypothesis must be modified considering our cytogenetic results indicate that the latter taxon contains two cytotypes treated herein as distinct species. Since *Y.* ×*gryphus* has been shown to be diploid (Fig. 5B), both its parents must be diploid as well. Therefore, tetraploid *Y. skinneri* s.str. is excluded from consideration, and the revised proposed parentage of *Y.* ×*gryphus* is *Y. fournieri* and *Y. subcordata*.

Ynesmexia ×*gryphus* is a documented diploid with normal chromosome pairing during meiosis (Fig. 5B). Its average spore lengths are completely congruent with those of other known diploids in the genus except for one collection that is slightly smaller than normal (Fig. 6). This supports the hypothesis that *Y.* ×*gryphus* is a fertile homoploid hybrid, a rare occurrence in ferns (Sigel, 2016). This is not too surprising, however, given the lack of sequence diversity observed among *Y.* ×*gryphus* and its proposed parents (Fig. 4A,B). The fertility of homoploid hybrids is inversely related to the genetic divergence between their progenitors (Mallet, 2005). Rare, completely fertile homoploid hybrids (e.g., *Pteris quadriaurita* × *multiaurita*; Walker, 1958, 1962) are known from crosses between sexual species with low genetic divergence and exhibit full pairing of homeologs at meiosis (as seen here for *Y.* ×*gryphus* in Fig. 5B). What is most striking here is the breadth of morphological diversity across these three taxa. *Ynesmexia fournieri* and *Y. subcordata* likely diverged recently and are actively hybridizing to form *Y.* ×*gryphus*. The fact that these three taxa are indistinguishable in a plastid phylogeny (Fig. 4A) may implicate chloroplast capture, but additional chloroplast loci are necessary to test this hypothesis.

Implications for the generic taxonomy of cheilanthoid ferns. — Tremendous progress has been made over the past 25 years in our understanding of the taxonomy of cheilanthoid ferns, leading to the circumscription of several novel, resurrected, and robustly monophyletic genera (Rothfels & al., 2008; Yesilyurt & Schneider, 2010; Link-Pérez & al., 2011; Li & al., 2012; Grusz & Windham, 2013; Yesilyurt & al., 2015; George & al., 2019; Kao & al., 2019; Ponce & Scataglini, 2022). These studies have advanced a nuanced understanding of evolutionary relationships within Cheilanthoideae, firmly moving closer to a monophyletic *Cheilanthes* (see Schuettpelz & al., 2025). By contrast, Christenhusz & al. (2018) proposed what is in our opinion a heavy-handed approach, dismantling decades of systematic progress by lumping the entire Cheilanthoideae into *Hemionitis*. This sweeping taxonomic revision—creating 468 new nomenclatural combinations—was driven by speculation that intergeneric hybridization had occurred between *Cheilanthes* and *Hemionitis*, despite the complete lack of phylogenetic evidence. Our analyses collectively refute this claim of Cheilanthoideae harboring deeply diverged intergeneric hybrids; *Ynesmexia* ×*gryphus* (formerly ×*Hemionanthes gryphus*) is neither a deeply diverged hybrid nor intergeneric. Instead, it is a homoploid hybrid maintaining fertility with its closely related progenitors with no evidence to support its treatment as an intergeneric anomaly (Figs. 4, 5). The Christenhusz & al. (2018) taxonomic treatment of cheilanthoid ferns thus appears to be a scientifically unsupported taxonomic overhaul that disregards both evidence and progress in cheilanthoid fern systematics. Such broad generic concepts are out-of-step with past and present treatments (Schuettpelz & al., 2018). Based on the findings presented here, we unequivocally reject the Christenhusz & al. (2018) classification. We advocate for a return to taxonomy grounded in robust phylogenetic evidence and detailed morphological study, recognizing the meticulous research that has clarified cheilanthoid fern relationships over recent decades.

■ TAXONOMIC TREATMENT

Ynesmexia Fauskee & Windham, **gen. nov.** – Type: *Ynesmexia skinneri* (Hook.) Fauskee & Windham (≡ *Pellaea skinneri* Hook.).

Monophyletic (Fig. 4) based on included sampling (5 of 5 species).

Diagnosis. – A small group of morphologically disparate species assigned to *Cheilanthes* and *Hemionitis* by recent authors (but the majority originally described in *Pellaea*). Differing from *Cheilanthes* s.str. (Schuettpelz & al., 2025) by having 64 (vs. 32 or 16) spores per sporangium, mostly pale-colored, dull (vs. dark brown, often lustrous) petioles and rachises, and

a primarily North American (vs. South American and Australasian) distribution. One species (*Y. subcordata*) usually included in *Hemionitis* s.str. but separable from that genus by having 1-pinnate leaves with glabrescent blade surfaces. Differing from *Pellaea* s.str. (Schuettpelz & al., 2025) by having the ultimate segments mostly broadly attached and sessile (vs. abruptly narrowed and stalked), chartaceous (vs. thick and leathery), with the secondary veins apparent on one or both surfaces (vs. obscure in mature leaves).

Distribution. – (compiled from World Ferns database; Hassler, 1994–2024) México (Baja California Norte, Baja California Sur, Chiapas, Chihuahua, Colima, Ciudad de México, Durango, Guanajuato, Guerrero, Jalisco, México Distrito Federal, Estado de México, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sinaloa, Sonora, Tamaulipas, Tres Marías Islands, Veracruz, Zacatecas); Guatemala; El Salvador; Nicaragua; Costa Rica; Panama; Colombia (Magdalena).

Etymology. – The genus *Ynesmexia* is named in honor of U.S.-born Mexican American Ynés Mexía (1870–1938), who began her short scientific career at age 51, conducting botanical expeditions across North, Central, and South America. Known for saying "I don't think there's any place in the world where a woman can't venture", she became one of the most accomplished plant collectors of her time both in terms of the number of plant specimens she collected (>145,000) and the miles traveled on her expeditions. She discovered over 500 new plant species of which 50 are named in her honor. Dozens of specimens of cheilanthoid ferns collected by Ynés Mexía are deposited at MO and UC, including members of the new genus named here in her honor. For more information on Ynés Mexía, see Kiernan (2015).

Ynesmexia fournieri (Baker) Fauskee & Windham, **comb. nov.** ≡ *Pellaea flavescens* E.Fourn., Mexic. Pl. 1: 119. 1872, nom. illeg., non Fée 1869, ≡ *Pellaea fournieri* Baker in Hooker & Baker, Syn. Fil., ed. 2: 476. 1874 ≡ *Allosorus fournieri* (Baker) Kuntze, Revis. Gen. Pl. 2: 806. 1891 ≡ *Doryopteris fournieri* (Baker) C.Chr., Index Fil.: 244. 1905 – Holotype: Mexico, Cuernavaca, *Bourgeau s.n*. (P barcode P01278110!).

Ynesmexia* ×*gryphus (Mickel) Fauskee & Windham, **comb. nov.** ≡ *Cheilanthes gryphus* Mickel in Amer. Fern J. 77: 112. 1987 ≡ ×*Hemionanthes gryphus* (Mickel) Mickel in McVaugh, Flora Novo-Galiciana 17: 288. 1992 ≡ *Hemionitis* ×*gryphus* (Mickel) Christenh. in Christenhusz & al., Global Fl. 4: 14. 2018 – Holotype: Mexico, Colima, low mountain summits 7 mi N of Santiago, road to Durazno, Jalisco, via the bridge over Rio Cihuatlan, *McVaugh 15908* (MICH barcode 1191314 [image!]).

Ynesmexia seemannii (Hook.) Fauskee & Windham, **comb. nov.** ≡ *Pellaea seemannii* Hook., Sp. Fil. 2: 141. 1858 ≡ *Cheilanthes lozanoi* var. *seemannii* (Hook.) Mickel & Beitel in Mem. New York Bot. Gard. 46: 118. 1988 – Holotype: Mexico, Sinaloa, Mazatlan, *Seemann 1447* (K barcode K000633020 [image!]).

= *Pellaea lozanoi* Maxon in Contr. U. S. Natl. Herb. 10: 500. 1908 ≡ *Cheilanthes lozanoi* (Maxon) R.M.Tryon & A.F. Tryon in Rhodora 83: 133. 1981 ≡ *Hemionitis lozanoi* (Maxon) Christenh. in Christenhusz & al., Global Fl. 4: 17. 2018 – Holotype: Mexico, Guerrero, near Iguala, *Lozano s.n*. [*Pringle 13947*] (US barcode 00142026 [image!]).

Ynesmexia skinneri (Hook.) Fauskee & Windham, **comb. nov**. ≡ *Pellaea skinneri* Hook., Sp. Fil. 2: 141. 1858 ≡ *Cheilanthes skinneri* (Hook.) T.Moore, Index Filic.: 253. 1861 ≡ *Allosorus skinneri* (Hook.) Kuntze, Revis. Gen. Pl. 2: 806. 1891 ≡ *Doryopteris skinneri* (Hook.) C.Chr., Index Fil.: 245. 1905 ≡ *Cheilanthes skinneri* (Hook.) R.M.Tryon & A.F.Tryon in Rhodora 83: 133. 1981, nom. illeg. superfl., non T.Moore 1861 ≡ *Hemionitis skinneri* (Hook.) Christenh. in Christenhusz & al., Global Fl. 4: 21. 2018 – Holotype: Guatemala, *Skinner s.n*. (K barcode K000633015 [image!]).

Ynesmexia subcordata (D.C.Eaton ex Davenp.) Fauskee & Windham, **comb. nov.** ≡ *Gymnogramma subcordata* D.C.Eaton ex Davenp. in Contr. U. S. Natl. Herb. 5: 138. 1897 ≡ *Coniogramme subcordata* (D.C.Eaton ex Davenp.) Maxon in Contr. U. S. Natl. Herb. 17: 174. 1913 ≡ *Coniogramme americana* Maxon in Contr. U. S. Natl. Herb. 17: 607. 1916, nom. illeg. superfl. ≡ *Hemionitis subcordata* (D.C.Eaton ex Davenp.) Mickel in Brittonia 31: 411. 1979 ≡ *Cheilanthes subcordata* (D.C.Eaton ex Davenp.) Mickel in Amer. Fern J. 77: 112. 1987 – Lectotype (designated by Mickel & Beitel in Mem. New York Bot. Gard. 46: 209. 1988): Mexico, Ymala and Lodiego, *E. Palmer 1572* (US barcode 00731129 [image!]).

Key to the taxa of *Ynesmexia*

1. Sporangia extending along veins from submarginal hydathodes toward segment midvein, forming a peripheral soral band >2 mm wide; segment margins not modified to form distinct pseudoindusia, flat to slightly recurved but not covering the majority of sporangia.....2
1. Sporangia confined to vicinity of submarginal hydathodes, forming discrete sori or confluent laterally to form a peripheral soral band <2 mm wide; segment margins modified to form pseudoindusia, recurved and covering the sporangia when young but often spreading outward at maturity.....3
2. Blades 1-pinnate, rarely with the lowermost pinnae irregularly lobed; sporangia following the veins for >½ their length; veins regularly anastomosing..... ***Y. subcordata***
2. Blades pinnate-pinnatifid to 2-pinnate, most pinnae regularly lobed; sporangia following the veins for <½ their length; veins free or rarely anastomosing..... ***Y. ×gryphus***

3. Petioles brown to dull gray throughout; blades oblong, elliptic or lanceolate, usually 1–2-pinnate ..... ***Y. seemannii***
3. Petioles straw-colored to greenish distally; blades broadly deltate to ovate-lanceolate, 2-pinnate-pinnatifid to 4-pinnate 4
4. Pseudoindusia consisting of smoothly integrated, entire or slightly crenate linear flaps arising from a ± continuous sporangial receptacle formed by laterally expanded (Y-shaped) vein tips; sporangia forming a wide (mostly >0.5 mm), nearly continuous band paralleling ultimate segment margins; abaxial blade surfaces very sparsely hairy distally, often somewhat glaucous; bicolored petiole base scales with poorly differentiated, dark brown central stripe grading into the broad, brown margins usually long-ciliate on the proximal half; spores averaging >39.3 µm in length..... ***Y. skinneri***
4. Pseudoindusia consisting of separate triangular or oblong flaps (relatively rare) or forming a partially to fully fused, scalloped-undulate margin arising from discrete ovoid vein tips; sporangia forming a narrow (mostly <0.5 mm), interrupted to confluent soral arrangement encircling ultimate segment margins; abaxial blade surfaces with more obvious indument, consisting of both hairs and linear scales, not glaucous; bicolored petiole base scales with sharply distinct blackish central stripe and narrow, tan margins that are eciliate or ciliate only near the point of attachment; spores averaging <39.3 µm in length ....***Y. fournieri***

■ DATA ACCESSIBILITY

All newly generated sequences used in phylogenetic analyses have been uploaded to GenBank, with accession numbers provided in Appendix 1. Alignments are available at https://github.com/bfauskee/Ynesmexia-alignments-Taxon2025.git.

■ AUTHOR CONTRIBUTION

BDF: Data curation, formal analysis, funding acquisition, molecular phylogenetic analyses, investigation, visualization, writing – original draft; MDW: conceptualization, funding acquisition, formal analysis, investigation, spore, cytogenetic, and morphological analyses, supervision, writing – original draft, review & editing; KMP: formal analysis, funding acquisition, investigation, supervision, visualization, writing – original draft, review & editing.

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Appendix 1. Vouchers, mean spore diameter measurements in µm, and GenBank accession numbers for taxa used in our spore and molecular phylogenetic analyses.

***Taxon*: COUNTRY. State**, collection locality/municipality, *Voucher collector and collector number* (HERBARIUM CODE), FernLab database number (https://fernlab.biology.duke.edu), mean spore diameter per sporangium (standard deviation; **unique identifier #** in Figs. 6 and 7) [sometimes more than one mean spore measurement separated by semicolons], GenBank accession numbers for *rbcL*, *atpA*, *trnG-R*, *gapCp* (number of *gapCp* clones analyzed), in that order. Loci missing from molecular analyses are indicated with a dash (–); NA = not applicable/available.

Ingroup. *Ynesmexia fournieri*: MEXICO. Baja California Sur, Comondú, *Brandegee s.n.* (UC), NA, 35.1 µm (2.10; **1**). **Chiapas**, Municipio de Cintalapa, *Breedlove 36706* (MEXU), 16575, [29.3 µm (1.53; **2**); 32.3 µm (2.38; **3**); 33.5 µm (1.57; **4**)], PQ474204, PQ474203, PQ474205, – (–). **Guerrero**, Municipio de Zirándaro, *Salas & Nuñez 1366* (MEXU), NA, 33.4 µm (2.38; **5**); 28 miles south of Alpuyeca and 1.5 miles west of river just inside Morelos, *Mickel 727* (DUKE), NA, 33.2 µm (2.45; **6**). **Jalisco**, Barranca near Guadalajara, *C.G. Pringle 2586* (P), NA, 32.6 µm (2.45; **7**); Municipio de Zapopan, *C.J. Rothfels 3108* (DUKE), 6540, [30.3 µm (1.95; **8**); 32.9 µm (2.0; **9**); 33.3 µm (1.39; **10**); 35.4 µm (1.87; **11**)]; (MEXU), NA, 29.9 µm (3.10; **12**). **México**, Municipio de Tejupilco, *J. Daniel Tejero Díez & R. Moreno 2415* (MEXU), NA, 35.8 µm (1.57; **13**); Municipio de Ixtapan de la Sal, *J. Daniel Tejero Díez 2185* (MEXU), NA, 33.0 µm (2.17; **14**). **Michoacán**, Sierra Las Cruces, Cañada Las Cruces, *Steinmann 4534* (MO), 4983, 32.7 µm (2.38, **15**). **Morelos**, Municipio de Xochitepec, *Sanchez 221* (MEXU), NA, 28.6 µm (1.78; **16**); Municipio de Puente de Ixtla, *R. Ramirez & al. 3541* (MEXU), NA, 33.4 µm (2.15; **17**); Cuernavaca, *Bourgeau s.n.* (P), NA, [34.0 µm (2.04; **18**); 35.3 µm (2.08; **19**); 35.9 µm (1.89; **20**); 38.2 µm (1.98; **21**)]. **Nayarit**, Municipio de Ixtlán, *Téllez & Salinas 12297* (MEXU), NA, 35.5 µm (2.80; **22**); Municipio de Xalisco, *Beck 1170* (DUKE), 6917, NA, –, –, –, PQ474231 (1). **Oaxaca**, Municipio de Tapanatepec, *Alvaro Campos V. 2051* (MEXU), NA, 31.4 µm (2.29; **23**). **Sinaloa**, Municipio de Culiacán, *Aviña 6532* (MEXU), NA, 32.9 µm (2.25; **24**). **Sonora**, Municipio de Álamos, *A.C. Sanders 12910* (UC), 1110, 35.6 µm (4.23; **25**). ***Ynesmexia* ×*gryphus*: MEXICO. Nayarit**, Municipio de Jalisco, *Beck 1169* (DUKE), NA, 31.2 µm (2.18; **26**); *Beck 1171* (DUKE), 6918, [35.5 µm (2.01; **27**); 35.9 µm (2.49; **28**)], PQ474207, PQ474208, PQ474209, – (–); *Beck 1172* (DUKE), 6919, 33.8 µm (1.79, **29**); *Beck 1173* (DUKE), 6920, [27.1 µm (2.13; **30**); 30.3 µm (1.66; **31**)], –, –, –, PQ474210 (1); Municipio de Santa María del Oro, *Dias Luna 9098* (UC), NA, 34.0 µm (2.28; **32**). ***Ynesmexia seemannii "lozanoi"*: MEXICO. Colima**, Municipio de Tecomán, *C.J. Rothfels 3202* (DUKE), 6616, NA, –, –, –, PQ474211 (1). **Guerrero**, *Pringle, C.G. 13947* (US; holotype), NA, 41.2 µm (2.80; **33**). **Jalisco**, Municipio de la Huerta, *Lott 3757* (UC), 1085, 32.6 µm (2.10; **34**); *Lott 1278* (UC), NA, 38.4 µm (1.89; **35**); Municipio de Autlán, *Dyer & al. 37* (DUKE), NA, 39.5 µm (2.28; **36**), –, –, –, PQ474206 (1). **México**, Municipio de Tlatlaya, *Tejero Diez 2649* (MEXU), NA, 38.6 µm (1.78; **37**); *Matuda 31053* (MEXU), NA, 36.9 µm (2.73; **38**); *Matuda 31144* (MEXU), NA, 44.5 µm (3.15; **39**); Municipio de Luvianos, *Matuda 31543* (MEXU), 17108, 34.9 µm (2.45; **40**), PQ474212, PQ474213, PQ474214, – (–); Municipio de Zacazonapan, *Tejero Diez 2825* (MEXU), NA, 35.9 µm (2.03; **41**). **Michoacán**, Municipio de Apatzingán, *McVaugh 17942* (MEXU), NA, 38.2 µm (2.11; **42**); Municipio de San Lucas, *Martínez Salas 1286* (MEXU), NA, 33.3 µm (2.01; **43**). **Nayarit**, Municipio de Ahuacatlán, *C.J. Rothfels 3121* (DUKE), 6558, 34.1 µm (2.15; **44**), –, –, –, PQ474215 (1); (MEXU), NA, 39.4 µm (3.09; **45**). **Oaxaca**, Municipio de Ciudad Ixtepec, *del Castillo 2555* (MEXU), NA, 41.8 µm (3.34; **46**). ***Ynesmexia seemannii "seemannii"*: MEXICO. Baja California Sur**, Municipio de La Paz, *Pray 1780* (UC), NA, 35.7 µm (2.22; **47**). **Guerrero**, Municipio de Acapulco, *Christ s.n.* (P), NA, 39.2 µm (3.20; **48**). **Jalisco**, Municipio de Tlajomulcho de Zuniga, *Cortes 580* (MEXU), NA, 36.6 µm (2.49; **49**). **Michoacán**, Morelia, Punguato, *Arsene 2865* (MEXU), NA, 37.7 µm (1.90; **50**); Penjamillo, Barranca O. de Arroyuelos, *Labat 1605* (MEXU), NA, [38.3 µm (2.36; **51**); 39.8 µm (1.90; **52**)]. **Morelos**, Municipio de Puente de Ixtla, *R. Ramirez 3431* (MEXU), 17106, [40.1 µm (2.45; **53**); 41.6 µm (2.88; **54**)], PQ474216, PQ474217, PQ474218, – (–). **Nayarit**, Municipio de Tepic, *Flores-Franco 2780* (MEXU), NA, 33.9 µm (2.29; **55**). **Oaxaca**, Municipio de Zimatlán de Álvarez, *Garcia 2438*: NA, 39.3 µm (3.72; **56**); Municipio de Cuicatlán, *Salinas 7233* (MEXU), NA, [38.9 µm (2.61; **57**); 39.1 µm (2.03; **58**)]; Municipio de San Pedro Juchatengo, *Yatskievych & Gastony 89-259* (IND), 5053, 37.4 µm (2.22; **59**). **Puebla**, Municipio de Acatatlán de Osorio, *Rojas-Martínez 189* (MEXU), 17107, [37.1 µm (2.66; **60**); 37.5 µm (2.17; **61**)], PQ474219, PQ474220, PQ474221, – (–). **Querétaro**, Municipio de Arroyo Seco, *Carranza 3417* (MEXU), NA, 38.1 µm (2.08; **62**). **San Luis Potosí**, Municipio de Ciudad Valles, *Purpus 5492* (MEXU), NA, 35.6 µm (2.31; **63**). **Sonora**, ca. 37.1 miles NE Alamos, *Lehto 24797* (ASU), NA, [33.0 µm (1.91; **64**); 33.1 µm (2.20; **65**)]; 35.7 miles NE Alamos, *Lehto 24807A*, NA, [34.9 µm (1.69; **66**); 36.3 µm (1.93; **67**); 38.4 µm (2.03; **68**)]. ***Ynesmexia skinneri* s.str.: COLOMBIA.** Santa Marta, *Smith 1087* (DUKE), NA, 42.7 µm (2.16; **69**); (UC), NA, 41.7 µm (2.13; **70**). **COSTA RICA. Guanacaste**, Bagaces, Parque Nacional Palo Verde, *C.J. Rothfels 2645* (DUKE), 5580, [40.2 µm (2.16; **71**); 42.9 µm (3.03; **72**); 43.5 µm (2.89; **73**); 43.7 µm (2.71; **74**)], –, –, –, PQ474222/PQ474223 (2); Canton de Nandayure, *Estrada & Rodriquez 140* (UC), NA, 42.0 µm (2.98; **75**); Catalina, *Stork 2790* (UC), NA, 42.4 µm (2.34; **76**); Estación Biológica Palo Verde, *Boyle & al. 6519* (UC), NA, [43.2 µm (3.02; **77**), 43.8 µm (2.18; **78**)]; *Bishop & al. s.n.* (UC), NA, 43.4 µm (2.69; **79**). **MEXICO. Veracruz**, Barranca de Pachuquilla, *Medina & Vazquez 437* (MEXU), NA, 40.1 µm (2.75; **80**); Barranca de Panoya, *Purpus 8461* (UC), NA, 43.6 µm (2.05; **81**); Municipio de Puente Nacional, *F. Ventura A. 18905* (MEXU), 17105, 42.5 µm (2.98; **82**), PQ474224, PQ474225, PQ474226, – (–); *F. Ventura A. 10471* (P), NA, 40.5 µm (2.5; **83**); Municipio de Tlaltetela, *F. Ventura A. 8841* (MEXU), NA, 40.4 µm (2.95; **84**). **NICARAGUA.** Managua, *Chaves s.n.* (P01278112), NA, 41.5 µm (3.06; **85**); *Chaves s.n.* (P01278115), NA, 41.6 µm (2.03; **86**).

Appendix 1. Continued.

***Ynesmexia subcordata*: GUATEMALA.** Huehuetenango, *J.A. Steyermark 51433* (DUKE), NA, 30.3 µm (1.95; **87**). **MEXICO. Nayarit**, Municipio de Xalisco, *Beck 1175* (DUKE), 6922, 34.8 µm (1.60, **88**); *Beck 1176* (DUKE), 6923, NA, –, –, –, PQ474227 (1); Municipio Santa María del Oro, *C.J. Rothfels 3163* (DUKE), 6588, [31.1 µm (1.63; **89**); 31.8 µm (1.53; **90**); 32.3 µm (1.60; **91**); 32.6 µm (2.10; **92**); 33.8 µm (1.93; **93**)]. **Oaxaca**, 10 km NE of bridge at Juchatengo on Highway 131 from Oaxaca to Puerto Escondido, *Yatskievych & Gastony 89-261* (IND), 5050, 30.6 µm (2.42; **94**); Distrito Pochutla, *Mickel 5151* (UC), NA, 30.7 µm (2.34; **95**); Highway 125: 5.25 km N of Ixcapa, *Ranker 729* (UC), 4746, [36.1 µm (1.92; **96**); 36.6 µm (2.03; **97**), 37.1 µm (2.0; **98**), 37.2 µm (1.95; **99**), 37.5 µm (2.04; **100**); 38.2 µm (1.98; **101**)], PQ474228, PQ474229, PQ474230, – (–). **Sinaloa**, Concordia, *Reina G. 2005-1509* (MO), NA, 29.9 µm (1.84; **102**). **Durango/Sinaloa**, Ymala and Lodiego, *Palmer 1572* (US), NA, 38.2 µm (2.76; **103**). **Outgroups. *Bommeria hispida*: MEXICO. San Luis Potosí**, Municipio de Santa María del Río, *Beck 1130* (DUKE), 6939, NA, MH173074.1, MH173074.1, MH173074.1, – (–). ***Cheilanthes micropteris*: BRASIL. Rio Grande do Sul**, Municipio do Jaquirana, *Prado 2132* (DUKE), 7859, NA, MH173078.1, MH173078.1, MH173078.1, – (–). ***Hemionitis palmata*:** Cultivated, Duke University Greenhouse, *Schuettpelz 297*: 2557, NA, KC984525.1, EU268743.1, EU268690.1, – (–). ***Myriopteris marsupianthes*: MEXICO**. NA, *Jankiewicz 13* (UC), 6158, NA, KF961803.1, KF961739.1, KF961864.1, – (–). ***Myriopteris wrightii*: U.S.A. Arizona**, Yavapai County, *Schuettpelz 441* (DUKE), 3148, NA, HM003030.1, KF961760.1, HM003034.1, – (–). ***Notholaena trichomanoides*: JAMAICA.** NA, *Ranker 860* (UT), 4054, NA, EU268807.1, EU268807.1, EU268807.1, – (–). ***Pellaea atropurpurea*:** Cultivated, Juniper Level Botanic Garden, *Schuettpelz 312* (DUKE), 2957, NA, KF961814.1, KF961814.1, JQ855913.1, KC984471.1 (1). ***Pellaea breweri*: U.S.A. Utah**, Salt Lake County, *Windham 3447 & Pryer*, 3930, NA, EU268764.1, EU268764.1, EU268712.1, – (–). ***Pentagramma triangularis*: U.S.A. California**, Mariposa County, *Schuettpelz 1332* (DUKE), 5975, NA, MH173070.1, MH173070.1, MH173070, – (–).