RESEARCH ARTICLE

A phylogenetically informed generic reclassification of the hemionitid ferns (Pteridaceae: Cheilanthoideae)

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Abstract The roughly 500 species of cheilanthoid ferns exhibit a diversity of morphological adaptations to xeric environments. However, most of these traits have evolved independently multiple times, impeding past efforts to establish a natural classification for the group. Considerable progress has been made over the past three decades resolving most of the major lineages, with the notable exception of the hemionitids, the largest and most widely distributed clade. The nearly 350 hemionitid species can be found in dry regions across the globe and account for two-thirds of cheilanthoid diversity. While some of the 17 genera commonly attributed to this group are easily recognized and demonstrably monophyletic, others have been shown to be clearly non-monophyletic. Here, we explore phylogenetic relationships among hemionitid species using a dataset that greatly expands on earlier studies. We carefully consider generic lines and propose a phylogenetically informed classification that better aligns with morphology, geography, and evolutionary history. Based on our analyses and morphological investigations, we propose the recognition of 22 monophyletic hemionitid genera. Nine of our generic circumscriptions are consistent with those of most other recent studies. Two other genera are expanded relative to these studies, while two are more narrowly defined. Two generic names are resurrected herein and seven genera are newly described to accommodate divergent clades. In all, 106 new species-level (plus 9 subspecific) combinations are made.

Keywords cheilanthoid ferns; desert environments; generitype; hemionitids; monophyly

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

Our ability to discern species relationships and circumscribe natural groups has been revolutionized by recent advances in molecular biology, facilitating the development of more robust, phylogenetically informed classifications across the tree of life (e.g., Laumer & al., 2019 [metazoans]; Li & al., 2021 [fungi]; One Thousand Plant Transcriptomes Initiative, 2019 [plants]). Ferns are no exception (Nitta & al., 2022) and a consensus classification was recently published (PPG I, 2016) in which most genera were well supported as monophyletic. However, a few large lineages, long considered phylogenetically "intractable", remained poorly resolved. While some of these challenging groups have since received considerable attention (e.g., Thelypteridaceae; Fawcett & Smith, 2021; Fawcett & al., 2021), others, such as the xeric-adapted cheilanthoid ferns, continue to baffle taxonomic practitioners.

Cheilanthoid ferns comprise a well-supported clade (subfamily Cheilanthoideae) within the Pteridaceae (Schuettpelz & al., 2007; Nitta & al., 2022), accounting for about 500 species. Their reputation as "the most contentious group of ferns with respect to a practical and natural generic classification" (Tryon & Tryon, 1982: 248) is reflected in the fact that 7 of the 23 genera recognized in PPG I (2016) were identified as non- (or questionably) monophyletic. Notably, these seven unnatural genera were estimated to comprise more than half the documented biodiversity of the cheilanthoid lineage.

Among cheilanthoids, both life cycle phases exhibit remarkable adaptations to living in xeric environments and, in turn, thrive in niches that are rarely exploited by other fern groups (Tryon, 1979; Tryon & Tryon, 1982; Yatskievych & Hooper, 2001). The free-living gametophytes of some species can survive for years in a desiccated state (Pickett, 1931). Many others are capable of initiating a new sporophyte in the absence of fertilization, which typically requires the availability of water to mediate sperm swimming from antheridium to archegonium (Haufler & al., 2016), through a process known as apomixis (see Grusz & al., 2021). The more conspicuous sporophytes display a wide variety of morphological

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features that are interpreted as adaptations to dry and exposed environments (Hevly, 1963; Nobel, 1978). These traits have been traditionally used to define large genera, including: (1) *Cheilanthes* Sw., characterized by leaf surfaces densely covered with indument (i.e., hairs and/or scales); (2) *Notholaena* R.Br., with leaf surfaces producing a waxy exudate (i.e., farina); and (3) *Pellaea* Link, bearing highly divided leaves with a thickened cuticle (Tryon & Tryon, 1982). Another large genus (*Doryopteris* J.Sm.) was commonly recognized based on the continuous distribution of sporangia (i.e., coenosori) along a network of marginal veins.

Phylogenetic analyses over the last three decades have established that each of these large cheilanthoid genera (*Cheilanthes*, *Doryopteris*, *Notholaena*, *Pellaea*) are polyphyletic as traditionally circumscribed (Gastony & Rollo, 1998; Kirkpatrick, 2007; Prado & al., 2007; Schuettpelz & al., 2007; Zhang & al., 2007; Rothfels & al., 2008; Windham & al., 2009; Yesilyurt & Schneider, 2010; Eiserhardt & al., 2011; Link-Pérez & al., 2011; F.-W. Li & al., 2012; Grusz & al., 2014; Yesilyurt & al., 2015; George & al., 2019; Kao & al., 2019), with the various morphological traits having evolved independently in distantly related lineages (Fig. 1). As previously defined, the genus *Cheilanthes* included representatives spanning the phylogenetic tree from the early-diverging bommeriid (George & al., 2019) and myriopterid (Grusz & al., 2014) clades to the derived hemionitid lineage (wherein the type of *Cheilanthes* resides). Although the typification of *Notholaena* has been the focus of a decades-long dispute (see Yatskievych & Smith, 2003), even the largely New World farinose group has been shown to comprise two distantly related lineages (Gastony & Rollo, 1998; Rothfels & al., 2008). One of these comprises the notholaenid clade as defined by Windham & al. (2009, see below), whereas the other species group belongs to the pellaeid clade where it is assigned to the segregate genus *Argyrochosma* (J.Sm.) Windham. The traditional concept of *Pellaea*, in turn, greatly exceeds the circumscription of the pellaeid clade to encompass multiple independent lineages in the hemionitid group (Kirkpatrick, 2007; Eiserhardt & al., 2011; Yesilyurt & al., 2015). Species formerly assigned to *Doryopteris* span the entire phylogenetic tree from the earliest branch (*Calciphilopteris* Yesilyurt & Schneider) to the hemionitid crown (Yesilyurt & Schneider, 2010).

Recent phylogenetically based studies of cheilanthoid ferns have described new genera, recircumscribed existing genera, or resurrected old generic names in the pursuit of monophyly. For example, *Calciphilopteris* was newly described to accommodate a small clade of species previously placed in *Doryopteris* that was found to be sister to all other cheilanthoids (Yesilyurt & Schneider, 2010). *Adiantopsis* Fée was expanded to incorporate a few species previously treated in *Cheilanthes* (Link-Pérez & al., 2011). *Gaga* Pryer & al. and *Myriopteris* Fée were newly described and resurrected, respectively, to accommodate well-defined clades of species formerly ascribed to *Cheilanthes* that were phylogenetically distant from the clade containing the generitype (Li & al., 2012; Grusz & Windham, 2013). *Lytoneuron* (Klotzsch) Yesilyurt was elevated to accommodate species previously recognized in *Doryopteris*, and *Ormopteris* J.Sm. ex J.Sm. was resurrected for a largely Brazilian clade of species formerly in *Pellaea* (Yesilyurt & al., 2015). Most recently, *Baja* Windham & L.O.George (George & al., 2019) and *Mineirella* Ponce & Scataglini (Ponce & Scataglini, 2022) were described to accommodate other isolated species previously assigned to *Cheilanthes*.

Cheilanthoid ferns are now understood to comprise seven major lineages (Windham & al., 2009) (Fig. 1). *Calciphilopteris* (previously referred to as the "ludens clade"; 4 species) and the bommeriids (6 species) are successively sister to all other cheilanthoids. The pellaeids (ca. 60 species) are sister to the myriopterids (ca. 45 species) and together these are sister to the "skinneri clade" (ca. 5 species). The notholaenids (ca. 30 species) are sister to a large hemionitid clade that accounts for perhaps 70% of cheilanthoid diversity (Windham & al., 2009).

Cheilanthoid species are concentrated in six xeric biogeographic centers (Tryon & Tryon, 1973): Mexican; Andean; Brazilian; African; Sino-Himalayan; and Australian. Whereas *Calciphilopteris* is associated with the Sino-Himalayan and Australian centers, bommeriids, pellaeids, myriopterids, the skinneri clade, and notholaenids are all closely tied to the Mexican center of diversity. Only the hemionitids are broadly distributed, with multiple species occurring in each of the major geographic centers.

The major cheilanthoid clades tied to the Mexican center of diversity are deeply diverged and mostly well defined and the generic taxonomy for these groups is largely resolved by recent molecular analyses (Rothfels & al., 2008; Grusz & al., 2014, 2021; George & al., 2019; Kao & al., 2019). However, the hyperdiverse, cosmopolitan hemionitid lineage remains problematic. Within this clade, many species currently treated in *Cheilanthes*, and others still ascribed to *Pellaea* and *Notholaena* (despite their ample phylogenetic divergence from the relevant generitypes), are intermixed with more than a dozen long-standing and well-defined genera (Eiserhardt & al., 2011; Ponce & Scataglini, 2022).

Resolving this situation calls for a careful balancing of taxonomic splitting and lumping to optimize both monophyly and nomenclatural stability (Schuettpelz & al., 2018). However, some recent authors (e.g., Christenhusz & al., 2018) have, instead, proposed a taxonomy that lumps all hemionitids (indeed all cheilanthoids) into a single genus, *Hemionitis* L. As noted by Schuettpelz & al. (2018), this expansion of a small, well-defined species group associated with the generitype of *Hemionitis* is inimical to nomenclatural stability and required 468 new combinations for the roughly 500 taxa involved (Christenhusz & al., 2018). And, although this group is consistently resolved as monophyletic (Schuettpelz & al., 2007; Eiserhardt & al., 2011; Yesilyurt & al., 2015; Nitta & al., 2022; Ponce & Scataglini, 2022), it is morphologically undiagnosable, effectively erasing the phylogenetically and geographically localized character combinations that have

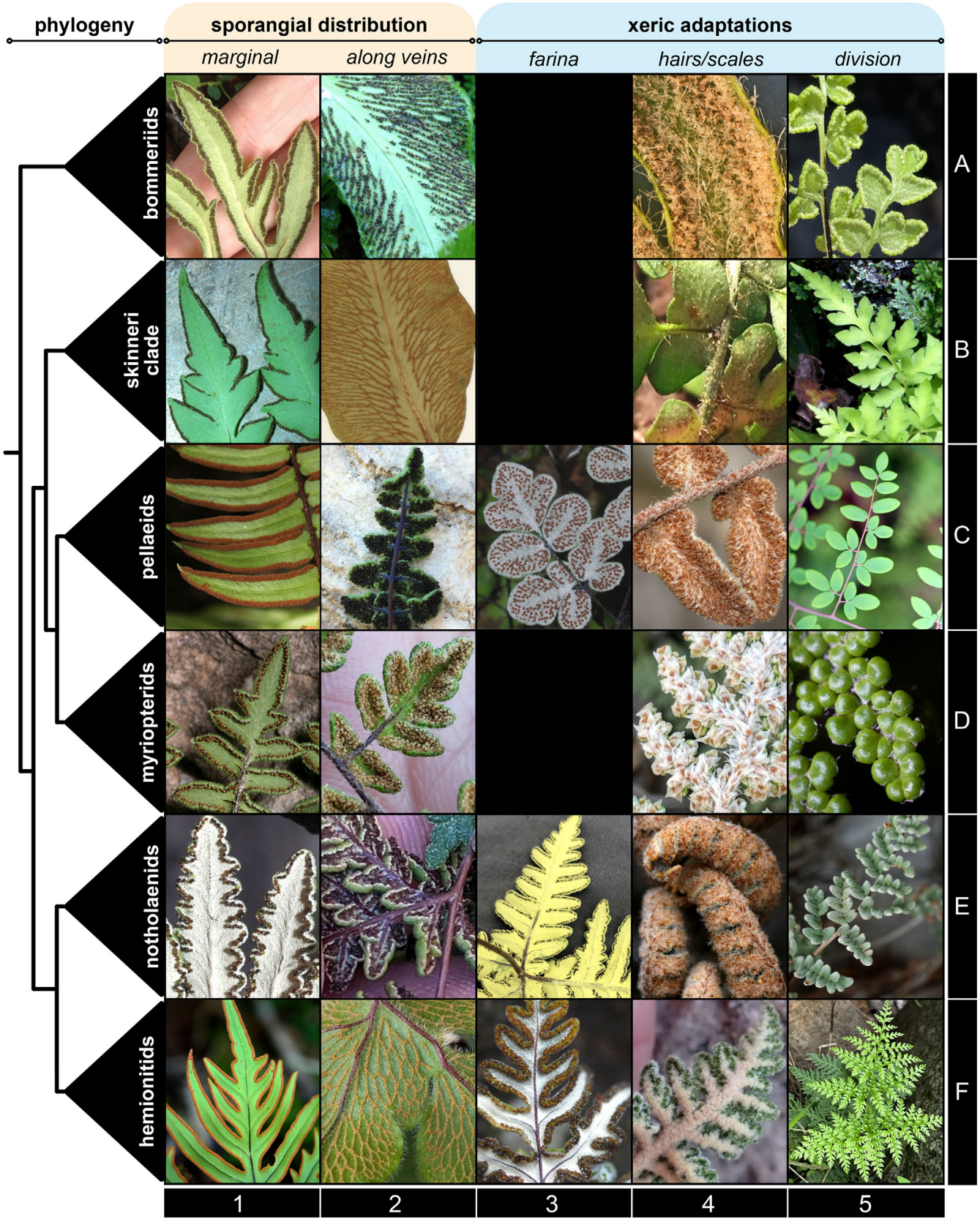

Fig. 1. Caption on opposite page

arisen through nearly 100 million years of evolution (Schuettpelz & al., 2018). This inclusive approach for *Hemionitis* has not gained broad acceptance from the botanical community and the best option for moving forward thus depends on a combination of improved molecular sampling and more comprehensive morphological studies. Here, we explore phylogenetic relationships within the hemionitid clade using a dataset that greatly expands on earlier work and includes nearly two-thirds of the hemionitid species. We carefully consider generic lines among hemionitid ferns and propose a phylogenetically informed classification that better aligns with the morphology, geography, and evolutionary history of this intriguing lineage.

■ MATERIALS AND METHODS

Taxonomic sampling. — Our aim was to include a representative sample of as many hemionitid fern species as possible in our phylogenetic analyses. We initially compiled a list of candidate species using the World Ferns database (Hassler, 2004–2023), which was amended and further refined by consulting other databases and Floras to arrive at a comprehensive set of 354 generally accepted hemionitid species. A total of 564 samples from 223 hemionitid species were ultimately included in this study, with many coming from recent fieldwork conducted in Brazil, China, Mexico, Nepal, and the southwestern United States (Appendices 1–3; suppl. Appendix S1). This sample accounts for 63% of the generally accepted hemionitid species, with 38%–100% species-level coverage within genera (based on predominant usage prior to this study, but see discussion of *Notholaena solitaria* below).

DNA isolation, amplification, and sequencing. — We isolated DNA from all available hemionitid samples for which sequences had not previously been published, using an established protocol (Schuettpelz & Pryer, 2007). For each of these samples, we then amplified and sequenced the most commonly used molecular marker for ferns: plastid *rbcL* (following Schuettpelz & Pryer, 2007). For select samples (see below), we also sequenced two other plastid regions that were commonly utilized in earlier studies of this lineage: *atpA* (following Schuettpelz & al., 2006) and *trnG-R* (following Nagalingum & al., 2007). In total, 478 sequences were newly generated for this study (attributed as such in Appendices 1 and 3).

Sequence assembly and alignment. — Through a joint search of GenBank (Sayers & al., 2020) and the relevant literature, we compiled all published *rbcL* sequences (366) understood to have been derived from members of the focal hemionitid clade. A small number of sequences (21) had problematic ends or small insertions that were trimmed (Appendices 1, 3). We standardized the names associated with the published sequences, as well as those that were newly generated for this study, seeking to apply the most commonly used existing taxonomy. The initial set of 366 published and 228 unpublished hemionitid sequences was then aligned and subjected to preliminary phylogenetic analyses to assess the affinities of sequences attributed to each species. We revisited voucher specimen determinations whenever possible, especially for anomalous sequences or in cases where sequences thought to have been derived from a single species were not resolved together. Duplicate (i.e., derived from the same voucher) or questionable sequences, as well as those from unnamed species or hybrids, were excluded (30 sequences total). The remaining 564 *rbcL* sequences were aligned in AliView v.1.28 (Larsson, 2014) to yield a final "all-samples" *rbcL* dataset (Table 1; suppl. Appendix S2).

Following analysis of the all-samples dataset (see below), one representative sample was selected for each available hemionitid species, based on the availability of voucher specimens and corresponding *atpA* and *trnG-R* region sequences from the same individual. For each marker, the relevant sequences were then assembled and aligned in AliView to yield three single-gene datasets and a combined "three-gene" dataset for analysis (Table 1; suppl. Appendix S3).

Phylogenetic analyses. — For the all-samples *rbcL* dataset and the three-gene dataset, the best-fitting substitution model for each locus (Table 1) was determined using ModelFinder (Kalyaanamoorthy & al., 2017) as implemented in IQ-TREE v.2.1.2 (Minh & al., 2020). Maximum likelihood (ML) analysis of the all-samples *rbcL* dataset was performed in IQ-TREE with 1000 ultrafast bootstrap replicates (Hoang & al., 2018) to aid in the selection of representative sequences for downstream analyses. Similarly, preliminary ML analyses of the refined *rbcL*, *atpA*, and *trnG-R* datasets were performed in IQ-TREE to identify any well-supported conflicts in the

Fig. 1. Photographs of key leaf traits typical for major cheilanthoid fern lineages (phylogeny at left from Windham & al., 2009). Rows **A–F**, from top, correspond to six of the seven major cheilanthoid lineages (*Calciphilopteris* not shown): **A**, Bommeriids; **B**, Skinneri clade; **C**, Pellaeids; **D**, Myriopterids; **E**, Notholaenids; **F**, Hemionitids. Columns **1** & **2**, from left, show distribution of sori on abaxial leaf surfaces: **1**, Marginal; **2**, Along veins. Columns **3–5**, from left, show leaf modifications indicating adaptations to xeric conditions: **3**, Presence of farina; **4**, Presence of hairs and/or scales; and **5**, Presence of highly divided penultimate leaf segments. **A1**, *Bommeria ehrenbergiana*; **A2**, *Bommeria elegans*; **A3**, not applicable; **A4**, *Bommeria hispida*; **A5**, *Baja brandegeei*; **B1**, *Cheilanthes skinneri*; **B2**, *Hemionitis subcordata*; **B3**, not applicable; **B4**, *Cheilanthes lozanoi*; **B5**, *Cheilanthes skinneri*; **C1**, *Pellaea falcata*; **C2**, *Argyrochosma jonesii*; **C3**, *Argyrochosma incana*; **C4**, *Astrolepis integerrima*; **C5**, *Pellaea andromedifolia*; **D1**, *Myriopteris scabra*; **D2**, *Myriopteris lanosa*; **D3**, not applicable; **D4**, *Myriopteris covillei*; **D5**, *Myriopteris covillei*; **E1**, *Notholaena standleyi*; **E2**, *Notholaena californica*; **E3**, *Notholaena standleyi*; **E4**, *Notholaena aschenborniana*; **E5**, *Notholaena bryopoda*; **F1**, *Doryopteris concolor*; **F2**, *Hemionitis palmata*; **F3**, *Aleuritopteris argentea*; **F4**, *Estrella mollis*; **F5**, *Aspidotis californica*. — Images via iNaturalist, cropped from originals, and used with CC BY-NC 4.0 license (https://creativecommons.org/licenses/by-nc/4.0), unless otherwise specified (see Appendix 4 for details).

topologies. With no significant conflicts identified, the datasets were concatenated. ML analyses were performed on the partitioned, concatenated three-gene dataset using RAxML-NG v.1.1.0 (Kozlov & al., 2019), with branch support for the most likely tree calculated from 1000 bootstrap replicates (MLBS). Bayesian analysis of the three-gene dataset was conducted in MrBayes v.3.2.7 (Ronquist & al., 2012). Four independent, simultaneous runs, each with four chains (three heated, one cold) were run for 10 million generations. Runs were initiated from random starting trees with trees saved every 1000 generations. Output parameters were visualized in Tracer v.1.7.1 (Rambaut & al., 2018) to ensure runs reached convergence. After discarding the burn-in (25%), the remaining trees were summarized in a consensus tree and used to calculate clade posterior probabilities (BPP). All trees were rooted with the genus *Pentagramma*, which is well-established as sister to the remainder of the hemionitid clade (Gastony & Rollo, 1998; Schuettpelz & al., 2007; Rothfels & al., 2008; Ponce & Scataglini, 2018; Nitta & al., 2022). All phylogenetic analyses were performed on the CIPRES computing cluster (Miller & al., 2010).

■ RESULTS

Relying primarily on World Ferns (Hassler, 2004–2023), along with other databases and Floras, we assembled a list of 354 generally accepted hemionitid species (Appendices 1, 2). A total of 564 samples from 223 of these species had a plastid *rbcL* sequence suitable for inclusion in our study (Appendices 1, 3). Phylogenetic analysis of this all-samples *rbcL* dataset yielded a tree with variable levels of branch support (suppl. Fig. S1). The resolved backbone was poorly supported, but the situation typically improved for smaller clades closer to the tips of the tree. When multiple samples of a species were included, they were generally well-supported as monophyletic, with a maximum likelihood bootstrap (MLBS) ≥ 70, and/or identical to one another. The exceptions included: *Adiantopsis radiata* (one of seven samples differing from the others, which are poorly supported as paraphyletic to *A. hickeyi*); *Aleuritopteris grisea* (two samples poorly supported as sister to *A. bullosa* and two others sister to this clade); *Aleuritopteris krameri* (four samples resolved together but not well-supported or identical); *Aleuritopteris mexicana* (six samples poorly supported as paraphyletic to *A. krameri*); *Aleuritopteris subargentea* (two samples poorly supported as paraphyletic to *A. argentea*); *Aleuritopteris veitchii* (one sample identical to *A. likiangensis* and the other sister to this pair); *Doryopteris patula* (three samples resolved together but not well-supported or identical); *Doryopteris varians* (two samples resolved together but not well-supported or identical); *Gaga marginata* (one of twelve samples differing from the others, which are identical to the samples of two other species); *Lytoneuron crenulans* (one sample poorly supported as sister to *L. acutilobum* and three others sister to this clade); *Mildella intramarginalis* (one sample identical to *M. fallax* and the other sister to this pair); *Oeosporangium stramineum* (two samples resolved together but not well-supported or identical); and *Ormopteris riedelii* (one of four samples differing from the others, which are identical to the samples of three other species). These minor exceptions (all visible in suppl. Fig. S1), had no bearing on our results as they are all associated in slightly larger clades and were accounted for when selecting exemplars (details below).

Based on the availability of *atpA* and *trnG-R* region sequences and voucher specimens, one sample was selected for each of the 223 available hemionitid species (Appendix 1). For all species, and especially in the exceptional cases noted above, we were careful to select a representative sample (suppl. Fig. S1). Phylogenetic analysis of the assembled three-gene dataset yielded a tree with much higher levels of MLBS support than that from the all-samples *rbcL* dataset, and a majority of branches also received significant (≥0.95) Bayesian posterior probability (BPP) support (suppl. Fig. S2). *Pentagramma* has consistently appeared as sister to all other hemionitids in previous studies (Gastony & Rollo, 1998; Schuettpelz & al., 2007; Rothfels & al., 2008; Ponce & Scataglini, 2018; Nitta & al., 2022), and this genus was used to root the tree; this bifurcation is strongly supported (MLBS = 100; BPP = 1.0). Within the larger sister clade, most other hemionitid species occurring in the Mexican center (typically treated in *Aspidotis* or the recently described *Gaga*) composed a well supported clade, but its sister clade did not receive comparable support (suppl. Fig. S2). Therein, two additional species occurring in the Mexican center (typically treated in *Mildella*), are resolved with most hemionitid species occurring in the Sino-Himalayan center, typically treated in *Aleuritopteris* and *Oeosporangium* (MLBS = 81; BPP = 1.0). Species assigned to *Aleuritopteris* and *Oeosporangium*, usually differentiated based on the presence or

Table 1. Molecular datasets, with summary statistics and best-fitting substitution models.

Dataset	Sequences	Sites included	Sites variable	Missing	ML model	BI model
rbcL (all samples)	564	1310	465	3.7%	GTR + F + I + R3	(not applicable)
rbcL (refined)	223	1310	428	3.2%	GTR + F + R5	GTR + F + I + G4
atpA	189	1776	654	3.3%	TN + F + R5	GTR + F + I + G4
trnG-R	163	1023	961	5.7%	GTR + F + R4	GTR + F + I + G4
Three-gene	223	4109	2043	16.1%	(partitioned)	(partitioned)

absence of farina, do not form reciprocally monophyletic groups (suppl. Fig. S2).

The species most commonly treated as *Cheilanthes poeppigiana* occupies a rather isolated position within the hemionitid clade (suppl. Fig. S2), poorly supported as sister to a large, well-supported (MLBS = 100; BPP = 1.0) clade of species variously ascribed to *Adiantopsis*, *Cheilanthes*, *Doryopteris*, *Lytoneuron*, *Mineirella*, *Ormopteris*, *Pellaea*, and *Trachypteris*. *Trachypteris* and *Adiantopsis* are each monophyletic (MLBS = 100; BPP = 1.0) and strongly supported as sister to one another (MLBS = 90; BPP = 0.98). *Mineirella*, a small genus recently segregated from *Cheilanthes* (Ponce & Scataglini, 2022), is here resolved as monophyletic and sister to two other species from the Brazilian center commonly placed in *Cheilanthes* (MLBS = 88; BPP = 1.0). Collectively, these are sister to a well-supported (MLBS = 94; BPP = 1.0) assemblage of species from the African center predominantly treated in *Cheilanthes* and *Pellaea*. In our analysis, the narrowed circumscription of *Doryopteris* proposed by Yesilyurt & al. (2015) is strongly supported as monophyletic (MLBS = 100; BPP = 1.0), but support is mixed for *Ormopteris* and *Lytoneuron* (MLBS = 60 and 65; BPP = 1.0 and 1.0), which nevertheless form a strongly supported clade (MLBS = 100; BPP = 1.0) sister to *Doryopteris* s.str.

Another well supported (MLBS = 100; BPP = 1.0) hemionitid clade comprises species predominantly treated in *Cheilanthes*, *Hemionitis*, *Doryopteris*, *Parahemionitis*, and *Pellaea*. *Hemionitis* itself is monophyletic therein (MLBS = 100; BPP = 1.0), and sister to two species typically placed in *Cheilanthes* (MLBS = 100; BPP = 1.0). The lone species of *Parahemionitis* is, in turn, sister to a single species treated in *Doryopteris*. The other species in this clade are all found in the African center and compose a well-supported lineage (MLBS = 100; BPP = 1.0); however, they are variously treated in *Cheilanthes*, *Doryopteris*, and *Pellaea*.

The remaining clade, which has mixed support (MLBS = 43; BPP = 0.99), consists entirely of species presently treated in *Cheilanthes*. The subclades therein are generally better supported and there is a correspondingly high level of geographic structure.

■ DISCUSSION

Analysis of our three-gene dataset resulted in a tree with broadly acceptable levels of branch support. While some parts of the backbone are effectively unresolved, most mid-level branches pertinent to generic delimitation are well-supported (suppl. Fig. S2). Most of the recently described genera are monophyletic, but most of the larger genera with longer nomenclatural histories are paraphyletic or polyphyletic (suppl. Fig. S2). This is true for most genera based on their predominant usage today, but is especially pronounced for the traditional definitions of *Cheilanthes*, *Notholaena*, and *Pellaea* (Fig. 2). Remarkably, there is considerable geographic structure present in the tree (Fig. 2). While many clades contain species that were previously treated in several genera, most are confined to just one or two of the cheilanthoid biodiversity centers recognized by Tryon & Tryon (1973).

The 354 confirmed or suspected hemionitid species considered herein represent 17 genera based on predominant usage prior to this study (Table 2). Following these circumscriptions, just one genus is monospecific, but its name and that of its sole species has been the subject of considerable debate (see Fraser-Jenkins & al., 2016; Lindsay & Middleton, 2021). It has been recognized as either *Parahemionitis arifolia* (Panigrahi, 1993) or *Mickelopteris cordata* (Fraser-Jenkins & al., 2016). However, a proposal to conserve the name *Asplenium arifolium* (*Hemionitis arifolia*, *Parahemionitis arifolia*) with a conserved type was recently recommended for acceptance by the Nomenclature Committee for Vascular Plants (Applequist, 2023), and approved by the General Committee (Wilson, 2024). We use the name *Parahemionitis arifolia* herein to reflect its formal acceptance at the XX International Botanical Congress. This species is included in our analyses, confirming that it is a hemionitid fern closely related to, but distinct from, *Hemionitis* (suppl. Fig. S2). Note that although the genus *Notholaena* may also appear to be monospecific (Table 2), this genus actually consists of about 30 species, most of which are clearly ascribed to the clade sister to hemionitids (Rothfels & al., 2008). The lone species suspected to be a hemionitid fern (*N. solitaria* R.M.Tryon) was not included in our molecular analysis and may well have affinities elsewhere.

Nine other genera to which hemionitid species have been ascribed in recent treatments are here resolved as monophyletic with strong support, based on available sampling (suppl. Fig. S2): *Hemionitis* (sampled 4 of 7 species; Appendices 1, 2); *Adiantopsis* (27/35); *Ormopteris* (5/5); *Trachypteris* (2/4); *Aspidotis* (3/4); *Pentagramma* (6/6); *Gaga* (18/19); *Lytoneuron* (6/16); and *Mineirella* (3/5). We see little reason to cease recognizing any of these morphologically distinct taxa. However, species ascribed to the remaining six genera (Table 2) are intermixed and/or resolved in multiple places across the phylogeny (suppl. Fig. S2). Because we seek to recognize only monophyletic genera in our revised classification, these are here discussed in greater detail. The paraphyletic or polyphyletic genera present in our sampling are: *Aleuritopteris* (sampled 34 of 57 species; Appendices 1, 2); *Oeosporangium* (21/38); *Mildella* (3/4); *Doryopteris* (19/47); *Pellaea* (10/16); and *Cheilanthes* (61/89).

Species recently partitioned between *Aleuritopteris* and *Oeosporangium* (Hassler, 2004–2023; Fraser-Jenkins & al., 2016) are here resolved together in a large, well-supported clade (suppl. Fig. S2), but the species attributed to these two "genera" are completely interspersed. The primary morphological feature used to differentiate *Aleuritopteris* from *Oeosporangium* is the presence of foliar farina in the former and its absence in the latter (Fraser-Jenkins & al., 2016). However, farina has been repeatedly gained and lost within other cheilanthoid genera such as *Notholaena* (Rothfels & al., 2008; Johnson & al., 2012; Kao & al., 2019) and *Argyrochosma*

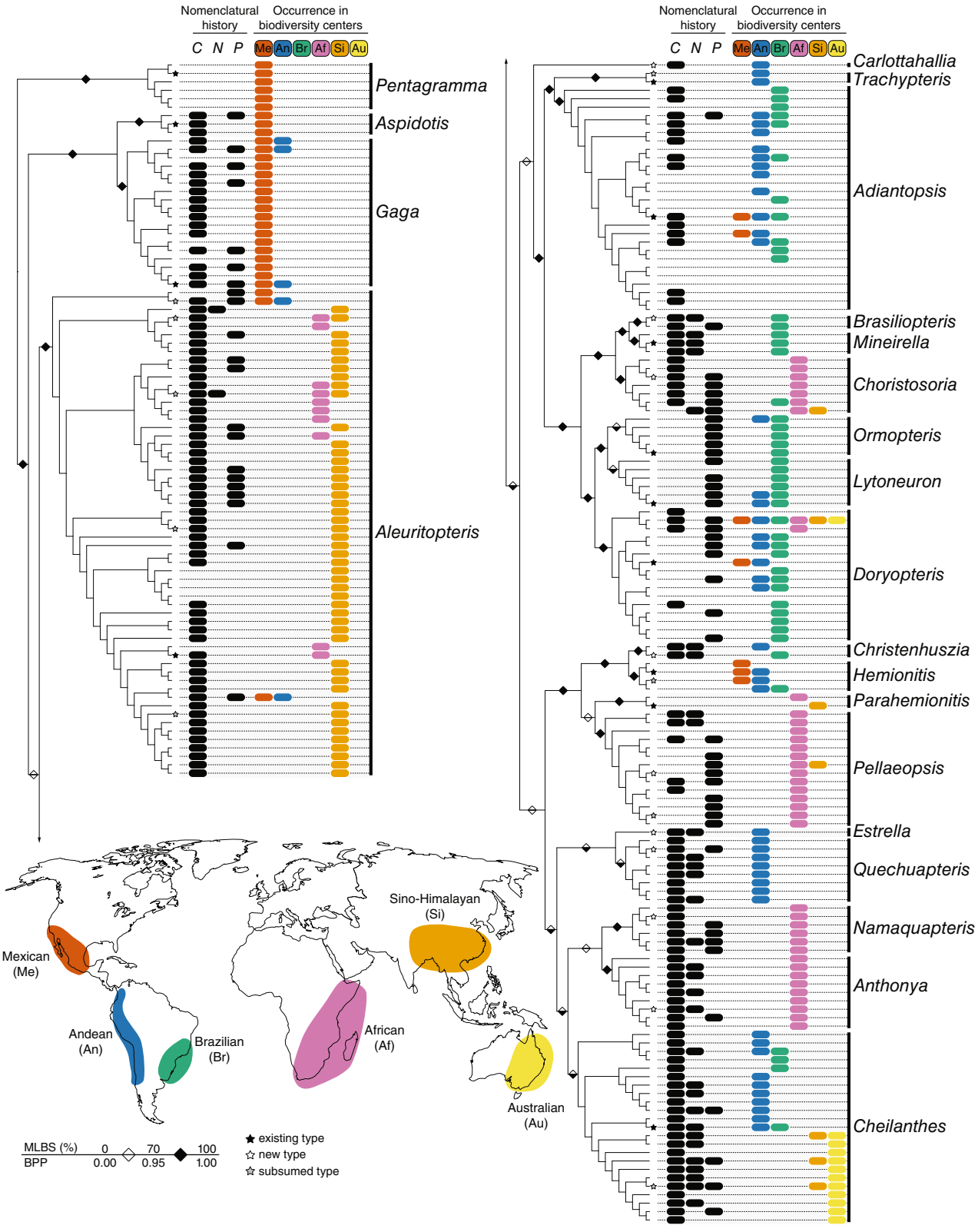

Fig. 2. Phylogeny, nomenclatural history, and distributions of hemionitid ferns. Cladogram based on consensus tree derived from Bayesian analysis of the three-gene dataset (223 species). Maximum likelihood bootstrap support (MLBS) and Bayesian posterior probability (BPP) are indicated for select nodes with triangles above and below branches, respectively (open for poor support and filled for strong support). Black ovals indicate species that have current or historical combinations in *Cheilanthes*, C; *Notholaena*, N; or *Pellaea*, P. Colored ovals indicate presence of a given taxon in cheilanthoid biodiversity centers, as defined by Tryon & Tryon (1973; see map). Stars at tips denote existing (black), new (white, this study), or subsumed (gray) types.

(Sigel & al., 2011), and its occurrence is sporadic even within some species of *Aleuritopteris* (e.g., *A. argentea*, *A. tamburii*, and *A. duclouxii*; Zhang & al., 2013). Considering the overall morphological similarity of *Aleuritopteris* and *Oeosporangium* and the fact that the species assigned to them are inextricably intermingled in our phylogenetic tree (suppl. Fig. S2), we see no other option than to combine these groups under the older generic name *Aleuritopteris*.

Mildella is circumscribed by Hassler (2004–2023) to include three Mexican/Caribbean species (*M. fallax*, *M. intramarginalis*, *M. leonardii*), and one east Asian species (*M. nitidula*). The topology of our phylogenetic tree mirrors these geographic differences, with *M. nitidula* deeply nested in the largely Eurasian *Aleuritopteris* s.l. clade (see above), while *M. intramarginalis* (the type of *Mildella*) and *M. fallax* form a strongly supported clade sister to this group (suppl. Fig. S2). Several additional Asian species assigned to *Mildella* in the monographic treatment of Hall & Lellinger (1967) are nested within *Aleuritopteris* s.l. and, like *M. nitidula*, they are easily accommodated within the expanded genus. Although the name *Mildella* could be maintained for the Mexican-Caribbean species based on the tree topology shown (suppl. Fig. S2), we have been unable to identify any morphological features distinguishing this small clade from *Aleuritopteris* s.l. and therefore accommodate them here within the larger group.

Table 2. Generic placements of 354 confirmed or suspected hemionitid species.

Genus	Prior	Current	Change	New combinations
Adiantopsis	35	35	–	–
Aleuritopteris	57	100	43	40
Anthonya	–	11	11	11 + 5
Aspidotis	4	4	–	–
Brasiliopteris	–	2	2	2
Carlottahallia	–	1	1	1
Cheilanthes	89	29	(60)	–
Choristosoria	–	14	14	13 + 3
Christenhusziа	–	2	2	2
Doryopteris	47	41	(6)	1
Estrella	–	1	1	1
Gaga	19	19	–	–
Hemionitis	7	7	–	–
Lytoneuron	16	16	–	–
Mildella	4	–	(4)	–
Mineirella	5	5	–	–
Namaquapteris	–	6	6	6 + 1
Notholaena	1	–	(1)	–
Oeosporangium	38	–	(38)	–
Ormopteris	5	5	–	–
Parahemionitis	1	3	2	2
Pellaea	16	–	(16)	–
Pellaeopsis	–	18	18	18
Pentagramma	6	6	–	–
Quechuapteris	–	9	9	9
Trachypteris	4	3	(1)	–
Incertae sedis	–	17	17	–

Prior placements are based on predominant usage, in most cases extrapolated from PPG I (2016) and aligning with World Ferns (Hassler, 2004–2023). Current placements follow the revised classification presented herein, with increases and (decreases) noted. Newly described genera appear in bold. Counts of new species-level + subspecific combinations are also provided.

Species commonly treated in *Doryopteris* are resolved in several places in our tree (suppl. Fig. S2). Most, including the generitype *D. palmata*, compose a large clade (here recognized as *Doryopteris* s.str.) sister to *Lytoneuron* and *Ormopteris*. All three of these genera are largely or exclusively distributed in South America, and most species previously ascribed to *Doryopteris* but not found in this region are phylogenetically divergent. Several "*Doryopteris*" species from southeast Asia form a clade sister to all other members of Pteridaceae subfam. Cheilanthoideae; these are not hemionitids and have been placed in the genus *Calciphilopteris* by Yesilyurt & Schneider (2010). Our study indicates that the Malagasy endemic, *Doryopteris cordifolia*, is phylogenetically isolated from *Doryopteris* s.str. as well, situated in an altogether different part of the hemionitid tree sister to *Parahemionitis arifolia* (suppl. Fig. S2). Although these two species share some obvious morphological similarities (e.g., the sterile leaves of the former and all leaves of the latter are cordate), they were not previously thought to be related. Here, we treat them together as *Parahemionitis* s.l.

Three additional African/Malagasy species typically ascribed to *Doryopteris* (*D. pedatoides*, *D. pilosa*, *D. madagascariensis*) are resolved in a clade sister to *Parahemionitis* s.l., where they are intermixed with similarly distributed species usually placed in either *Pellaea* or *Cheilanthes*. The type of *Pellaea* (*P. atropurpurea*) falls well outside the hemionitid clade (Fig. 1) and, as such, that generic name would be inappropriately applied here. And, although the type of *Cheilanthes* (*C. micropteris*) is a hemionitid, it belongs to a lineage that is deeply separated from this largely African clade sister to *Parahemionitis* s.l. and its application here would be blocked by the nomenclatural priority of the more closely related *Hemionitis*. In any case, the focal clade does include the types of both *Pellaeopsis* (*P. articulata* = *P. angulosa*) and *Pteridella* (*P. doniana*); we here take up the older name *Pellaeopsis* for this morphologically diverse group of African species.

Two other species predominantly ascribed to *Pellaea* (*P. pteroides*, *P. calomelanos*) are resolved within hemionitids (suppl. Fig. S2), forming a mostly African clade with species often attributed to *Cheilanthes*. Because both *Pellaea* and

Cheilanthes are unavailable (see discussion above), a different name is required. Given that the type of *Choristosoria* (*C. pteroides*) is resolved therein, we here take up this name for the lineage.

All remaining species included in our analysis have generally been treated in *Cheilanthes*. However, they do not form a monophyletic group and instead appear in several distinct positions in our tree (suppl. Fig. S2). Two narrow Brazilian endemics (*C. regnelliana*, *C. pohliana*) form a small well-supported clade that is sister to the (recently named) South American genus *Mineirella*. These two species are quite distinct from *Mineirella* morphologically and we here describe a new genus (*Brasiliopteris*; Fig. 3) to accommodate them. In another part of the phylogeny, two additional South American "*Cheilanthes*" species (*C. cantangensis*, *C. hassleri*) are together strongly supported as sister to *Hemionitis* s.str. However, these lineages are highly divergent and we therefore treat *C. cantangensis* and *C. hassleri* in a new genus, *Christenhuszia*. The South American taxon commonly called *Cheilanthes poeppigiana* occupies a remarkably isolated position in our phylogeny (suppl. Fig. S2). The species itself is morphologically heterogeneous and our molecular analyses reveal significant genetic divergence between the sampled morphotypes (suppl. Fig. S1), together suggesting that more than one species may be present. We here propose the new genus *Carlottahallia* to encompass this species complex.

The remaining 47 species in our analyses that were previously ascribed to *Cheilanthes* do form a clade that includes the type of *Cheilanthes*, but it is weakly supported and not morphologically definable. The five clades therein, however, are generally better supported and more easily circumscribed (and, in many cases, also geographically distinct). We advocate treating each of these clades as a separate genus, with four of five newly described herein. A group of nine Andean endemics is weakly supported as sister to the other species in this lineage (suppl. Fig. S2). The earliest divergence in this Andean group reveals *C. mollis* (also referred to as *Notholaena mollis*) as sister to the others. Given its morphological distinctiveness (and the poor support for its placement), we here treat it in the new monospecific genus *Estrella* (Fig. 3). The other eight species are here accommodated in the new genus *Quechuapteris* (Fig. 4). All of the African species recently included in *Cheilanthes* s.str. by Ponce & Scataglini (2022) form a weakly supported clade in our analyses (Fig. 2, suppl. Fig. S2). However, the two subclades therein are considerably more robust, and we propose recognizing two genera, *Namaquapteris* and *Anthonya* (Fig. 4), based on their morphological divergence. The remaining sampled species are distributed in the Andean, Brazilian, Sino-Himalayan, and Australian centers. Although morphologically quite diverse, members of this clade share a distinctive trait (reduction in spore number per sporangium in sexual species from 64 to 32) and are here treated together as *Cheilanthes* s.str.

Based on our phylogenetic analyses of 223 species and our morphological investigations, we favor the recognition of 22 hemionitid genera (Fig. 2). All but four of these (*Ormopteris*, *Lytoneuron*, *Quechuapteris*, *Cheilanthes*) are reasonably well-supported, with both maximum likelihood bootstrap score greater than 70 and a Bayesian posterior probability greater than 0.95 (suppl. Fig. S2). Nine circumscriptions (*Hemionitis*, *Adiantopsis*, *Ormopteris*, *Trachypteris*, *Aspidotis*, *Pentagramma*, *Gaga*, *Lytoneuron*, *Mineirella*) are consistent with those of most other recent studies. *Aleuritopteris* is expanded (to include *Oeosporangium* and *Mildella*) and the previously monospecific *Parahemionitis* is likewise expanded to include two additional species. *Doryopteris* and *Cheilanthes* are, in turn, more narrowly defined, whereas *Choristosoria* and *Pellaeopsis* are resurrected. Seven genera (*Carlottahallia*, *Brasiliopteris*, *Christenhuszia*, *Estrella*, *Quechuapteris*, *Namaquapteris*, *Anthonya*) are newly described to accommodate divergent clades.

There are 131 species thought to belong to the hemionitid clade that are not included in our analyses (Appendix 2). For the most part, these species can be confidently ascribed to one of the 22 recognized genera based on morphology and we provide new combinations for them, if applicable, in our Taxonomic Treatment below. However, there are 17 species (listed as "incertae sedis" in Appendix 2) for which additional study will be necessary to ascertain their proper generic placement.

■ TAXONOMIC TREATMENT

Adiantopsis Fée, Mém. Foug. 5. (Gen. Filic.): 145. 1852 – Type (designated by Christensen, Index Filic.: xli. 1906): ***Adiantopsis radiata*** (L.) Fée (≡ *Adiantum radiatum* L.).

Comments. – Monophyletic (Fig. 2, suppl. Fig. S2) based on included sampling (27 of 35 species; Table 2; Appendices 1, 2). See also Link-Pérez & al. (2011) and Schuettpelz & al. (2014).

Aleuritopteris Fée, Mém. Foug. 5. (Gen. Filic.): 153–154. 1852 – Type (designated by Christensen, Index Filic.: xlii. 1906): ***Aleuritopteris farinosa*** (Forssk.) Fée (≡ *Pteris farinosa* Forssk.).

= *Oeosporangium* Vis. in Atti Reale Ist. Veneto Sci. Lett. Arti, ser. 6, 12: 663. 1867 – Type: *Oeosporangium szovitsii* (Fisch. & C.A.Mey ex Hohen.) Vis. (≡ *Cheilanthes szovitsii* Fisch. & C.A.Mey ex Hohen.) [= ***Aleuritopteris persica*** (Bory) Windham].

= *Mildella* Trevis. in Rendiconti Reale Ist. Lombardo Sci. 9: 810. 1877 – Type: *Mildella intramarginalis* (Kaulf. ex Link) Trevis. (≡ *Pteris intramarginalis* Kaulf. ex Link ≡ ***Aleuritopteris intramarginalis*** (Kaulf. ex Link) Windham).

= *Sinopteris* C.Chr. & Ching in Bull. Fan Mem. Inst. Biol. 4 (10): 359. 1933 – Type: *Sinopteris grevilleoides* (Christ) C.Chr. & Ching (≡ *Cheilanthes grevilleoides* Christ ≡ ***Aleuritopteris grevilleoides*** (Christ) X.C. Zhang).

= *Negripteris* Pic.Serm. in Nuovo Giorn. Bot. Ital., n.s., 53: 130. 1946 – Type: *Negripteris scioana* (Chiov.) Pic.Serm. (≡ *Mohria scioana* Chiov. ≡ ***Aleuritopteris scioana*** (Chiov.) Fraser-Jenk.).

= *Leptolepidium* K.H.Shing & S.K.Wu in Acta Bot. Yunnan. 1(1): 115. 1979 – Type (designated by Fraser-Jenkins in Pakistan Syst. 5: 89. 1991): ***Aleuritopteris leptolepis*** (Fraser-Jenk.) Fraser-Jenk. (≡ *Cheilanthes leptolepis* Fraser-Jenk.).

Comments. – Monophyletic (Fig. 2, suppl. Fig. S2) based on included sampling (58 of 100 species; Table 2; Appendices 1, 2). Note that over the last two centuries, numerous

Fig. 3. Photographs of newly described hemionitid fern genera *Brasiliopteris* (**A–F**) and *Estrella* (**G–I**). **A**, *B. pohliana*, habit; **B**, *B. pohliana*, habit; **C**, *B. pohliana*, detail of fertile leaf; **D**, *B. regnelliana*, habit; **E**, *B. regnelliana*, leaf; **F**, *B. regnelliana*, detail of fertile leaf; **G**, *E. mollis*, habit; **H**, *E. mollis*, adaxial view of lamina; **I**, *E. mollis*, abaxial view of lamina. — Images via iNaturalist, cropped from originals, and used with CC BY-NC 4.0 license (https://creativecommons.org/licenses/by-nc/4.0), unless otherwise specified (see Appendix 4 for details).

hemionitid fern species have been placed in *Allosorus*, which predates all other hemionitid genera except *Hemionitis*. Nonetheless, this name is not applicable to hemionitid ferns and has been proposed for rejection (Fraser-Jenkins & al., 2017); both the Nomenclature Committee for Vascular Plants and the General Committee subsequently recommended acceptance of the proposal, which was formally approved at the XX International Botanical Congress.

Aleuritopteris acrostica (Balb.) Windham & Schuettp., **comb. nov.** ≡ *Pteris acrostica* Balb., Elenco: 98. 1801 ≡ *Cheilanthes acrostica* (Balb.) Tod. in Giorn. Sci. Nat.

Fig. 4. Photographs of newly described hemionitid fern genera *Quechuapteris* (**A–C**), *Namaquapteris* (**D–F**), and *Anthonya* (**G–I**). **A**, *Q. pruinata*, habit; **B**, *Q. pruinata*, detail of pinnae; **C**, *Q. glauca*, habit; **D**, *Namaquapteris robusta*, habit; **E**, *N. hastata*, habit; **F**, *N. hastata*, adaxial view of lamina; **G**, *A. eckloniana*, habit; **H**, *A. hirta*, habit; **I**, *A. hirta*, detail of pinnae. — Images via iNaturalist, cropped from originals, and used with CC BY 4.0 license (https://creativecommons.org/licenses/by/4.0), unless otherwise specified (see Appendix 4 for details).

Econ. Palermo 1(10): 215. 1866 ≡ *Allosorus acrosticus* (Balb.) Christenh. in Willdenowia 42(2): 284. 2012 ≡ *Oeosporangium pteridioides* subsp. *acrosticum* (Balb.) Fraser-Jenk. & Pariyar in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 259. 2016 ≡ *Oeosporangium acrosticum* (Balb.) L.Sáez & Aymerich in Orsis 31: 33. 2017 ≡ *Hemionitis acrostica* (Balb.) Mosyakin in Phytotaxa 373 (2): 165. 2018.

Aleuritopteris belangeri (Bory) Windham & Schuettp., **comb. nov.** ≡ *Pteris belangeri* Bory in Bélanger, Voy. Indes Or. 2: 44. 1833 ≡ *Pteridella belangeri* (Bory) Mett. ex Kuhn in Kersten, Reis. Ost-Afr. 3(3): 16. 1879 ≡ *Cheilanthes belangeri* (Bory) C.Chr., Index Filic. 3: 172. 1905 ≡ *Cheilosoria belangeri* (Bory) Ching & K.H.Shing, Gloss. Terms Names Ferns: 39. 1982 ≡ *Oeosporangium belangeri* (Bory) Fraser-Jenk. in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 255. 2016 ≡ *Hemionitis belangeri* (Bory) Christenh. in Christenhusz & al., Global Fl. 4: 10. 2018.

Aleuritopteris chinensis (Baker) Windham & Schuettp., **comb. nov.** ≡ *Notholaena chinensis* Baker in Gard. Chron., n.s., 14: 494. 1880 ≡ *Cheilanthes chinensis* (Baker) Domin in Biblioth. Bot. 85(1): 133. 1913 ≡ *Oeosporangium chinense* (Baker) Fraser-Jenk. in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 2: 451. 2018 ≡ *Hemionitis chinensis* (Baker) Christenh. in Christenhusz & al., Global Fl. 4: 11. 2018.

Aleuritopteris chusana (Hook.) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes chusana* Hook., Sp. Fil. 2: 95, t. 106B. 1852 ≡ *Cheilanthes mysurensis* var. *chusana* (Hook.) Christ in Bull. Acad. Int. Géogr. Bot. 17: 149. 1907 ≡ *Cheilosoria chusana* (Hook.) Ching in J. Arnold Arbor. 64(1): 19. 1983 ≡ *Oeosporangium chusanum* (Hook.) Fraser-Jenk. in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 256. 2016 ≡ *Hemionitis chusana* (Hook.) Christenh. in Christenhusz & al., Global Fl. 4: 11. 2018.

Aleuritopteris coriacea (Decne.) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes coriacea* Decne. in Arch. Mus. Hist. Nat. 2: 190. 1841 ≡ *Allosorus coriaceus* (Decne.) Christenh. in Willdenowia 42(2): 284. 2012 ≡ *Oeosporangium coriaceum* (Decne.) Fraser-Jenk. & Pariyar in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 264. 2016 ≡ *Hemionitis morla* Christenh. in Christenhusz & al., Global Fl. 4: 18. 2018.

Aleuritopteris delicatula (Tagawa & K.Iwats.) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes delicatula* Tagawa & K.Iwats. in Acta Phytotax. Geobot. 25(1): 19. 1971 ≡ *Oeosporangium delicatulum* (Tagawa & K. Iwats.) Fraser-Jenk. & Pariyar in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 265. 2016 ≡ *Hemionitis delicatessa* Christenh. in Christenhusz & al., Global Fl. 4: 12. 2018, non *Hemionitis delicatula* (Maxon & Wheath.) Christenh. in Christenhusz & al., Global Fl. 4: 13. 2018.

Aleuritopteris ×duriensis (Mendonça & Vasc.) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes ×duriensis* Mendonça & Vasc. in Anais Inst. Vinho Porto 15(4): 47. 1956.

Aleuritopteris elegans (Poir.) Windham & Schuettp., **comb. nov.** ≡ *Pteris elegans* Poir. in Lamarck, Encycl. 5: 718. 1804 ≡ *Oeosporangium elegans* (Poir.) Fraser-Jenk. & Pariyar in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 256. 2016.

Aleuritopteris erythraea (Pic.Serm.) E.A.Hooper, **comb. nov.** ≡ *Cheilanthes erythraea* Pic.Serm. in Webbia 27: 420. 1973 ("1972") ≡ *Hemionitis erythraea* (Pic.Serm.) Christenh. in Christenhusz & al., Global Fl. 4: 13. 2018.

Aleuritopteris fallax (M.Martens & Galeotti) Windham & Schuettp., **comb. nov.** ≡ *Pteris fallax* M.Martens & Galeotti in Nouv. Mém. Acad. Roy. Sci. Bruxelles 15: 53, t. 14, fig. 2. 1842 ≡ *Mildella fallax* (M.Martens & Galeotti) G.L.Nesom in Phytologia 75(5): 384. 1993.

Aleuritopteris fragilis (Hook.) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes fragilis* Hook., Fil. Exot.: t. 96. 1859 ≡ *Cheilosoria fragilis* (Hook.) Ching & K.H.Shing, Gloss. Terms Names Ferns: 39. 1982 ≡ *Oeosporangium fragile* (Hook.) Fraser-Jenk. in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 265. 2016 ≡ *Hemionitis fragilis* (Hook.) Christenh. in Christenhusz & al., Global Fl. 4: 14. 2018.

Aleuritopteris guanchica (Bolle) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes guanchica* Bolle in Bonplandia 7: 107. 1859 ≡ *Allosorus guanchicus* (Bolle) Christenh. in Willdenowia 42(2): 284. 2012 ≡ *Oeosporangium guanchicum* (Bolle) Fraser-Jenk. & Pariyar in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 265. 2016 ≡ *Hemionitis guanchica* (Bolle) Christenh. in Christenhusz & al., Global Fl. 4: 15. 2018.

Aleuritopteris hancockii (Baker) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes hancockii* Baker in Bull. Misc. Inform. Kew 1895(99): 54. 1895 ≡ *Cheilosoria hancockii* (Baker) Ching & K.H.Shing, Gloss. Terms Names Ferns: 39. 1982 ≡ *Oeosporangium hancockii* (Baker) Fraser-Jenk. in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 257. 2016 ≡ *Hemionitis hancockii* (Baker) Christenh. in Christenhusz & al., Global Fl. 4: 15. 2018.

Aleuritopteris hispanica (Mett.) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes hispanica* Mett. in Abh. Senckenberg. Naturf. Ges. 3: 74. 1859 ≡ *Allosorus hispanicus*

(Mett.) Christenh. in Willdenowia 42(2): 284. 2012 ≡ *Oeosporangium hispanicum* (Mett.) Fraser-Jenk. & Pariyar in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 264. 2016 ≡ *Hemionitis hispanica* (Mett.) Christenh. in Christenhusz & al., Global Fl. 4: 15. 2018.

Aleuritopteris* ×*iberica (Rasbach & Reichst.) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes* ×*iberica* Rasbach & Reichst. in Webbia 35(2): 264. 1982 ≡ *Allosorus* ×*ibericus* (Rasbach & Reichst.) Rumsey in Fern Gaz. 19(7): 277. 2014 ≡ *Oeosporangium* ×*ibericum* (Rasbach & Reichst.) Arana & Mor.-Saiz in Phytotaxa 433(3): 191. 2020 ≡ *Hemionitis* ×*iberica* (Rasbach & Reichst.) F.M.Vázquez in Folia Bot. Extremadur. 15: 149. 2021.

Aleuritopteris insignis (Ching) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes insignis* Ching in Northwest Institute of Botany CAS, Fl. Tsinling. 2: 208, t. 18, fig. 7–9. 1974 ≡ *Cheilosoria insignis* (Ching) Ching & K.H.Shing, Gloss. Terms Names Ferns: 39. 1982 ≡ *Oeosporangium insigne* (Ching) Fraser-Jenk. in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 265. 2016 ≡ *Hemionitis insignis* (Ching) Christenh. in Christenhusz & al., Global Fl. 4: 16. 2018.

Aleuritopteris* ×*insularis (Rasbach & Reichst.) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes* ×*insularis* Rasbach & Reichst. in Webbia 35(2): 266. 1982 ≡ *Allosorus* ×*insularis* (Rasbach & Reichst.) Rumsey in Fern Gaz. 19(7): 277. 2014 ≡ *Oeosporangium* ×*insulare* (Rasbach & Reichst.) Arana & Mor.-Saiz in Phytotaxa 433(3): 191. 2020 ≡ *Hemionitis* ×*insularis* (Rasbach & Reichst.) F.M.Vázquez in Folia Bot. Extremadur. 15: 149. 2021.

Aleuritopteris intramarginalis (Kaulf. ex Link) Windham & Schuettp., **comb. nov.** ≡ *Pteris intramarginalis* Kaulf. ex Link, Hort. Berol. 2: 34. 1833 ≡ *Cheilanthes intramarginalis* (Kaulf. ex Link) Hook., Sp. Fil. 2: 112. 1852 ≡ *Pellaea intramarginalis* (Kaulf. ex Link) J.Sm., Cult. Ferns: 31. 1857 ≡ *Mildella intramarginalis* (Kaulf. ex Link) Trevis. in Rendiconti Reale Ist. Lombardo Sci., ser. 2, 9: 810. 1877 ≡ *Hemionitis intramarginalis* (Kaulf. ex Link) Christenh. in Christenhusz & al., Global Fl. 4: 16. 2018.

Aleuritopteris* ×*kochiana (Rasbach, Reichst. & Schneller) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes* ×*kochiana* Rasbach, Reichst. & Schneller in Webbia 37(1): 48. 1983 ≡ *Allosorus* ×*kochianus* (Rasbach, Reichst. & Schneller) Rumsey in Fern Gaz. 19(7): 277. 2014 ["*Allosorus* ×*kochianus* (Rasbach, Reichst. & Schneller) L. Sáez & Aymerich in Orsis 29: 26. 2015", isonym] ≡ *Oeosporangium* ×*kochianus* (Rasbach, Reichst. & Schneller) L.Sáez & Aymerich in Orsis 31: 33. 2017 ≡ *Hemionitis* ×*kochiana* (Rasbach, Reichst. & Schneller) F.M.Vázquez in Folia Bot. Extremadur. 15: 149. 2021.

Aleuritopteris* ×*kurdica (Rasbach & Reichst.) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes* ×*kurdica* Rasbach & Reichst. in Webbia 37(1): 58. 1983 ≡ *Allosorus* ×*kurdicus* (Rasbach & Reichst.) Rumsey in Fern Gaz. 19(7): 2014 ≡ *Oeosporangium* ×*kurdicum* (Rasbach & Reichst.) Fraser-Jenk. & Pariyar in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 266. 2016.

Aleuritopteris leonardii (Maxon) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes leonardii* Maxon in J. Wash. Acad. Sci. 14: 87. 1924 ≡ *Mildella leonardii* (Maxon) C.C.Hall & Lellinger in Amer. Fern J. 57(3): 126. 1967 ≡ *Hemionitis leonardii* (Maxon) Christenh. in Christenhusz & al., Global Fl. 4: 16. 2018.

Aleuritopteris mairei (Brause) Windham & Schuettp., **comb. nov.** ≡ *Pellaea mairei* Brause in Hedwigia 54(2): 201–202, t. 4. 1914 ≡ *Mildella mairei* (Brause) C.C.Hall & Lellinger in Amer. Fern J. 57(3): 133. 1967 ≡ *Cheilanthes brausei* Fraser-Jenk., Taxon. Revis. Indian Subcontinental Pteridophytes: 122. 2008, non Brause (1914) ≡ *Oeosporangium mairei* (Brause) Fraser-Jenk. in Annot. Checkl. Ind. Pterid. 1: 265. 2016.

Aleuritopteris* ×*malacitensis (Rasbach & Reichst.) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes* ×*malacitensis* Rasbach & Reichst. in Webbia 35(2): 269. 1982 ≡ *Allosorus* ×*malacitensis* (Rasbach & Reichst.) Rumsey in Fern Gaz. 19(7): 277. 2014 ≡ *Oeosporangium* ×*malacitense* (Rasbach & Reichst.) Arana & Mor.-Saiz in Phytotaxa 433(3): 191. 2020 ≡ *Hemionitis* ×*malacitensis* (Rasbach & Reichst.) F.M.Vázquez in Folia Bot. Extremadur. 15: 149. 2021.

Aleuritopteris* ×*marchettiana (Rasbach, Reichst. & Schneller) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes* ×*marchettiana* Rasbach, Reichst. & Schneller in Webbia 37(1): 55. 1983 ≡ *Allosorus* ×*marchettianus* (Rasbach, Reichst. & Schneller) Rumsey in Fern Gaz. 19(7): 277. 2014 ≡ *Oeosporangium* ×*marchettianum* (Rasbach, Reichst. & Schneller) Arana & Mor.-Saiz in Phytotaxa 433(3): 191. 2020 ≡ *Hemionitis* ×*marchettiana* (Rasbach, Reichst. & Schneller) F.M.Vázquez in Folia Bot. Extremadur. 15: 149. 2021.

Aleuritopteris* ×*meridionalis (F.M.Vazquez) Windham & Schuettp., **comb. nov.** ≡ *Hemionitis* ×*meridionalis* F.M. Vázquez in Folia Bot. Extremadur. 15: 150. 2021.

Aleuritopteris nitidula (Wall. ex Hook.) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes nitidula* Wall. ex Hook., Sp. Fil. 2: 112. 1852 ≡ *Pellaea nitidula* (Wall. ex Hook.) Baker in Hooker & Baker, Syn. Fil.: 149. 1867 ≡ *Mildella nitidula* (Wall. ex Hook.) C.C.Hall & Lellinger in Amer. Fern J. 57(3): 127. 1967 ≡ *Oeosporangium nitidulum* (Wall. ex Hook.) Fraser-Jenk. in

Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 257. 2016 ≡ *Hemionitis nitidula* (Wall. ex Hook.) Christenh. in Christenhusz & al., Global Fl. 4: 18. 2018.

Aleuritopteris patula (Baker) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes patula* Baker in J. Bot. 26(7): 225. 1888 ≡ *Pellaea patula* (Baker) Ching in Acta Phytotax. Sin. 10(4): 302. 1965 ≡ *Cheilosoria patula* (Baker) P.S. Wang in Wang & Wang, Pterid. Fl. Guizhou: 188. 2001 ≡ *Oeosporangium patulum* (Baker) Fraser-Jenk. in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 265. 2016 ≡ *Hemionitis patula* (Baker) Christenh. in Christenhusz & al., Global Fl. 4: 19. 2018.

Aleuritopteris paupercula (Christ) Windham & Schuettp., **comb. nov.** ≡ *Pteris paupercula* Christ in Bull. Acad. Int. Géogr. Bot., n.s., 16: 131. 1906 ≡ *Pellaea paupercula* (Christ) Ching in Bull. Fan Mem. Inst. Biol. 2(10): 203, t. 17. 1931 ('*pauperculae*') ≡ *Mildella paupercula* (Christ) C.C.Hall & Lellinger in Amer Fern J. 57(3): 131. 1967 ≡ *Cheilanthes christii* Fraser-Jenk. & Yatsk. in Indian Fern J. 27(1–2): 213. 2010, non Mett. (1856) ≡ *Oeosporangium pauperculum* (Christ) Fraser-Jenk. & Pariyar in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid.: 1: 265. 2016.

Aleuritopteris persica (Bory) Windham & Schuettp., **comb. nov.** ≡ *Notholaena persica* Bory in Bélanger, Voy. Indes Or., 2: 23. 1833 ≡ *Cheilanthes persica* (Bory) Mett. ex Kuhn in Bot. Zeitung (Berlin) 26: 234. 1868 ≡ *Allosorus persicus* (Bory) Christenh. in Willdenowia 42(2): 284. 2012 ≡ *Hemionitis persica* (Bory) Christenh. in Christenhusz & al., Global Fl. 4: 19. 2018.

Aleuritopteris pteridioides (Reichard) Windham & Schuettp., **comb. nov.** ≡ *Polypodium pteridioides* Reichard, Syst. Pl. 4: 424. 1780 ≡ *Cheilanthes pteridioides* (Reichard) C.Chr., Index Filic.: 178. 1905 ≡ *Allosorus pteridioides* (Reichard) Christenh. in Willdenowia 42(2): 284. 2012 ≡ *Oeosporangium pteridioides* (Reichard) Fraser-Jenk. & Pariyar in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 258. 2016 ≡ *Hemionitis pteridioides* (Reichard) Christenh. in Christenhusz & al., Global Fl. 4: 19. 2018.

Aleuritopteris pulchella (Bory ex Willd.) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes pulchella* Bory ex Willd., Sp. Pl. 5(1): 456. 1810 ≡ *Oeosporangium pulchellum* (Bory ex Willd.) Fraser-Jenk. & Pariyar in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 264. 2016 ≡ *Hemionitis pulchella* (Bory ex Willd.) Christenh. in Christenhusz & al., Global Fl. 4: 20. 2018.

Aleuritopteris smithii (C.Chr.) Windham & Schuettp., **comb. nov.** ≡ *Pellaea smithii* C.Chr. in Acta Horti Gothob. 1(2): 84, t. 18a–c. 1924 ≡ *Mildella smithii* (C.Chr.) C.C.Hall & Lellinger in Amer. Fern J. 57(3): 132. 1967 ≡ *Cheilanthes smithii* (C.Chr.) R.M.Tryon in Amer. Fern J. 76(4): 185. 1986 ≡ *Oeosporangium smithii* (C.Chr.) Fraser-Jenk. & Pariyar in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 265. 2016 ≡ *Hemionitis smithii* (C.Chr.) Christenh. in Christenhusz & al., Global Fl. 4: 11. 2018.

Aleuritopteris straminea (Ching) Windham & Schuettp., **comb. nov.** ≡ *Pellaea straminea* Ching in Bull. Fan Mem. Inst. Biol. 2(10): 203, t. 17. 1931 ≡ *Mildella straminea* (Ching) C.C.Hall & Lellinger in Amer. Fern J. 57(3): 130. 1967 ≡ *Oeosporangium stramineum* (Ching) Fraser-Jenk. in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 260. 2016 ≡ *Hemionitis straminea* (Ching) Christenh. in Christenhusz & al., Global Fl. 4: 21. 2018.

Aleuritopteris ×teneriffae (Rasbach & Reichst.) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes ×teneriffae* Rasbach & Reichst. in Webbia 35(2): 262. 1982 ≡ *Allosorus ×teneriffae* (Rasbach & Reichst) Rumsey in Fern Gaz. 19(7): 277. 2014 ≡ *Oeosporangium ×teneriffae* (Rasbach & Reichst.) Arana & Mor.-Saiz in Phytotaxa 433(3): 191. 2020.

Aleuritopteris tinaei (Tod.) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes tinaei* Tod. in Giorn. Sci. Nat. Econ. Palermo 1: 217. 1866 ≡ *Allosorus tinaei* (Tod.) Christenh. in Willdenowia 42(2): 284. 2012 ≡ *Oeosporangium tinaei* (Tod.) Fraser-Jenk. in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 265. 2016.

Aleuritopteris tirajanae (T.S.Velázquez) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes tirajanae* T.S.Velázquez in Bot. Macaronés. 28: 22. 2013.

Aleuritopteris ×tolocensis (Rasbach, Reichst. & Schneller.) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes ×tolocensis* Rasbach, Reichst. & Schneller in Webbia 37(1): 52. 1983 ≡ *Allosorus ×tolocensis* (Rasbach, Reichst. & Schneller.) Rumsey in Fern Gaz. 19(7): 277. 2014 ≡ *Oeosporangium ×tolocense* (Rasbach, Reichst. & Schneller.) Arana & Mor.-Saiz in Phytotaxa 433(3): 192. 2020 ≡ *Hemionitis ×tolocensis* (Rasbach, Reichst. & Schneller.) F.M.Vázquez in Folia Bot. Extremadur. 15: 150. 2021.

Aleuritopteris trichophylla (Baker) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes trichophylla* Baker in Ann. Bot. (Oxford) 5(18): 211. 1891 ≡ *Pellaea trichophylla* (Baker) Ching in Acta Phytotax. Sin. 10(4). 302. 1965 ≡ *Oeosporangium trichophyllum* (Baker) Fraser-Jenk. in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 262. 2016 ≡ *Hemionitis trichophylla* (Baker) Christenh. in Christenhusz & al., Global Fl. 4: 22. 2018.

Aleuritopteris velutina (Tardieu & C.Chr.) Windham & Schuettp., **comb. nov.** ≡ *Notholaena velutina* Tardieu

& C.Chr. in Notul. Syst. (Paris) 6: 167, t. 1(5–7). 1938 ≡ *Cheilanthes velutina* (Tardieu & C.Chr.) Fraser-Jenk., New Sp. Syndr. Indian Pteridol.: 84. 1997 ≡ *Hemionitis velutina* (Tardieu & C.Chr.) Christenh. in Christenhusz & al., Global Fl. 4: 22. 2018.

Aleuritopteris yunnanensis (Ching) Windham & Schuettp., **comb. nov.** ≡ *Pellaea yunnanensis* Ching in Acta Phytotax. Sin. 20(2): 235. 1982 ≡ *Cheilanthes bhutanica* Fraser-Jenk. & Wangdi in Fern Gaz. 18(5): 220. 2009, non Brause (1913) ≡ *Oeosporangium yunnanense* (Ching) Fraser-Jenk. & Pariyar in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 264. 2016 ≡ *Hemionitis bhutanica* (Fraser-Jenk. & Wangdi) Christenh. in Christenhusz & al., Global Fl. 4: 10. 2018.

Anthonya Windham & Pryer, **gen. nov.** – Type: ***Anthonya hirta*** (Sw.) Windham & Pryer (≡ *Cheilanthes hirta* Sw.).

Diagnosis. – A clade of Subsaharan and Malagasy endemics differing from the strictly South American and Australasian genus *Cheilanthes* in having 64 (vs. 32 or 16) spores per sporangium or, if 32, the spores larger than those of 32-spored individuals of *Cheilanthes* s.str. (>57 μm vs. <57 μm); differing from most species of the newly described *Namaquapteris* and recircumscribed *Choristosoria* in having pubescent or glutinous leaf blades and terete rachises; further distinguished from most *Namaquapteris* species by having predominantly sclerotic, dark brown, black or bicolored (vs. membranous, pale, and concolorous) rhizome scales; differing from the recircumscribed genus *Pellaeopsis* in having discontinuous sori with relatively few (<20) sporangia arrayed on small (usually <2 mm) semicircular, triangular or oblong lobes of ultimate segments (vs. ± continuous sori with many [20 to >1000] sporangia paralleling the margins of larger [2 to 90 mm], entire or sparingly lobed ultimate segments).

Etymology. – Named for botanist Nicola C. Anthony, whose incredibly detailed study of South African cheilanthoid ferns (Anthony, 1984) made possible our taxonomic revision of the group.

Comments. – Monophyletic (Fig. 2, suppl. Fig. S2) based on included sampling (9 of 11 species; Table 2; Appendices 1, 2). The distribution of *Anthonya* extends from Kenya west to the Democratic Republic of the Congo, south to the Cape of Good Hope and east to the islands of Madagascar and Mauritius. The Republic of South Africa is the center of species diversity for the genus, with 10 of the 11 named species occurring in this region and two endemic to it.

Anthonya bergiana (Schltdl.) Windham & Pryer, **comb. nov.** ≡ *Cheilanthes bergiana* Schltdl., Adumbr. Pl. 5: 51. 1832 ≡ *Hypolepis bergiana* (Schltdl.) Hook., Sp. Fil. 2: 67. 1852 ≡ *Hemionitis bergiana* (Schltdl.) Christenh. in Christenhusz & al., Global Fl. 4: 10. 2018.

Anthonya ceterachoides (A.W.Klopper & Klopper) Windham & Pryer, **comb. nov.** ≡ *Cheilanthes ceterachoides* A.W.Klopper & Klopper in Crouch & al., Ferns S. Afr. Compreh. Guide: 747. 2011 ≡ *Hemionitis ceterachoides* (A.W.Klopper & Klopper) Christenh. in Christenhusz & al., Global Fl. 4: 11. 2018.

Anthonya contracta (Kunze) Windham & Pryer, **comb. nov.** ≡ *Cheilanthes hirta* var. *contracta* Kunze in Linnaea 10(5): 539. 1836 ≡ *Myriopteris contracta* (Kunze) Fée, Mém. Foug. 5 (Gen. Filic.): 149. 1852 ≡ *Cheilanthes contracta* (Kunze) Mett. ex Kuhn, Filic. Afr.: 70. 1868 ≡ *Hemionitis contracta* (Kunze) Christenh. in Christenhusz & al., Global Fl. 4: 12. 2018.

Anthonya depauperata (Baker) Windham & Pryer, **comb. nov.** ≡ *Cheilanthes depauperata* Baker in Ann. Bot. (Oxford) 5: 210. 1891 ≡ *Hemionitis depauperata* (Baker) Christenh. in Christenhusz & al., Global Fl. 4: 13. 2018.

Anthonya dinteri (Brause) Windham & Pryer, **comb. nov.** ≡ *Cheilanthes dinteri* Brause in Bot. Jahrb. Syst. 53(3–5): 385. 1915 ≡ *Hemionitis dinteri* (Brause) Christenh. in Christenhusz & al., Global Fl. 4: 13. 2018.

Anthonya eckloniana (Kunze) Windham & Pryer, **comb. nov.** ≡ *Notholaena eckloniana* Kunze in Linnaea 10(5): 501. 1836 ≡ *Cheilanthes eckloniana* (Kunze) Mett., Abh. Senckenberg. Naturf. Ges. 3: 66. 1859 ≡ *Hemionitis eckloniana* (Kunze) Christenh. in Christenhusz & al., Global Fl. 4: 13. 2018.

Anthonya hirta (Sw.) Windham & Pryer, **comb. nov.** ≡ *Cheilanthes hirta* Sw., Syn. Fil.: 128, 329. 1806 ≡ *Adiantum hirtum* (Sw.) Poir. in Lamarck, Encycl. Suppl. 1: 142. 1810 ≡ *Notholaena hirta* (Sw.) J.Sm. in J. Bot. (Hooker) 4: 50. 1841 ≡ *Myriopteris hirta* (Sw.) J.Sm., Ferns Brit. For.: 174. 1866 ≡ *Hemionitis hirta* (Sw.) Christenh. in Christenhusz & al., Global Fl. 4: 15. 2018.

Anthonya hirta subsp. ***brevipilosa*** (W.Jacobsen & N.H.G.Jacobsen) Windham & Pryer, **comb. & stat. nov.** ≡ *Cheilanthes hirta* var. *brevipilosa* W.Jacobsen & N.H.G. Jacobsen in Bothalia 18(1): 64, fig. 4g, h, 8, 9. 1988.

Anthonya hirta subsp. ***inferacampestris*** (W.Jacobsen & N.H.G.Jacobsen) Windham & Pryer, **comb. & stat. nov.** ≡ *Cheilanthes hirta* var. *inferacampestris* W.Jacobsen & N.H.G.Jacobsen in Bothalia 18(1): 71, fig. 18d, e, 20, 21. 1988.

Anthonya hirta subsp. ***laxa*** (Kunze) Windham & Pryer, **comb. & stat nov.** ≡ *Cheilanthes hirta* var. *laxa* Kunze in Linnaea 10(5): 540. 1836 ≡ *Cheilanthes hirta* [var. *brevipilosa* W.Jacobsen & N.H.G.Jacobsen] f. *laxa* (Kunze) W.Jacobsen & N.H.G.Jacobsen in Bothalia 18(1): 65. 1988.

Anthonya hirta subsp. ***nemorosa*** (W.Jacobsen & N.H.G. Jacobsen) Windham & Pryer, **comb. & stat. nov.** ≡ *Cheilanthes hirta* var. *nemorosa* W.Jacobsen & N.H.G. Jacobsen in Bothalia 18(1): 69, fig. 16, 17, 18a–c. 1988.

Anthonya hirta subsp. ***watermeyeri*** (Verdc.) Windham & Pryer, **comb. & stat. nov.** ≡ *Cheilanthes hirta* var. *watermeyeri* Verdc. in Polhill, Fl. Trop. E. Afr. Adiant.: 36. 2002.

Anthonya hyaloglandulosa (W.Jacobsen & N.H.G.Jacobsen) Windham & Pryer, **comb. nov.** ≡ *Cheilanthes hyaloglandulosa* W.Jacobsen & N.H.G.Jacobsen in S. African J. Bot. 51(2): 145. 1985 ≡ *Cheilanthes hirta* var. *hyaloglandulosa* (W.Jacobsen & N.H.G.Jacobsen) J.E.Burrows, S. African Ferns & Fern Allies: 138. 1990.

Anthonya marlothii (Hieron.) Windham & Pryer, **comb. nov.** ≡ *Notholaena marlothii* Hieron. in Bot. Jahrb. Syst. 46(3): 384. 1911 ≡ *Cheilanthes marlothii* (Hieron.) Domin in Biblioth. Bot. 85: 133. 1913 ["*Cheilanthes marlothii* (Hieron.) Schelpe" in Contr. Bolus Herb. 1: 74. 1969, isonym] ≡ *Hemionitis marlothii* (Hieron.) Christenh. in Christenhusz & al., Global Fl. 4: 17. 2018.

Anthonya nielsii (W.Jacobsen) Windham & Pryer, **comb. nov.** ≡ *Cheilanthes nielsii* W.Jacobsen, Ferns & Fern Allies of Southern Africa: 252. 1983 ≡ *Hemionitis nielsii* (W.Jacobsen) Christenh. in Christenhusz & al., Global Fl. 4: 18. 2018.

Anthonya parviloba (Sw.) Windham & Pryer, **comb. nov.** ≡ *Adiantum parvilobum* Sw. in J. Bot. (Schrader) 1800(2): 85. 1801 ≡ *Cheilanthes parviloba* (Sw.) Sw., Syn. Fil.: 128, 331. 1806 ≡ *Cheilanthes hirta* var. *parviloba* (Sw.) Kunze in Linnaea 10(5): 541. 1836 ≡ *Hemionitis parviloba* (Sw.) Christenh. in Christenhusz & al., Global Fl. 4: 19. 2018.

Aspidotis (Nutt. ex Hook.) Copel. in Ann. Cryptog. Phytopathol. 5 (Gen. Fil.): 68. 1947 ≡ *Hypolepis* sect. *Aspidotis* Nutt. ex Hook., Sp. Fil. 2: 70. 1852 – Type: ***Aspidotis californica*** (Hook.) Nutt. ex Copel. (≡ *Hypolepis californica* Hook.).

Comments. – Monophyletic (Fig. 2, suppl. Fig. S2) based on included sampling (3 of 4 species; Table 2; Appendices 1, 2). See also Li & al. (2012).

Brasiliopteris J.Prado, Schuettp. & Yatsk., **gen. nov.** – Type: ***Brasiliopteris pohliana*** (Mett.) J.Prado, Schuettp. & Yatsk. (≡ *Cheilanthes pohliana* Mett.).

Diagnosis. – Differs from *Mineirella* in having lamina 1–3-pinnate-pinnatisect throughout, linear-lanceolate to oblong-lanceolate (vs. lamina 1-pinnate only at base or lamina not fully divided, pentagonal or deltate); abaxial lamina surface visible through matted hairs (vs. abaxial lamina surface concealed by densely-matted hairs); segments short-stipitate (vs. segments adnate).

Etymology. – Named for Brazil (Portuguese spelling Brasil), to which the genus is endemic.

Comments. – Monophyletic (Fig. 2, suppl. Fig. S2) based on included sampling (2 of 2 species; Table 2; Appendices 1, 2). Endemic to Brazil.

Brasiliopteris pohliana (Mett.) J.Prado, Schuettp. & Yatsk., **comb. nov.** ≡ *Cheilanthes pohliana* Mett. in Abh. Senckenberg. Naturf. Ges. 3: 67. 1859 ≡ *Hemionitis pohliana* (Mett.) Christenh. in Christenhusz & al., Global Fl. 4: 19. 2018.

– "*Notholaena pohliana* Kunze", Farrnkräuter 1: 45. 1840, nom. nud.

Brasiliopteris regnelliana (Mett. ex Baker) J.Prado, Schuettp. & Yatsk., **comb. nov.** ≡ *Cheilanthes regnelliana* Mett. ex Baker in Martius, Fl. Bras. 1(2): 391. t. 43, fig. 1. 1870 ≡ *Pellaea regnelliana* (Mett. ex Baker) Prantl in Bot. Jahrb. Syst. 3(5): 420. 1882 ≡ *Gymnogramma regnelliana* (Mett. ex Baker) Christ in Schwacke, Pl. Nov. Mineir. 2: 18. 1900 ≡ *Hemionitis regnelliana* (Mett. ex Baker) Christenh. in Christenhusz & al., Global Fl. 4: 20. 2018.

Carlottahallia Windham, **gen. nov.** – Type: ***Carlottahallia poeppigiana*** (Mett. ex Kuhn) Windham (≡ *Cheilanthes poeppigiana* Mett. ex Kuhn).

Diagnosis. – Endemic to Andean South America and differing from other hemionitid ferns in having broad (mostly >2 mm wide), completely glabrous ultimate segments with raised, often laterally undulate midveins, and strongly differentiated, largely continuous pseudoindusia originating from prominent, abaxially situated, mostly triangular hydathodes.

Etymology. – Named for Carlotta C. Hall (1880–1949), a botanist at the University of California, Berkeley and an avid pteridologist who was working on a taxonomic treatment of this species complex at the time of her death.

Comments. – Seemingly monospecific, with the sole species sampled herein (Table 2; Appendices 1, 2).

Carlottahallia poeppigiana (Mett. ex Kuhn) Windham, **comb. nov.** ≡ *Cheilanthes poeppigiana* Mett. ex Kuhn in Linnaea 36(1): 84. 1869 ≡ *Hemionitis poeppigiana* (Mett. ex Kuhn) Christenh. in Christenhusz & al., Global Fl. 4: 19. 2018.

Cheilanthes Sw., Syn Fil.: 5, 126. 1806, nom. cons. – Type (designated by Maxon, Pteridophyt. Porto Rico 6(3): 428. 1926): ***Cheilanthes micropteris*** Sw.

= *Neurosoria* Mett. ex Kuhn. in Bot. Zeitung (Berlin) 27: 437. 1869 – Type: *Neurosoria pteroides* (R.Br.) Mett. & Kuhn. (≡ *Acrostichum pteroides* R.Br.).

= *Cheilosoria* Trevis. in Atti Reale Ist. Veneto Sci. Lett. Arti, ser. 6, 5(3): 579. 1877 – Type (designated by Weatherby in Amer. Fern J. 33(2): 68. 1943): *Cheilosoria tenuifolia*

(Burm.f.) Trevis. (≡ *Trichomanes tenuifolium* Burm.f. ≡ ***Cheilanthes tenuifolia*** (Burm.f.) Sw.).

Comments. – Monophyletic (Fig. 2, suppl. Fig. S2) based on included sampling (23 of 29 species; Table 2; Appendices 1, 2).

Choristosoria Mett. ex Kuhn in Kersten, Reis. Ost-Afr. 3(3): 13. 1879 – Type: ***Choristosoria pteroides*** (L.) Mett. ex Kuhn (≡ *Adiantum pteroides* L.).

Comments. – Monophyletic (Fig. 2, suppl. Fig. S2) based on included sampling (7 of 14 species; Table 2; Appendices 1, 2).

Choristosoria botswanae (Schelpe & N.C.Anthony) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes botswanae* Schelpe & N.C.Anthony in Contr. Bolus Herb. 10: 151. 1982 ≡ *Hemionitis botswanae* (Schelpe & N.C.Anthony) Christenh. in Christenhusz & al., Global Fl. 4: 10. 2018.

Choristosoria calomelanos (Sw.) Windham & Schuettp., **comb. nov.** ≡ *Pteris calomelanos* Sw. in J. Bot. (Schrader) 1800(2): 70. 1801 ≡ *Allosorus calomelanos* (Sw.) C.Presl, Tent. Pterid.: 153. 1836 ≡ *Pellaea calomelanos* (Sw.) Link, Fil. Spec.: 61. 1841 ≡ *Platyloma calomelanos* (Sw.) J.Sm. in Bot. Mag. 72(Companion): 21. 1846 ≡ *Notholaena calomelanos* (Sw.) Keyserl., Polyp. Herb. Bunge: 29. 1873 ≡ *Pteridella hastata* var. *calomelanos* (Sw.) Pirotta in Annuario Reale Ist. Bot. Roma 8(1): 18. 1903 ≡ *Hemionitis calomelanos* (Sw.) Christenh. in Christenhusz & al., Global Fl. 1(4): 11. 2018.

Choristosoria calomelanos subsp. ***swynnertoniana*** (Sim) Windham & Schuettp., **comb. & stat. nov.** ≡ *Pellaea swynnertoniana* Sim, Ferns S. Afr., ed. 2: 213, t. 101. 1915 ≡ *Pellaea calomelanos* var. *swynnertoniana* (Sim) Schelpe in J. S. African Bot. 30(4): 187. 1964.

Choristosoria dolomiticola (Schelpe) Windham & Schuettp., **comb. nov.** ≡ *Pellaea dolomiticola* Schelpe in J. S. African Bot. 34: 239, t. 3. 1968 ≡ *Cheilanthes dolomiticola* (Schelpe) Schelpe & N.C.Anthony in Contr. Bolus Herb. 10: 155. 1982 ≡ *Hemionitis dolomiticola* (Schelpe) Christenh. in Christenhusz & al., Global Fl. 4: 13. 2018.

Choristosoria glauca (Sim) Windham & Schuettp., **comb. & stat. nov.** ≡ *Pellaea hastata* var. *glauca* Sim, Handb. Ferns Kaffraria: 30, t. 19. 1891 ≡ *Pellaea viridis* var. *glauca* (Sim) Sim, Ferns S. Afr., ed. 2: 209, 210, t. 97. 1915 ≡ *Cheilanthes viridis* var. *glauca* (Sim) Schelpe & N.C.Anthony in Contr. Bolus Herb. 10: 155. 1982.

Choristosoria induta (Kunze) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes induta* Kunze in Linnaea 10(5): 538. 1836 ≡ *Myriopteris induta* (Kunze) Fée, Mém. Foug. 5 (Gen. Filic.): 149. 1852 ≡ *Hemionitis induta* (Kunze) Christenh. in Christenhusz & al., Global Fl. 4: 16. 2018.

Choristosoria involuta (Sw.) Windham & Schuettp., **comb. nov.** ≡ *Pteris involuta* Sw. in J. Bot. (Schrader) 1800(2): 69. 1801 ≡ *Allosorus involutus* (Sw.) C.Presl, Tent. Pterid.: 153. 1836 ≡ *Pellaea involuta* (Sw.) Baker in Hooker & Baker, Syn. Fil., ed. 2: 148. 1874 ≡ *Pteridella involuta* (Sw.) Mett. ex Kuhn in Kersten, Reis. Ost-Afr. 3(3): 15. 1879 ≡ *Pellaea viridis* var. *involuta* (Sw.) Schelpe in Bol. Soc. Brot., sér. 2, 41: 214. 1967 ≡ *Cheilanthes involuta* (Sw.) Schelpe & N.C.Anthony in Contr. Bolus Herb. 10: 155. 1982.

Choristosoria involuta subsp. ***obscura*** (N.C.Anthony) Windham & Schuettp., **comb. & stat. nov.** ≡ *Pellaea viridis* var. *obscura* N.C.Anthony in Contr. Bolus Herb. 10: 154. 1982 ≡ *Cheilanthes viridis* var. *obscura* N.C.Anthony in Contr. Bolus Herb. 10: 155. 1982 ≡ *Cheilanthes involuta* var. *obscura* (N.C.Anthony) N.C.Anthony in Contr. Bolus Herb. 11: 146. 1984 ≡ *Pellaea involuta* var. *obscura* (N.C.Anthony) Verdc. in Polhill, Fl. Trop. E. Africa, Adiant.: 18. 2002.

Choristosoria lacerata (N.C.Anthony & Schelpe) Windham & Schuettp., **comb. & stat. nov.** ≡ *Cheilanthes multifida* subsp. *lacerata* N.C.Anthony & Schelpe in Contr. Bolus Herb. 10: 153. 1982.

Choristosoria leucomelas (Mett. ex Kuhn) Windham & Schuettp., **comb. nov.** ≡ *Pteris leucomelas* Mett. ex Kuhn, Filic. Afr.: 83. 1868 ≡ *Pellaea leucomelas* (Mett.) Baker in Hooker & Baker, Syn. Fil., ed. 2: 478. 1874 ≡ *Pteridella leucomelas* (Mett.) Kuhn in Kersten, Reis. Ost-Afr. 3(3): 14, 90. 1879 ≡ *Allosorus leucomelas* (Mett.) Kuntze, Revis. Gen. Pl. 2: 806. 1891 ≡ *Pellaea calomelanos* var. *leucomelas* (Mett.) J.E.Burrows, S. African Ferns & Fern-Allies: 177. 1990.

Choristosoria multifida (Sw.) Windham & Schuettp., **comb. nov.** ≡ *Adiantum multifidum* Sw. in J. Bot. (Schrader) 1800(2): 85. 1801 ≡ *Cheilanthes multifida* (Sw.) Sw., Syn. Fil.: 129, 334. 1806 ≡ *Hemionitis multifida* (Sw.) Christenh. in Christenhusz & al., Global Fl. 4: 18. 2018.

Choristosoria namaquensis (Baker) Windham & Schuettp., **comb. nov.** ≡ *Pellaea namaquensis* Baker in J. Bot. 12: 199. 1874 ≡ *Allosorus namaquensis* (Baker) Kuntze, Revis. Gen. Pl. 2: 806. 1891 ≡ *Cheilanthes namaquensis* (Baker) Schelpe & N.C.Anthony in Contr. Bolus Herb. 10: 155. 1982 ≡ *Hemionitis namaquensis* (Sw.) Christenh. in Christenhusz & al., Global Fl. 4: 18. 2018.

Choristosoria pentagona (Schelpe & N.C.Anthony) Windham & Schuettp., **comb. nov.** ≡ *Cheilanthes pentagona* Schelpe & N.C.Anthony in Contr. Bolus Herb. 10: 152. 1982.

– "*Hemionitis pentagona* (Schelpe & N.C.Anthony) Christenh." in Christenhusz & al., Global Fl. 4: 20. 2018, not validly published.

Choristosoria quadripinnata (Forssk.) Windham & Schuettp., **comb. nov.** ≡ *Pteris quadripinnata* Forssk., Fl. Aegypt.-Arab.: 186. 1775 ≡ *Allosorus quadripinnatus* (Forssk.) C.Presl, Tent. Pterid.: 154. 1836 ≡ *Cheilanthes quadripinnata* (Forssk.) Kuhn, Filic. Afr.: 74. 1868 ≡ *Pteridella quadripinnata* (Forssk.) Mett. ex Kuhn in Kersten, Reis. Ost-Afr. 3(3): 16.1879 ≡ *Pellaea quadripinnata* (Forssk.) Prantl in Bot. Jahrb. Syst. 3: 420. 1882 ≡ *Hemionitis quadripinnata* (Forssk.) Christenh. in Christenhusz & al., Global Fl. 4: 20. 2018.

Choristosoria viridis (Forssk.) Windham & Schuettp., **comb. nov.** ≡ *Pteris viridis* Forssk., Fl. Aegypt.-Arab.: 186. 1775 ≡ *Adiantum viride* (Forssk.) Vahl, Symb. Bot. 3: 104. 1794 ≡ *Cheilanthes viridis* (Forssk.) Sw., Syn. Fil.: 127. 1806 ≡ *Pteridella viridis* (Forssk.) Mett. ex Kuhn in Kersten, Reis. Ost-Afr. 3(3): 16. 1879 ≡ *Pellaea viridis* (Forssk.) Prantl in Bot. Jahrb. Syst. 3: 420. 1882 ≡ *Allosorus viridis* (Forssk.) Kuntze, Revis. Gen. Pl. 2: 806. 1891 ≡ *Cassebeera viridis* (Forssk.) Kaulf. ex Farw. in Amer. Midl. Naturalist 12: 281. 1931 ≡ *Oeosporangium viride* (Forssk.) Fraser-Jenk. & Pariyar in Fraser-Jenkins & al., Annot. Checkl. Ind. Pterid. 1: 263. 2016 ≡ *Hemionitis viridis* (Forssk.) Christenh. in Christenhusz & al., Global Fl. 4: 22. 2018.

Choristosoria viridis subsp. ***macrophylla*** (Kunze) Windham & Schuettp., **comb. & stat. nov.** ≡ *Cheilanthes hastata* var. *macrophylla* Kunze in Linnaea 10(5): 532. 1836 ≡ *Cheilanthes macrophylla* (Kunze) Kunze in Linnaea 28: 244, 307. 1850 ≡ *Pellaea macrophylla* (Kunze) Fée, Mém. Foug. 5 (Gen. Filic.): 129. 1852 ≡ *Allosorus hastatus* var. *macrophyllus* (Kunze) Pappe & Rawson, Syn. Fil. Afr. Austr.: 30. 1858 ≡ *Pellaea hastata* var. *macrophylla* (Kunze) Hook., Sp. Fil.: 146. 1858 ≡ *Pellaea viridis* var. *macrophylla* (Kunze) Sim, Ferns S. Afr., ed. 2: 208, 209, t. 99. 1915 ≡ *Cheilanthes viridis* var. *macrophylla* (Kunze) Schelpe & N.C.Anthony in Contr. Bolus Herb. 10: 155. 1982.

Christenhuszia Schuettp. & J.Prado, **gen. nov.** – Type: ***Christenhuszia hassleri*** (Weath.) Schuettp. & J.Prado (≡ *Notholaena hassleri* Weath.).

Diagnosis. – Differing from superficially similar, densely scaly species of *Cheilanthes* in having 64 (vs. 32 or 16) spores per sporangium, cristate or rugulate (vs. verrucate, echinate, or psilate) spore surfaces, and ultimate segments with sporadic, segmented hairs (vs. glabrous or with scattered, linear-lanceolate scales) on adaxial surfaces; differing from densely scaly species of *Notholaena* (their original taxonomic placement) in having sporangia distributed along the veins for much of their length (vs. confined to segment margins) as well as the absence of whitish or yellowish powder (farina) on abaxial blade surfaces; differing from *Hemionitis* (their sister clade) in having bipinnate-pinnatifid leaves with ultimate segments <5 mm (vs. simple, palmatifid, or pinnate leaves with much larger ultimate segments).

Etymology. – The generic name recognizes Maarten J.M. Christenhusz (1976–), a prominent botanist who has made significant contributions to fern and angiosperm classifications. He has had an outsized impact on the taxonomy of hemionitids by establishing a new combination or new name (in *Hemionitis*) for the vast majority of species in this diverse group.

Comments. – Presumably monophyletic (Fig. 2, suppl. Fig. S2) with both accepted species sampled herein (Table 2; Appendices 1, 2).

Christenhuszia cantangensis (R.M.Tryon) Schuettp. & J.Prado, **comb. nov.** ≡ *Notholaena cantangensis* R.M. Tryon in Rhodora 63: 81, t. 1257, fig. 6. 1961 ≡ *Cheilanthes cantangensis* (R.M.Tryon) R.M.Tryon in Fieldiana, Bot. 22: 32. 1989 ≡ *Hemionitis cantangensis* (R.M. Tryon) Christenh. in Christenhusz & al., Global Fl. 4: 11. 2018.

Christenhuszia hassleri (Weath.) Schuettp. & J.Prado, **comb. nov.** ≡ *Notholaena hassleri* Weath. in Lilloa 6: 274, t. 4. 1941 ≡ *Cheilanthes hassleri* (Weath.) Ponce in Darwiniana 45(2): 240. 2007 ≡ *Hemionitis hassleri* (Weath.) Christenh. in Christenhusz & al., Global Fl. 4: 15. 2018.

Doryopteris J.Sm. in J. Bot. (Hooker) 3: 404. 1841, emend. Yesilyurt in Phytotaxa 221(2): 115. 2015, nom. cons. – Type (designated by Morton in Amer. Fern J. 34: 26. 1944): ***Doryopteris palmata*** (Willd.) J.Sm. (≡ *Pteris palmata* Willd.).

= *Cassebeera* Kaulf., Enum. Filic.: 216. 1824, nom. rej. – Type: *Cassebeera triphyllum* (Lam.) Kaulf. (≡ *Adiantum triphyllum* Lam.).

= *Bakeriopteris* C.Chr., Index Filic.: 148. 1905 – Type: *Bakeriopteris pinnata* (Kaulf.) Kuntze (≡ *Cassebeera pinnata* Kaulf.).

= *Tryonella* Pic.Serm. in Webbia 29: 14. 1975 ("1974") ≡ *Heteropteris* Fée, Crypt. Vasc. Brésil 1: 123. 1869, nom. illeg. non Kunth (1822).

Comments. – Monophyletic (Fig. 2, suppl. Fig. S2) based on included sampling (16 of 41 species; Table 2; Appendices 1, 2). See also Yesilyurt & al. (2015).

Doryopteris incisa (Kunze ex Mett.) J.Prado & Schuettp., **comb. nov.** ≡ *Cheilanthes incisa* Kunze ex Mett. in Abh. Senckenberg. Naturf. Ges. 3: 88, t. 3, fig. 28–31. 1859 ≡ *Hypolepis incisa* (Kunze ex Mett.) C.Chr., Index Filic.: 371. 1905 ≡ *Hemionitis xayide* Christenh. in Christenhusz & al., Global Fl. 4: 23. 2018, non Blanco (1837).

Although generally treated in *Cheilanthes*, this species is here resolved within *Doryopteris* s.str. Its gross morphology is strikingly different; however, like other species of *Doryopteris*, it has sclerified leaf sinuses (these most common proximally and most visible abaxially).

Estrella Windham, **gen. nov.** – Type: ***Estrella mollis*** (Kunze) Windham (≡ *Notholaena mollis* Kunze).

Diagnosis. – Distinguished from most cheilanthoid ferns by an abundance of appressed, stellate trichomes forming a dense mat concealing abaxial blade surfaces. Separable from the few other cheilanthoid taxa having stellate trichomes (i.e., isolated, non-hemionitid species of *Notholaena*, *Pellaea*, and *Myriopteris*) by the following combination of traits: (1) mostly entire rhizome scales, at least some of which are bicolored with a dark midstripe and narrow, pale margins; (2) oblong to narrowly lanceolate leaf blades that are fully 2–3-pinnate; (3) the lack of either a powdery exudate (farina) or multiseriate scales on abaxial blade surfaces; and (4) nearly exclusive production of 32 small (<57 μm) spores per sporangium.

Etymology. – Named for its distinctive stellate leaf trichomes as well as its near-endemic occurrence in Chile, a country symbolized by its single-starred flag known as "La Estrella Solitaria."

Comments. – Seemingly monospecific, with the sole species sampled herein (Table 2; Appendices 1, 2).

Estrella mollis (Kunze) Windham, **comb. nov.** ≡ *Notholaena mollis* Kunze in Linnaea 9(1): 54. 1834 ≡ *Cheilanthes mollis* (Kunze) C.Presl, Tent. Pterid.: 160. 1836 ≡ *Hemionitis mollis* (Kunze) Christenh. in Christenhusz & al., Global Fl. 4: 18. 2018.

Gaga Pryer, Fay W.Li & Windham in Syst. Bot. 37(4): 855. 2012 – Type: ***Gaga marginata*** (Kunth) Fay W.Li & Windham (≡ *Cheilanthes marginata* Kunth).

Comments. – Monophyletic (Fig. 2, suppl. Fig. S2) based on included sampling (18 of 19 species; Table 2; Appendices 1, 2). See also Li & al. (2012).

Hemionitis L., Sp. Pl.: 1077. 1753 – Type (designated by Kaulfuss, Enum. Filic.: 68, 198. 1824): ***Hemionitis palmata*** L.

= *Gymnopteris* Bernh. in J. Bot. (Schrader) 1799(1): 297. 1799 ≡ *Gymnogramma* Desv. in Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin 5(3): 304. 1811, nom. superfl. ≡ *Neurogramma* Link, Fil. Spec.: 138. 1841, nom. superfl. – Type: *Gymnopteris rufa* (L.) Bernh. ex Underw. (≡ *Pteris rufa* L.).

Comments. – Monophyletic (Fig. 2, suppl. Fig. S2) based on included sampling (4 of 7 species; Table 2; Appendices 1, 2).

Lytoneuron (Klotzsch) Yesilyurt in Phytotaxa 221(2): 116. 2015 ≡ *Doryopteris* sect. *Lytoneuron* Klotzsch in Linnaea 20(3): 343. 1847 – Type: ***Lytoneuron lomariaceum*** (Klotzsch) Yesilyurt (≡ *Doryopteris lomariacea* Klotzsch).

Comments. – Monophyletic (Fig. 2, suppl. Fig. S2) based on included sampling (6 of 16 species; Table 2; Appendices 1, 2). See also Yesilyurt & al. (2015).

Mineirella Ponce & Scataglini in J. Syst. Evol. 60(2): 274. 2022 – Type: ***Mineirella geraniifolia*** (Weath.) Ponce & Scataglini (≡ *Notholaena geraniifolia* Weath.).

Comments. – Monophyletic (Fig. 2, suppl. Fig. S2) based on included sampling (3 of 5 species; Table 2; Appendices 1, 2). See also Ponce & Scataglini (2022).

Namaquapteris Windham & Pryer, **gen. nov.** – Type: ***Namaquapteris capensis*** (Thunb.) Windham & Pryer (≡ *Adiantum capense* Thunb.).

Diagnosis. – A clade of African endemics differing from the strictly South American and Australasian genus *Cheilanthes* in having 64 (vs. 32 or 16) spores per sporangium (except for *N. schimperi*, which is distinct from the species of *Cheilanthes* s.str. in having nearly glabrous, 3-pinnate-pinnatifid, pentagonal leaf blades with narrow, prominently serrate ultimate segments and prominent pseudoindusial lobes protecting sori confined to sinuses between the teeth); differing from the newly described *Anthonya* and recircumscribed *Pellaeopsis* by their combination of largely glabrous leaf blades, rachises with a rounded, longitudinal groove (often bordered by narrow wings) adaxially, and predominantly membranous, pale, and concolored rhizome scales; differing from the recircumscribed genus *Choristosoria* by their generally smaller stature (mostly <12 cm tall but up to 50 cm in *N. schimperi*), almost complete lack of leaf hairs, and predominantly membranous, pale, and concolored rhizome scales.

Etymology. – The genus is named for Namaqualand (northwestern South Africa and southern Namibia), the center of species diversity for the genus, with five of the six named species occurring in this area.

Comments. – Monophyletic (Fig. 2, suppl. Fig. S2), with all six accepted species sampled herein (Table 2; Appendices 1, 2). Endemic to Africa extending from Ethiopia and South Sudan west to northern Nigeria and south to the Cape of Good Hope.

Namaquapteris capensis (Thunb.) Windham & Pryer, **comb. nov.** ≡ *Adiantum capense* Thunb., Prodr. Pl. Cap.: 173. 1800 ≡ *Cheilanthes capensis* (Thunb.) Sw., Syn. Fil.: 128. 1806 ≡ *Adiantopsis capensis* (Thunb.) Fée, Mém. Foug. (Gen. Filic.) 5: 145. 1852 ≡ *Hypolepis capensis* (Thunb.) Hook., Sp. Fil. 2: 71, t. 77C. 1852 ≡ *Hemionitis capensis* (Thunb.) Christenh. in Christenhusz & al., Global Fl. 4: 11. 2018.

Namaquapteris deltoidea (Kunze) Windham & Pryer, **comb. nov.** ≡ *Cheilanthes deltoidea* Kunze in Linnaea 10(5): 535. 1836 ≡ *Pellaea deltoidea* (Kunze) Baker in Hooker & Baker, Syn. Fil.: 146. 1867 ≡ *Allosorus deltoideus* (Kunze) Kuntze, Revis. Gen. Pl. 2: 806. 1891 ≡ *Doryopteris deltoidea* (Kunze) Diels in Engler & Prantl., Nat. Pflanzenfam. 1(4): 269. 1899 ≡ *Hemionitis deltoidea* (Hook. ex Baker) Christenh. in Christenhusz & al., Global Fl. 4: 13. 2018.

Namaquapteris deltoidea subsp. ***silicicola*** (Klopper & A.E. van Wyk) Windham & Pryer, **comb. nov.** ≡ *Cheilanthes deltoidea* subsp. *silicicola* Klopper & A.E.van Wyk in Bothalia 41: 204, fig. 21, 22. 2011.

Namaquapteris hastata (L.f.) Windham & Pryer, **comb. nov.** ≡ *Adiantum hastatum* L.f., Suppl.: 447. 1781 ≡ *Pteris hastata* (L.f.) Sw., J. Bot. (Schrader) 1800(2). 69. 1801, nom. illeg., non Thunb. (1800) ≡ *Cheilanthes hastata* (L.f.) Kunze in Linnaea 10(5): 532. 1836 ≡ *Allosorus hastatus* (L.f.) C.Presl, Tent. Pterid.: 153. 1836 ≡ *Cassebeera hastata* (L.f.) J.Sm. in J. Bot. (Hooker) 4: 159. 1841 ≡ *Pellaea hastata* (L.f.) Link, Fil. Spec.: 60. 1841 ≡ *Platyloma hastata* (L.f.) Lowe, Ferns 3: t. 32. 1857 ≡ *Pellaea hastata* (L.f.) Schelpe in J. S. African Bot. 29: 93. 1963, nom. illeg.

Namaquapteris kunzei (Mett.) Windham & Pryer, **comb. nov.** ≡ *Cheilanthes kunzei* Mett. in Abh. Senckenberg. Naturf. Ges. 27: 71, t. 3, fig. 6, 7. 1859 ≡ *Cheilosoria kunzei* (Mett.) Trev. in Atti Reale Ist. Veneto Sci. Lett. Arti, ser. 5, 5(3): 580. 1877 ≡ *Hemionitis kunzei* (Mett.) Christenh. in Christenhusz & al., Global Fl. 4: 16. 2018.

Namaquapteris robusta (Kunze) Windham & Pryer, **comb. nov.** ≡ *Allosorus robustus* Kunze in Linnaea 10(5): 502. 1836 ≡ *Onychium robustum* (Kunze) Fée, Mém. Foug. 5 (Gen. Filic.): 132. 1852 ≡ *Cryptogramma robusta* (Kunze) Pappe & Pappe & Rawson, Syn. Fil. Afr. Austr.: 32. 1858 ≡ *Pellaea robusta* (Kunze) Hook., Sp. Fil. 2: 147. 1858 ≡ *Doryopteris robusta* (Kunze) Diels in Engler & Prantl., Nat. Pflanzenfam. 1(4): 269. 1899 ≡ *Cheilanthes robusta* (Kunze) R.M.Tryon in Contr. Gray Herb 143: 72. 1942 ≡ *Hemionitis robusta* (Kunze) Christenh. in Christenhusz & al., Global Fl. 4: 20. 2018.

Namaquapteris schimperi (Kunze) Windham & Pryer, **comb. nov.** ≡ *Cheilanthes schimperi* Kunze, Farrnkräuter 1: 52, t. 26. 1840 ≡ *Hypolepis schimperi* (Kunze) Hook., Sp. Fil. 2: 70. 1852 ≡ *Adiantopsis schimperi* (Kunze) T.Moore, Index Fil. 1: 37. 1857 ≡ *Aspidotis schimperi* (Kunze) Pic.Serm. in Webbia 7: 326. 1950 ≡ *Hemionitis schimperi* (Kunze) Christenh. in Christenhusz & al., Global Fl. 4: 21. 2018.

Ormopteris J.Sm. ex J.Sm., Hist. Fil.: 281. 1875 – Type: ***Ormopteris gleichenioides*** (Gardner) J.Sm. (≡ *Cassebeera gleichenioides* Gardner).

Comments. – Monophyletic (Fig. 2, suppl. Fig. S2), with all five accepted species sampled herein (Table 2; Appendices 1, 2). See also Yesilyurt & al. (2015).

Parahemionitis Panigrahi in Indian Fern J. 9(1–2): 244. 1993 ("1992") – Type: ***Parahemionitis arifolia*** (Burm.f.) Panigrahi (≡ *Asplenium arifolium* Burm.f.).

Comments. – Presumably monophyletic (Fig. 2, suppl. Fig. S2), with two of three accepted species sampled herein (Table 2; Appendices 1, 2).

Parahemionitis cordifolia (Baker) Windham & Schuettp. **comb. nov.** ≡ *Pteris cordifolia* Baker in J. Bot. 29: 4. 1891 ≡ *Doryopteris cordifolia* (Baker) Diels in Engler & Prantl, Nat. Pflanzenfam. 1(4): 270. 1899 ≡ *Hemionitis goabica* Christenh. in Christenhusz & al., Global Fl. 4: 14. 2018.

Parahemionitis humbertii (Tardieu) Windham & Schuettp., **comb. nov.** ≡ *Doryopteris humbertii* Tardieu in Humbert, Fl. Madagasc. Fam. 5(1): 144. 1958 ≡ *Hemionitis humbertii* (Tardieu) Christenh. in Christenhusz & al., Global Fl. 4: 15. 2018.

Pellaeopsis J.Sm., Hist. Fil.: 289. 1875 – Type: *Pellaeopsis articulata* (Kaulf. ex Spreng.) J.Sm. (≡ *Pteris articulata* Kaulf. ex Spreng.) [= ***Pellaeopsis angulosa*** (Bory ex Willd.) Windham ≡ *Pellaea angulosa* (Bory ex Willd.) Baker].

= *Pteridella* Mett. ex Kuhn in Kersten, Reis. Ost-Afr. 3(3): 13. 1879 – Type (designated by Christensen, Index Filic.: xl. 1906): *Pteridella doniana* (Hook.) Mett. ex Kuhn (≡ *Pellaea doniana* Hook.).

Comments. – Monophyletic (Fig. 2, suppl. Fig. S2) based on included sampling (14 of 18 species; Table 2; Appendices 1, 2).

Pellaeopsis angulosa (Bory ex Willd.) Windham, **comb. nov.** ≡ *Pteris angulosa* Bory ex Willd., Sp. Pl. 5: 377. 1810 ≡ *Pteridella angulosa* (Bory ex Willd.) Mett. ex Kuhn in Kersten, Reis. Ost-Afr. 3(3): 15. 1879 ≡ *Hemionitis angulosa* (Bory ex Willd.) Christenh. in Christenhusz & al., Global Fl. 4: 19. 2018.

Pellaeopsis boivinii (Hook.) Windham, **comb. nov.** ≡ *Pellaea boivinii* Hook., Sp. Fil. 2: 147, t. 118A. 1858 ≡ *Hemionitis boivinii* (Hook.) Christenh. in Christenhusz & al., Global Fl. 4: 10. 2018.

Pellaeopsis buchananii (Baker) Windham, **comb. nov.** ≡ *Cheilanthes buchananii* Baker in Biblioth. Bot. 20 (85-1): 133. 1913.

Pellaeopsis deboeri (Verdc.) Windham, **comb. nov.** ≡ *Cheilanthes deboeri* Verdc. in Polhill, Fl. Trop. E. Africa, Adiant.: 40. 2002 ≡ *Hemionitis deboeri* (Verdc.) Christenh. in Christenhusz & al., Global Fl. 4: 12. 2018.

Pellaeopsis doniana (J.Sm.) Windham, **comb. nov.** ≡ *Pellaea doniana* J.Sm. in Hooker, Sp. Fil. 2: 137, t. 125A. 1858 ≡ *Pteridella doniana* (J.Sm.) Mett. ex Kuhn in Kersten, Reis. Ost-Afr. 3(3): 13. 1879 ≡ *Hemionitis doniana*

(J.Sm.) Christenh. in Christenhusz & al., Global Fl. 4: 13. 2018.

Pellaeopsis dura (Willd.) Windham, **comb. nov.** ≡ *Pteris dura* Willd., Sp. Pl. 5(1): 376. 1810 ≡ *Litobrochia dura* (Willd.) T.Moore, Index. Fil.: 44. 1857 ≡ *Pellaea dura* (Willd.) Hook., Sp. Fil. 2: 139, t. 113A. 1858 ≡ *Platyloma durum* (Willd.) J.Sm., Hist. Fil.: 165. 1875.

Pellaeopsis inaequalis (Kunze) Windham, **comb. nov.** ≡ *Notholaena inaequalis* Kunze, Farrnkräuter 1: 146, t. 64, fig. 1. 1844 ≡ *Cheilanthes inaequalis* (Kunze) Mett. in Abh. Senckenberg. Naturf. Ges. 3: 68, t. 3, fig. 4. 1859 ≡ *Hemionitis inaequalis* (Kunze) Christenh. in Christenhusz & al., Global Fl. 4: 16. 2018.

Pellaeopsis lanceolata (Bonap.) Windham, **comb. nov.** ≡ *Notholaena lanceolata* Bonap., Notes Ptéridol. 5: 65. 1917 ≡ *Notholaena madagascarica* Bonap., Notes Ptéridol. 5: 66. 1917 ≡ *Cheilanthes perrieri* J.P.Roux in Bothalia 40 (1): 81. 2010 ≡ *Hemionitis perrieri* (J.P.Roux) Christenh. in Christenhusz & al., Global Fl. 4: 19. 2018.

Pellaeopsis leachii (Schelpe) Windham, **comb. nov.** ≡ *Notholaena leachii* Schelpe in J. S. African Bot. 30: 185, fig. La. 1964 ≡ *Hemionitis leachii* (Schelpe) Christenh. in Christenhusz & al., Global Fl. 4: 16. 2018.

Pellaeopsis longipilosa (Bonap.) Windham, **comb. nov.** ≡ *Pellaea longipilosa* Bonap., Notes Ptéridol. 15: 33. 1924 ≡ *Hemionitis longipilosa* (Bonap.) Christenh. in Christenhusz & al., Global Fl. 4: 17. 2018.

Pellaeopsis madagascariensis (Tardieu) Windham, **comb. nov.** ≡ *Doryopteris madagascariensis* Tardieu in Humbert, Fl. Madagasc. Fam. 5(1): 148. 1958 ≡ *Hemionitis tenrecorum* Christenh. in Christenhusz & al., Global Fl. 4: 22. 2018, non Christenhusz (2018).

Pellaeopsis pectiniformis (Baker) Windham, **comb. nov.** ≡ *Pellaea pectiniformis* Baker in Hooker & Baker, Syn. Fil., ed. 2: 147. 1874 ≡ *Hemionitis pectinatiformis* (Baker) Christenh. in Christenhusz & al., Global Fl. 4: 19. 2018.

Pellaeopsis pedatoides (Desv.) Windham, **comb. nov.** ≡ *Pteris pedatoides* Desv. in Mém. Soc. Linn. Paris 6(3): 293, t. 7, fig. 2. 1827 ≡ *Doryopteris pedatoides* (Desv.) Kuhn in Kersten, Reis. Ost-Afr. 3(3): 63. 1879 ≡ *Hemionitis pedatoides* (Desv.) Christenh. in Christenhusz & al., Global Fl. 4: 19. 2018.

Pellaeopsis pilosa (Poir.) Windham, **comb. nov.** ≡ *Pteris pilosa* Poir. in Lamarck, Encycl. 5: 717. 1804 ≡ *Doryopteris pilosa* (Poir.) Kuhn in Kersten, Reis. Ost-Afr. 3(3): 63. 1879 ≡ *Hemionitis pilosa* (Poir.) Christenh. in Christenhusz & al., Global Fl. 4: 19. 2018.

Pellaeopsis schippersii (Verdc.) Windham, **comb. nov.** ≡ *Pellaea schippersii* Verdc. in Polhill, Fl. Trop. E. Africa, Adiant.: 12. 2002.

Pellaeopsis schweinfurthii (Hieron. ex Diels) Windham, **comb. nov.** ≡ *Pellaea schweinfurthii* Hieron. ex Diels in Engler & Prantl, Nat. Pflanzenfam. 1(4): 267. 1899.

Pellaeopsis similis (F.Ballard) Windham, **comb. nov.** ≡ *Cheilanthes similis* F.Ballard in Kew Bull. 12(1): 47. 1957 ≡ *Hemionitis similis* (F.Ballard) Christenh. in Christenhusz & al., Global Fl. 4: 21. 2018.

Pellaeopsis tomentosa (Bonap.) Windham, **comb. nov.** ≡ *Pellaea tomentosa* Bonap., Notes Ptérid. 5: 64. 1917 ≡ *Hemionitis hydornii* Christenh. in Christenhusz & al., Global Fl. 4: 15. 2018, non Raddi (1819).

Pentagramma Yatsk., Windham & E.Wollenw. in Amer. Fern J. 80(1): 13. 1990 – Type: ***Pentagramma triangularis*** (Kaulf.) Yatsk., Windham & E.Wollenw. (≡ *Gymnogramma triangularis* Kaulf.).

Comments. – Monophyletic (Fig. 2, suppl. Fig. S2), with all six accepted species sampled herein (Table 2; Appendices 1, 2). See also Schuettpelz & al. (2015).

Quechuapteris Windham, **gen. nov.** – Type: ***Quechuapteris glauca*** (Cav.) Windham (≡ *Pteris glauca* Cav.).

Diagnosis. – A clade of Andean South American endemics differing from *Cheilanthes* in having (1) 64 (vs. 32 or 16) spores per sporangium (or, if 32-spored, the spores significantly larger than those of *Cheilanthes* s.str. [>57 µm]) and (2) and sclerotic, shiny, mostly dark brown or bicolored (vs. membranous, dull, and mostly concolored light brown) petiole scales; distinguished from the only Andean species of *Gaga* (*G. marginata*) in having non-decurrent pseudoindusia; differing from superficially similar Andean species of *Myriopteris* in: (1) the absence of multiseriate scales on leaf rachises and costae (present in *M. myriophylla* and *M. notholaenoides*), (2) dimorphic abaxial blade trichomes in *Q. buchtienii* and *Q. fraseri* (monomorphic in their doppelganger *M. aurea*), and (3) sclerotic, shiny, mostly dark brown or bicolored petiole scales (membranous, dull, and mostly concolored light brown in *M. lendigera* and *M. microphylla*).

Etymology. – This genus is endemic to the Andes of South America and is named for the largest indigenous group in the region.

Comments. – Monophyletic (Fig. 2, suppl. Fig. S2), with 8 of 9 accepted species sampled herein (Table 2; Appendices 1, 2).

Quechuapteris andina (Hook.) Windham, **comb. nov.** ≡ *Cheilanthes andina* Hook., Sp. Fil. 2: 115. 1852.

Quechuapteris buchtienii (Rosenst.) Windham, **comb. nov.** ≡ *Notholaena buchtienii* Rosenst. in Repert. Spec. Nov.

Regni Veg. 5: 238. 1908 ≡ *Hemionitis buchtienii* (Rosenst.) Christenh. in Christenhusz & al., Global Fl. 4: 11. 2018.

Quechuapteris fraseri (Mett. ex Kuhn) Windham, **comb. nov.** ≡ *Cheilanthes fraseri* Mett. ex Kuhn in Linnaea 36: 83. 1869 ≡ *Hemionitis fraseri* (Mett. ex Kuhn) Christenh. in Christenhusz & al., Global Fl. 4: 14. 2018.

Quechuapteris glauca (Cav.) Windham, **comb. nov.** ≡ *Pteris glauca* Cav., Descr. Pl.: 269. 1802 ≡ *Cheilanthes glauca* (Cav.) Mett. in Abh. Senckenberg. Naturf. Ges. 3: 75, t. 3, fig. 18, 19. 1859 ≡ *Hemionitis glauca* (Cav.) Christenh. in Christenhusz & al., Global Fl. 4: 14. 2018.

Quechuapteris glutinosa (M.Kessler & A.R.Sm.) Windham, **comb. nov.** ≡ *Cheilanthes glutinosa* M.Kessler & A.R. Sm. in Brittonia 59(2): 188, fig. 2A, B. 2007 ≡ *Hemionitis glutinosa* **(**M.Kessler & A.R.Sm.) Christenh. in Christenhusz & al., Global Fl. 4: 14. 2018.

Quechuapteris hypoleuca (Kunze) Windham, **comb. nov.** ≡ *Notholaena hypoleuca* Kunze in Linnaea 9(1): 54. 1834 ≡ *Cheilanthes hypoleuca* (Kunze) Mett. in Abh. Senckenberg. Naturf. Ges. 3: 66. 1859 ≡ *Hemionitis hypoleuca* (Kunze) Christenh. in Christenhusz & al., Global Fl. 4: 15. 2018.

Quechuapteris pilosa (Goldm.) Windham, **comb. nov.** ≡ *Cheilanthes pilosa* Goldm. in Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19 (Suppl. 1): 455. 1843 ≡ *Hemionitis graograman* Christenh. in Christenhusz & al., Global Fl. 4: 14. 2018.

Quechuapteris pruinata (Kaulf.) Windham, **comb. nov.** ≡ *Cheilanthes pruinata* Kaulf., Enum. Filic.: 210. 1824 ≡ *Hemionitis pruinata* (Kaulf.) Christenh. in Christenhusz & al., Global Fl. 4: 19. 2018.

Quechuapteris rufopunctata (Rosenst.) Windham, **comb. nov.** ≡ *Cheilanthes rufopunctata* Rosenst. in Meded. Rijks-Herb. 19: 9. 1913 ≡ *Hemionitis rufopunctata* (Rosenst.) Christenh. in Christenhusz & al., Global Fl. 4: 20. 2018.

Trachypteris André ex Christ in Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss. 36: 150. 1899 – Type: ***Trachypteris aureonitens*** (Hook.) André ex Christ (≡ *Acrostichum aureonitens* Hook.).

= *Saffordia* Maxon in Smithsonian Misc. Collect. 61(4): 2, t. 1–2. 1913 – Type: *Saffordia induta* Maxon (≡ *Trachypteris induta* (Maxon) R.M.Tryon & A.F.Tryon).

Comments. – Monophyletic (Fig. 2, suppl. Fig. S2) based on included sampling (2 of 3 species; Table 2; Appendices 1, 2).

■ AUTHOR CONTRIBUTIONS

Conceptualization: ES, MDW, GY & KMP. Validation: ES, MDW, JP & KTP. Formal analysis: ES & KTP. Investigation: ES, MDW, JP, EAH, GY, LH, KTP & KMP. Resources: ES, MDW, JP, EAH, GY, LH & KMP. Data curation: ES, MDW & KTP. Writing (original draft): ES & MDW. Writing (review and editing): ES, MDW, JP, EAH, GY, LH, KTP & KMP. Visualization: KTP & KMP. Project administration: ES. Funding acquisition: ES, MDW, JP, EAH, GY, LH, KTP & KMP.

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■ LITERATURE CITED

Anthony, N.C. 1984. A revision of the southern African species of *Cheilanthes* Swartz and *Pellaea* Link (Pteridaceae). *Contr. Bolus Herb.* 11: 1–293.

Applequist, W. 2023. Report of the Nomenclature Committee for Vascular Plants: 73. *Taxon* 72: 179–204. https://doi.org/10.1002/tax.12871

Bouma, W.L., Ritchie, P. & Perrie, L.R. 2010. Phylogeny and generic taxonomy of the New Zealand Pteridaceae ferns from chloroplast *rbcL* DNA sequences. *Austral. Syst. Bot.* 23: 143–151. https://doi.org/10.1071/SB09047

Chao, Y.S., Rouhan, G., Amoroso, V.B. & Chiou, W.L. 2014. Molecular phylogeny and biogeography of the fern genus *Pteris* (Pteridaceae). *Ann. Bot. (Oxford)* 114: 109–124. https://doi.org/10.1093/aob/mcu086

Christenhusz, M.J.M., Fay, M.F. & Byng, J.W. (eds.) 2018. *The global flora: A practical flora to vascular plant species of the world*, [ser. 3], vol. 4, *Special edition: GLOVAP nomenclature*, part 1. Bradford, U.K.: Plant Gateway

Ebihara, A., Nitta, J.H. & Ito, M. 2010. Molecular species identification with rich floristic sampling: DNA barcoding the pteridophyte flora of Japan. *PLoS One* 5(12): e15136. https://doi.org/10.1371/journal.pone.0015136

Eiserhardt, W.L., Rohwer, J.G., Russell, S.J., Yesilyurt, J.C. & Schneider, H. 2011. Evidence for radiations of cheilanthoid

ferns in the Greater Cape Floristic Region. *Taxon* 26: 1–15. https://doi.org/10.1002/tax.605004

Fawcett, S. & Smith, A.R. 2021. *A generic classification of the Thelypteridaceae*. Sida, Botanical Miscellany Series 59. Fort Worth: BRIT Press.

Fawcett, S., Smith, A.R., Sundue, M.A., Burleigh, J.G., Sessa, E.B., Kuo, L.-Y., Chen, C.-W., Testo, W.L., Kessler, M., GoFlag Consortium & Barrington, D.S. 2021. A global phylogenomic study of the Thelypteridaceae. *Syst. Bot.* 46: 891–915. https://doi.org/10.1600/036364421X16370109698650

Fraser-Jenkins, C.R., Gandhi, K.N., Kholia, B.S. & Benniamin, A. 2016. *An annotated checklist of Indian pteridophytes*, part 1. Dehra Dun: Bishen Singh Mahendra Pal Singh.

Fraser-Jenkins, C.R., Smith, A.R. & Windham, M.D. 2017. Proposal to reject the name *Allosorus* (Pteridaceae). *Taxon* 66: 517–518. https://doi.org/10.12705/662.21

Fujiwara, T., Liu, H., Meza-Torres, E.I., Morero, R.E., Vega, A.J., Liang, Z., Ebihara, A., Leitch, I.J. & Schneider, H. 2023. Evolution of genome space occupation in ferns: Linking genome diversity and species richness. *Ann. Bot. (Oxford)* 131: 59–70. https://doi.org/10.1093/aob/mcab094

Gastony, G.J. & Johnson, W.P. 2001. Phylogenetic placements of *Loxoscaphe thecifera* (Aspleniaceae) and *Actiniopteris radiata* (Pteridaceae) based on analysis of *rbcL* nucleotide sequences. *Amer. Fern J.* 91: 197–213. https://doi.org/10.1640/0002-8444(2001)091[0197:PPOLTA]2.0.CO;2

Gastony, G.J. & Rollo, D.R. 1995. Phylogeny and generic circumscriptions of cheilanthoid ferns (Pteridaceae: Cheilanthoideae) inferred from *rbcL* nucleotide sequences. *Amer. Fern J.* 85: 341–360. https://doi.org/10.2307/1547814

Gastony, G.J. & Rollo, D.R. 1998. Cheilanthoid ferns (Pteridaceae: Cheilanthoideae) in the southwestern United States and adjacent Mexico: A molecular phylogenetic reassessment of generic lines. *Aliso* 17: 131–144. https://doi.org/10.5642/aliso.19981702.04

George, L.O., Pryer, K.M., Kao, T.-T., Huiet, L. & Windham, M.D. 2019. Baja: A new monospecific genus segregated from *Cheilanthes* s. l. (Pteridaceae). *Syst. Bot.* 44: 471–482. https://doi.org/10.1600/036364419X15620113920536

Grusz, A.L. & Windham, M.D. 2013. Toward a monophyletic *Cheilanthes*: The resurrection and recircumscription of *Myriopteris* (Pteridaceae). *PhytoKeys* 32: 49–64. https://doi.org/10.3897/phytokeys.32.6733

Grusz, A.L., Windham, M.D., Yatskievych, G., Huiet, L., Gastony, G.J. & Pryer, K.M. 2014. Patterns of diversification in the xeric-adapted fern genus *Myriopteris* (Pteridaceae). *Syst. Bot.* 39: 698–714. https://doi.org/10.1600/036364414X681518

Grusz, A.L., Windham, M.D., Picard, K.T., Pryer, K.M., Schuettpelz, E. & Haufler, C.H. 2021. A drought-driven model for the evolution of obligate apomixis in ferns: Evidence from pellaeids (Pteridaceae). *Amer. J. Bot.* 108: 263–283. https://doi.org/10.1002/ajb2.1611

Hall, C.C. & Lellinger, D.B. 1967. A revision of the fern genus *Mildella*. *Amer. Fern J.* 57: 113–34. https://doi.org/10.2307/1546230.

Hasebe, M., Wolf, P.G., Pryer, K.M., Ueda, K., Ito, M., Sano, R., Gastony, G.J., Yokoyama, J., Manhart, J.R., Murakami, N. & Crane, E.H. 1995. Fern phylogeny based on *rbcL* nucleotide sequences. *Amer. Fern J.* 85: 134–181. https://doi.org/10.2307/1547807

Hassler, M. 2004–2023. World ferns: Synonymic checklist and distribution of ferns and lycophytes of the world. Version 17.0. https://www.worldplants.de/ferns/ (last accessed 16 Oct 2023).

Haufler, C.H., Pryer, K.M., Schuettpelz, E., Sessa, E.B., Farrar, D.R., Moran, R., Schneller, J.J., Watkins, J.E., Jr. & Windham, M.D. 2016. Sex and the single gametophyte: Revising the homosporous vascular plant life cycle in light of contemporary research. *BioScience* 66: 928–937. https://doi.org/10.1093/biosci/biw108

Hennequin, S., Kessler, M., Lindsay, S. & Schneider, H. 2014. Evolutionary patterns in the assembly of fern diversity on the oceanic Mascarene Islands. *J. Biogeogr.* 41: 1651–1663. https://doi.org/10.1111/jbi.12339

Hevly, R.H. 1963. Adaptations of cheilanthoid ferns to desert environments. *J. Arizona Acad. Sci.* 2: 164–175. https://doi.org/10.2307/40026172

Hoang, D.T., Chernomor, O., Haeseler, A. von, Minh, B.Q. & Vinh, L.S. 2018. UFBoot2: Improving the ultrafast bootstrap approximation. *Molec. Biol. Evol.* 35: 518–522. https://doi.org/10.1093/molbev/msx281

Johnson, A.K., Rothfels, C.J., Windham, M.D. & Pryer, K.M. 2012. Unique expression of a sporophytic character on the gametophytes of notholaenid ferns (Pteridaceae). *Amer. J. Bot.* 99: 1118–1124. https://doi.org/10.3732/ajb.1200049

Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K., Haeseler, A. von & Jermiin, L.S. 2017. ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Meth.* 14: 587–589. https://doi.org/10.1038/nmeth.4285

Kao, T.-T., Pryer, K.M., Freund, F.D., Windham, M.D. & Rothfels, C.J. 2019. Low-copy nuclear sequence data confirms homoplasy in farina expression in notholaenid ferns (Pteridaceae). *Molec. Phylogen. Evol.* 138: 139–155. https://doi.org/10.1016/j.ympev.2019.05.016

Kirkpatrick, R.E.B. 2007. Investigating the monophyly of *Pellaea* (Pteridaceae) in the context of a phylogenetic analysis of cheilanthoid ferns. *Syst. Bot.* 32: 504–518. https://doi.org/10.1600/036364407782250616

Kozlov, A.M., Darriba, D., Flouri, T., Morel, B. & Stamatakis, A. 2019. RAxML-NG: A fast, scalable and user-friendly tool for maximum-likelihood phylogenetic inference. *Bioinformatics* 35: 4453–4455. https://doi.org/10.1093/bioinformatics/btz305

Larsson, A. 2014. AliView: A fast and lightweight alignment viewer and editor for large data sets. *Bioinformatics* 30: 3276–3278. https://doi.org/10.1093/bioinformatics/btu531

Laumer, C.E., Fernández, R., Lemer, S., Combosch, D., Kocot, K.M., Riesgo, A., Andrade, S.C.S., Sterrer, W., Sørensen, M.V. & Giribet, G. 2019. Revisiting metazoan phylogeny with genomic sampling of all phyla. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 286: 20190831. https://doi.org/10.1098/rspb.2019.0831

Li, F.-W., Pryer, K.M. & Windham, M.D. 2012. *Gaga*, a new fern genus segregated from *Cheilanthes* (Pteridaceae). *Syst. Bot.* 37: 845–860. https://doi.org/10.1600/036364412X656626

Li, Y., Steenwyk, J.L., Chang, Y., Wang, Y., James, T.Y., Stajich, J.E., Spatafora, J.W., Groenewald, M., Dunn, C.W., Hittinger, C.T., Shen, X.X. & Rokas, A. 2021. A genome-scale phylogeny of the kingdom Fungi. *Curr. Biol.* 31: 1653–1665. https://doi.org/10.1016/j.cub.2021.01.074

Lindsay, S. & Middleton, D.J. 2021. (2836) Proposal to conserve the name *Asplenium arifolium* (*Hemionitis arifolia*, *Parahemionitis arifolia*) (Pteridaceae) with a conserved type. *Taxon* 70: 1133–1134. https://doi.org/10.1002/tax.12579

Link-Pérez, M.A., Watson, L.E. & Hickey, R.J. 2011. Redefinition of *Adiantopsis* Fée (Pteridaceae): Systematics, diversification, and biogeography. *Taxon* 60: 1255–1268. https://doi.org/10.1002/tax.605003

Link-Pérez, M.A., Ludwig, T.G., Ledford, C.J., Seabolt, M.H. & Sessa, E.B. 2016. Lectotypification of *Adiantopsis alata* (Pteridaceae) and descriptions of new palmate species in the Guiana Shield. *Syst. Bot.* 41: 906–918. https://doi.org/10.1600/036364416X694008

Little, D.P. 2014. A DNA mini-barcode for land plants. *Molec. Ecol. Resources* 14: 437–446. https://doi.org/10.1111/1755-0998.12194

Lu, J.M., Wen, J., Lutz, S., Wang, Y.P. & Li, D.Z. 2012. Phylogenetic relationships of Chinese *Adiantum* based on five plastid markers.

J. Pl. Res. 125: 237–249. https://doi.org/10.1007/s10265-011-0441-y

Miller, M.A., Pfeiffer, W. & Schwartz, T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Pp. 45–52 in: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, New Orleans, Louisiana, 14 Nov 2010. Piscataway: IEEE. https://doi.org/10.1109/GCE.2010.5676129

Minh, B.Q., Schmidt, H.A., Chernomor, O., Schrempf, D., Woodhams, M.D., von Haeseler, A. & Lanfear, R. 2020. IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. *Molec. Biol. Evol.* 37: 1530–1534. https://doi.org/10.1093/molbev/msaa015

Nagalingum, N.S., Schneider, H. & Pryer, K.M. 2007. Molecular phylogenetic relationships and morphological evolution in the heterosporous fern genus *Marsilea*. *Syst. Bot.* 32: 16–25. https://doi.org/10.1600/036364407780360256

Nitta, J.H., Meyer, J.Y., Taputuarai, R. & Davis, C.C. 2017. Life cycle matters: DNA barcoding reveals contrasting community structure between fern sporophytes and gametophytes. *Ecol. Monogr.* 87: 278–296. https://doi.org/10.1002/ecm.1246

Nitta, J.H., Schuettpelz, E., Ramírez-Barahona, S. & Iwasaki, W. 2022. An open and continuously updated fern tree of life. *Frontiers Pl. Sci. (Lausanne)* 13: 909768. https://doi.org/10.3389/fpls.2022.909768

Nobel, P.S. 1978. Microhabitat, water relations, and photosynthesis of a desert fern, *Notholaena parryi*. *Oecologia* 31: 293–309. https://doi.org/10.1007/BF00346249

One Thousand Plant Transcriptomes Initiative 2019. One thousand plant transcriptomes and the phylogenomics of green plants. *Nature* 574: 679–685. https://doi.org/10.1038/s41586-019-1693-2

Panigrahi, G. 1993. *Parahemionitis*, a new genus of Pteridaceae. *Amer. Fern J.* 83: 90–92. https://doi.org/10.2307/1547458.

Pickett, F.L. 1931. Notes on xerophytic ferns. *Amer. Fern J.* 21: 49–57. https://doi.org/10.2307/1543887

Ponce, M. & Scataglini, M.A. 2016. Do two South American species of *Cheilanthes* (Pteridaceae) traditionally linked to the *Cheilanthes marginata* group, belong to *Gaga*? *Phytotaxa* 257: 149–157. https://doi.org/10.11646/phytotaxa.257.2.4

Ponce, M.M. & Scataglini, M.A. 2018. Further progress towards the delimitation of *Cheilanthes* (Cheilanthoideae, Pteridaceae), with emphasis on South American species. *Organisms Diversity Evol.* 18: 175–186. https://doi.org/10.1007/s13127-018-0366-6

Ponce, M.M. & Scataglini, M.A. 2022. Phylogenetic position of South American *Cheilanthes* (Cheilanthoideae, Pteridaceae): Advances in the generic circumscription and segregation of the new genus *Mineirella*. *J. Syst. Evol.* 60: 266–80. https://doi.org/10.1111/jse.12723

PPG I 2016. A community-derived classification for extant lycophytes and ferns. *J. Syst. Evol.* 54: 563–603. https://doi.org/10.1111/jse.12229

Prado, J., Del Nero, R., Salatino, A. & Salatino, M.L.F. 2007. Phylogenetic relationships among Pteridaceae, including Brazilian species, inferred from *rbcL* sequences. *Taxon* 56: 355–368. https://doi.org/10.1002/tax.562008

Prado, J., Schuettpelz, E., Hirai, R.Y. & Smith, A.R. 2013. *Pellaea flavescens*, a Brazilian endemic, is a synonym of Old World *Pellaea viridis*. *Amer. Fern J.* 103: 21–26. https://doi.org/10.1640/0002-8444-103.1.21

Pryer, K.M., Schuettpelz, E., Huiet, L., Grusz, A.L., Rothfels, C.J., Avent, T., Schwartz, D. & Windham, M.D. 2010. DNA barcoding exposes a case of mistaken identity in the fern horticultural trade. *Molec. Ecol. Resources* 10: 979–985. https://doi.org/10.1111/j.1755-0998.2010.02858.x

Rambaut, A., Drummond, A.J., Xie, D., Baele, G. & Suchard, M. A. 2018. Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Syst. Biol.* 67: 901–904. https://doi.org/10.1093/sysbio/syy032

Robison, T.A., Grusz, A.L., Wolf, P.G., Mower, J.P., Fauskee, B.D., Sosa, K. & Schuettpelz, E. 2018. Mobile elements shape plastome evolution in ferns. *Genome Biol. Evol.* 10: 2558–2571. https://doi.org/10.1093/gbe/evy189

Ronquist, F., Teslenko, M., Van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model selection across a large model space. *Syst. Biol.* 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Rothfels, C.J. & Schuettpelz, E. 2014. Accelerated rate of molecular evolution for vittarioid ferns is strong and not driven by selection. *Syst. Biol.* 63: 31–54. https://doi.org/10.1093/sysbio/syt058

Rothfels, C.J., Windham, M.D., Grusz, A.L. Gastony, G.J. & Pryer, K.M. 2008. Toward a monophyletic *Notholaena* (Pteridaceae): Resolving patterns of evolutionary convergence in xeric-adapted ferns. *Taxon* 57: 712–724. https://doi.org/10.1002/tax.573005

Sayers, E.W., Cavanaugh, M., Clark, K., Ostell, J., Pruitt, K.D. & Karsch-Mizrachi, I. 2020. GenBank. *Nucl. Acids Res.* 48: D84–D86. https://doi.org/10.1093/nar/gkz956

Schuettpelz, E. & Pryer, K.M. 2007. Fern phylogeny inferred from 400 leptosporangiate species and three plastid genes. *Taxon* 56: 1037–1050. https://doi.org/10.2307/25065903

Schuettpelz, E., Korall, P. & Pryer, K.M. 2006. Plastid *atpA* data provide improved support for deep relationships among ferns. *Taxon* 55: 897–906. https://doi.org/10.2307/25065684

Schuettpelz, E., Schneider, H., Huiet, L., Windham, M.D. & Pryer, K.M. 2007. A molecular phylogeny of the fern family Pteridaceae: Assessing overall relationships and the affinities of previously unsampled genera. *Molec. Phylogen. Evol.* 44: 1172–1185. https://doi.org/10.1016/j.ympev.2007.04.011

Schuettpelz, E., Davila, A., Prado, J., Hirai, R.Y. & Yatskievych, G. 2014. Molecular phylogenetic and morphological affinities of *Adiantum senae* (Pteridaceae). *Taxon* 63: 258–264. https://doi.org/10.12705/632.7

Schuettpelz, E., Pryer, K.M. & Windham, M.D. 2015. A unified approach to taxonomic delimitation in the fern genus *Pentagramma* (Pteridaceae). *Syst. Bot.* 40: 629–644. https://doi.org/10.1600/036364415X689366

Schuettpelz, E., Rouhan, G., Pryer, K.M., Rothfels, C.J., Prado, J., Sundue, M.A., Windham, M.D., Moran, R.C. & Smith, A.R. 2018. Are there too many fern genera? *Taxon* 67: 473–480. https://doi.org/10.12705/673.1

Sigel, E.M., Windham, M.D., Huiet, L., Yatskievych, G. & Pryer, K.M. 2011. Species relationships and farina evolution in the cheilanthoid fern genus *Argyrochosma* (Pteridaceae). *Syst. Bot.* 36: 554–564. https://doi.org/10.1600/036364411X583547

Sosa, K., Pryer, K.M., Huiet, L., Yatskievych, G. & Windham, M.D. 2021. *Cheilanthes ecuadorensis*: A new species of *Cheilanthes* s.s. (Pteridaceae) from Northern South America. *Syst. Bot.* 46: 249–252. https://doi.org/10.1600/036364421X16231782047280

Tryon, R.M. 1979. Biogeography of the Antillean fern flora. Pp. 55–68 in: Bramwell, D. (ed.), *Plants and islands*. London: Academic Press.

Tryon, R.M. & Tryon, A.F. 1973. Geography, spores, and evolutionary relations in the cheilanthoid ferns. Pp. 145–153 in: Jermy, A.C., Crabbe, J.A. & Thomas, B.A. (eds.), *The phylogeny and classification of ferns*. New York: Academic Press.

Tryon, R.M. & Tryon, A.F. 1982. *Ferns and allied plants with special reference to tropical America*. Berlin: Springer. https://doi.org/10.1007/978-1-4613-8162-4

Wang, W., Yang, W., Dou, P. & Zhang, G. 2015a. Phylogenetic analysis of *Cheilosoria* Trevis. based on four chloroplast DNA sequences. *Chin. Bull. Bot.* 50: 310–320. https://doi.org/10.3724/SP.J.1259.2015.00310

Wang, W., Yang, W., Mao, X., Zhao, R., Dou, P. & Zhang, G. 2015b. The phylogenetic affinities of *Pellaea connectens*, a rare endemic

Chinese fern. *Phytotaxa* 220: 30–42. https://doi.org/10.11646/phytotaxa.220.1.2

Wang, W., Yang, W.-L., Dou, P., Zhao, R.-R. & Zhang, G.M. 2015c. The relationship between *Aleuritopteris humatifolia* and *A. chrysophylla* based on three chloroplast DNA sequences analyses. *Pl. Diversity & Resources* 37: 301–308.

Wilson, K.L. 2024. Report of the General Committee: 29. *Taxon* 73: 619–621. https://doi.org/10.1002/tax.13151

Windham, M.D., Huiet, L., Schuettpelz, E., Grusz, A.L., Rothfels, C.J., Beck, J.B., Yatskievych, G. & Pryer, K.M. 2009. Using plastid and nuclear DNA sequences to redraw generic boundaries and demystify species complexes in cheilanthoid ferns. *Amer. Fern J.* 99: 128–132.

Yatskievych, G. & Hooper, E.A. 2001. Evolution and adaptations of pteridophytes in dry climates. P. 82, Abstract 328 in: *Botany 2001: Plants and People*, Albuquerque, New Mexico, 12–16 August 2001: *Abstracts*, vol. 2. Albuquerque: Botanical Society of America. http://2001.botanyconference.org/botany2001b.pdf

Yatskievych, G. & Smith, A.R. 2003. Typification of *Notholaena* R.Br. (Pteridaceae). *Taxon* 52: 331–336. https://doi.org/10.2307/3647407

Yesilyurt, J.C. & Schneider, H. 2010. The new fern genus *Calciphilopteris* (Pteridaceae). *Phytotaxa* 7: 52–59. https://doi.org/10.11646/phytotaxa.7.1.7

Yesilyurt, J.C., Barbará, T., Schneider, H., Russell, S., Culham, A. & Gibby, M. 2015. Identifying the generic limits of the cheilanthoid genus *Doryopteris*. *Phytotaxa* 221: 101–122. https://doi.org/10.11646/phytotaxa.221.2.1

Zhang, G., Zhang, X. & Chen, Z. 2003. Phylogeny of cryptogrammoid ferns and related taxa based on *rbcL* sequences. *Nordic J. Bot.* 23: 485–493. https://doi.org/10.1111/j.1756-1051.2003.tb00421.x

Zhang, G., Zhang, X., Chen, Z., Liu, H. & Yang, W. 2007. First insights in the phylogeny of Asian cheilanthoid ferns based on sequences of two chloroplast markers. *Taxon* 56: 369–378. https://doi.org/10.1002/tax.562009

Zhang, G., Liu, H., Yang, W. & Zhang, X. 2009. Systematic position of *Hemionitis arifolia* based on the analysis of *rbcL* sequences. *J. Beijing Forest. Univ.* 31: 15–18.

Zhang, G., Yatskievych, G. & Hooper, E.A. 2013. *Aleuritopteris*. Pp. 224–235 in: Wu. Z.-Y., Raven, P.H. & Hong, D.-Y. (eds.), *Flora of China*, vol. 2–3. Beijing: Science Press; St. Louis: Missouri Botanical Garden Press.

Zumkeller, S.M., Knoop, V. & Knie, N. 2016. Convergent evolution of fern-specific mitochondrial group II intron atp1i361g2 and its ancient source paralogue rps3i249g2 and independent losses of intron and RNA editing among Pteridaceae. *Genome Biol. Evol.* 8: 2505–2519. https://doi.org/10.1093/gbe/evw173

Appendix 1. Hemionitid fern species included in our three-gene dataset. Species are listed by currently accepted name (following the classification presented herein), but we also provide the name most commonly used prior to this study (if different), as well as a summary of current or historical combinations (C = *Cheilanthes*, N = *Notholaena*, P = *Pellaea*, - = none) and the biogeographic centers occupied (Me = Mexican, An = Andean, Br = Brazilian, Af = African, Si = Sino-Himalayan, Au = Australian, - = none) in brackets. For each sample, we then include: voucher information with collector and collection number (plus herbarium code); country of origin; and *rbcL*, *atpA*, and *trnG-R* GenBank accession numbers (respectively, with corresponding citations; NA = sequence not available; * = sequence edited). The information included in this appendix also appears in a combined machine-readable suppl. Appendix S1.

Adiantopsis alata Prantl [-/Br]: *Matos 738* (UPCB); Brazil; KY020078, KY020081, NA (Link-Pérez & al., 2016). ***Adiantopsis aurea*** Link-Pérez, Seabolt & Ledford [-/-]: *Henkel 5721* (NY); Guyana; KY020080, JN709810, NA (Link-Pérez & al., 2011, 2016). ***Adiantopsis ×australopedata*** Hickey, M.S.Barker & Ponce [-/Br]: *Hickey 01-63* (MU); Argentina; JN709745, JN709791, NA (Link-Pérez & al., 2011). ***Adiantopsis chlorophylla*** (Sw.) Fée [C/AnBr]: *Meza Torres 337* (MU); Argentina; JN709741, JN709787, NA (Link-Pérez & al., 2011). ***Adiantopsis dactylifera*** Link-Pérez & Hickey [-/An]: *van der Werff 16380* (MO); Peru; JN709759, JN709805, NA (Link-Pérez & al., 2011). ***Adiantopsis dichotoma*** (Cav.) T.Moore [CP/AnBr]: *Deginani 1359* (MO); Argentina; JN709727, JN709773, PQ412337 (Link-Pérez & al., 2011; this study). ***Adiantopsis flexuosa*** (Kunze) Link-Pérez & Hickey [C/Br]: *Hatschbach 77948* (UC); Brazil; PQ417413, PQ429019, PQ412338 (this study). ***Adiantopsis hickeyi*** Link-Pérez, Seabolt & Ledford [-/-]: *Mori 25095* (NY); France; JN709762, JN709808, NA (Link-Pérez & al., 2011). ***Adiantopsis lindigii*** (Mett.) Prantl [C/An]: *Langenheim 3568* (UC); Colombia; JN709754, JN709800, NA (Link-Pérez & al., 2011). ***Adiantopsis monticola*** (Gardner) T.Moore [C/-]: *Cordeiro 2665* (UC); Brazil; JN709729, JN709775, NA (Link-Pérez & al., 2011). ***Adiantopsis orbignyana*** (Mett. ex Kuhn) Ponce & Scataglini [C/An]: *Sagástegui 14979* (UC); Peru; PQ417414, PQ417530, PQ412339 (this study). ***Adiantopsis parvisegmenta*** M.S.Barker & Hickey [-/-]: *Jack 6877* (NY); Cuba; JN709750, JN709796, NA (Link-Pérez & al., 2011). ***Adiantopsis paupercula*** (Kunze) Fée [C/-]: *Hespenheide 1191* (US); Jamaica; JN709765, JN709811, NA (Link-Pérez & al., 2011). ***Adiantopsis pedata*** (Hook.) Moore [C/-]: *Harris 10878* (NY); Jamaica; JN709748, JN709794, NA (Link-Pérez & al., 2011). ***Adiantopsis pentagona*** M.S.Barker & Hickey [-/-]: *Proctor 3229* (NY); Cuba; JN709749, JN709795, NA (Link-Pérez & al., 2011). ***Adiantopsis perfasciculata*** Sehnem [-/Br]: *Irwin 19130* (NY); Brazil; JN709747, JN709793, NA (Link-Pérez & al., 2011). ***Adiantopsis radiata*** (L.) Fée [C/MeAnBr]: *Christenhusz 4033* (TUR); France; EF452131, EU268718, EU268664 (Schuettpelz & al., 2007; Rothfels & al., 2008). ***Adiantopsis reesii*** (Jenman) C.Chr. [C/-]: *Ekman 7965* (NY); Haiti; JN709755, JN709801, NA (Link-Pérez & al., 2011). ***Adiantopsis regularis*** (Mett.) Moore [C/Br]: *Labiak 1966* (UC); Brazil; PQ417415, PQ417531, PQ412340 (this study). ***Adiantopsis rupicola*** Maxon [-/-]: *Britton 7497* (NY); Cuba; JN709753, JN709799, NA (Link-Pérez & al., 2011). ***Adiantopsis seemannii*** (Hook.) Maxon [C/MeAn]: *Lobo 14* (DUKE); Costa Rica; MK632704, PQ417532, PQ412341 (Kao & al., 2019; this study). ***Adiantopsis senae*** (Baker) Schuettp. & A.Davila [-/Br]: *Schuettpelz 1400* (SP); Brazil; KF800702, KF800704, PQ412342 (Schuettpelz & al., 2014; this study). ***Adiantopsis ternata*** Prantl [-/An]: *Haught 2402* (US); Colombia; JN709756, JN709802, NA (Link-Pérez & al., 2011). ***Adiantopsis timida*** Link-Pérez & Hickey [-/An]: *Wurdack 43734* (NY); Venezuela; JN709757, JN709803, NA (Link-Pérez & al., 2011). ***Adiantopsis trifurcata*** (Baker) Link-Pérez & Hickey [C/AnBr]: *Jimenez 2685* (UC); Bolivia; PQ417416, PQ417533, PQ412343 (this study). ***Adiantopsis tweediana*** (Hook.) Link-Pérez & Hickey [C/AnBr]: *Zardini 35665* (MO); Paraguay; PQ417417, PQ417534, PQ412344 (this study). ***Adiantopsis vincentii*** M.S.Barker & Hickey [-/-]: *Morton 10544* (US); Cuba; JN709751, JN709797, NA (Link-Pérez & al., 2011). ***Aleuritopteris acrostica*** (Balb.) Windham & Schuettp., *Oeosporangium acrosticum* (Balb.) L.Sáez & Aymerich [C/AfSi]: *Stevens 25959* (MO); Spain; PQ417500, PQ417637, PQ412427 (this study). ***Aleuritopteris albofusca*** (Baker) Pic.Serm. [C/Si]: *Zhang 243* (PE); China; DQ432647, NA, NA (Zhang & al., 2007). ***Aleuritopteris albomarginata*** (C.B.Clarke) Ching [C/Si]: *Yatskievych 09-086A* (MO); Nepal; PQ417418, PQ417535, PQ412345 (this study). ***Aleuritopteris anceps*** (Blanf.) Panigrahi [C/Si]: *Yatskievych 09-98* (MO); Nepal; PQ417419, PQ417536, PQ412346 (this study). ***Aleuritopteris argentea*** (S.G.Gmel.) Fée [C/Si]: *Yatskievych 01-23* (MO); China; EF452137, EU268719, EU268665 (Schuettpelz & al., 2007; Rothfels & al., 2008). ***Aleuritopteris argyrophylla*** (Sw.) Fée [-/Af]: *Vorontsova 54* (MO); Kenya; PQ417420, PQ417537, PQ412347 (this study). ***Aleuritopteris belangeri*** (Bory) Windham & Schuettp., *Oeosporangium belangeri* (Bory) Fraser-Jenk. [CP/Si]: *Wu WS-1890* (MO); Laos; PQ417501, PQ417638, PQ412428 (this study). ***Aleuritopteris bicolor*** (Roxb.) Fraser-Jenk. [C/Si]: *Yatskievych 09-071* (MO); Nepal; PQ417421, PQ417538, PQ412348 (this study). ***Aleuritopteris bullosa*** (Kunze) Ching [C/Si]: *Fraser-Jenkins FN17* (MO); India; PQ417422, PQ417539, PQ412349 (this study). ***Aleuritopteris chinensis*** (Baker) Windham & Schuettp., *Oeosporangium chinense* (Baker) Fraser-Jenk. [CN/Si]: *Zhang 684* (MO); China; JQ855929, PQ417639, PQ412429 (Johnson & al., 2012; this study). ***Aleuritopteris chrysophylla*** (Hook.) Ching [C/Si]: *Fraser-Jenkins FN202* (MO); Bhutan; PQ417423, PQ417540, PQ412350 (this study). ***Aleuritopteris chusana*** (Hook.) Windham & Schuettp., *Oeosporangium chusanum* (Hook.)

Appendix 1. Continued.

Fraser-Jenk. [C/Si]: *Zhang 632* (MO); China; PQ417502, PQ417640, PQ412430 (this study). ***Aleuritopteris coriacea*** (Hook.) Windham & Schuettp., *Oeosporangium coriaceum* (Decne.) Fraser-Jenk. & Pariyar [CP/Af]: *Gastony s.n.* (MO); Cultivated; PQ417503, PQ417641, PQ412431 (this study). ***Aleuritopteris dealbata*** (C.Presl) Fée [C/Si]: *Yatskievych 09-070* (MO); Nepal; PQ417424, PQ417541, PQ412351 (this study). ***Aleuritopteris dubia*** (C.Hope) Ching [C/Si]: *Yatskievych 09-59* (MO); Nepal; PQ417425, PQ417542, PQ412352 (this study). ***Aleuritopteris duclouxii*** (Christ) Ching [C/Si]: *Zhang 375* (MO); China; PQ417426, PQ417543, PQ412353 (this study). ***Aleuritopteris duthiei*** (Baker) Ching [C/Si]: *Fraser-Jenkins 31626* (MO); Bhutan; PQ417427, PQ417544, PQ412354 (this study). ***Aleuritopteris ebenipes*** X.C.Zhang [-/Si]: *Zhang 364* (MO); China; PQ417428, PQ417545, PQ412355 (this study). ***Aleuritopteris elegans*** (Poir.) Windham & Schuettp., *Oeosporangium elegans* (Poir.) Fraser-Jenk. & Pariyar [C/Si]: *Dong 747* (PE); China; KP126966*, NA, NA (Wang & al., 2015c). ***Aleuritopteris fallax*** (M.Martens & Galeotti) Windham & Schuettp., *Mildella fallax* (M.Martens & Galeotti) G.L.Nesom [P/Me]: *Yatskievych 89-207* (IND); Mexico; MK632713, PQ417633, PQ412425 (Kao & al., 2019; this study). ***Aleuritopteris farinosa*** (Forssk.) Fée [C/Af]: *Kamau 529* (MO); Kenya; PQ417429, PQ417546, PQ412356 (this study). ***Aleuritopteris formosana*** (Hayata) Tagawa [C/Si]: *Yatskievych 09-084* (MO); Nepal; PQ417430, PQ417547, PQ412357 (this study). ***Aleuritopteris fragilis*** (Hook.) Windham & Schuettp., *Oeosporangium fragile* (Hook.) Fraser-Jenk. [C/Si]: *Boonkerd 519* (BJFC); Thailand; KP126967*, NA, NA (Wang & al., 2015c). ***Aleuritopteris gongshanensis*** G.M.Zhang [-/Si]: *Zhang 2743* (PE); China; PQ417431, PQ417548, PQ412358 (this study). ***Aleuritopteris grevilleoides*** (Christ) G.M.Zhang & X.C.Zhang [C/Si]: *Zhang 639* (PE); China; DQ432648, NA, NA (Zhang & al., 2007). ***Aleuritopteris grisea*** (Blanf.) Panigrahi [C/Si]: *Wen 9237* (MO); China; PQ417432, PQ417549, PQ412359 (this study). ***Aleuritopteris guanchica*** (Bolle) Windham & Schuettp., *Oeosporangium guanchicum* (Bolle) Fraser-Jenk. & Pariyar [C/Af]: *Eiserhardt AND2-1* (HBG); Spain; GU935504, GU935459, GU935554 (Eiserhardt & al., 2011). ***Aleuritopteris hancockii*** (Baker) Windham & Schuettp., *Oeosporangium hancockii* (Baker) Fraser-Jenk. [C/Si]: *Zhang 282* (PE); China; DQ432649, NA, NA (Zhang & al., 2007). ***Aleuritopteris insignis*** (Ching) Windham & Schuettp., *Oeosporangium insigne* (Ching) Fraser-Jenk. [C/Si]: *Dong S32* (PE); China; AY266413, NA, NA (Zhang & al., 2003). ***Aleuritopteris intramarginalis*** (Kaulf. ex Link) Windham & Schuettp., *Mildella intramarginalis* (Kaulf. ex Link) Trevis. [CP/MeAn]: *Steinmann 2549* (MO); Mexico; MH170427, PQ417634, PQ412426 (Sosa & al., 2021; this study). ***Aleuritopteris krameri*** (Franch. & Sav.) Ching [C/Si]: *Schuettpelz 1062A* (DUKE); Taiwan; PQ417433, PQ417550, PQ412360 (this study). ***Aleuritopteris kuhnii*** (Milde) Ching, *Oeosporangium kuhnii* (Milde) Fraser-Jenk. [C/Si]: *Woo 495* (DUKE); China; PQ417504, PQ417642, PQ412432 (this study). ***Aleuritopteris leptolepis*** (Fraser-Jenk.) Fraser-Jenk. [C/Si]: *Yatskievych 09-056* (MO); Nepal; PQ417434, PQ417551, PQ412361 (this study). ***Aleuritopteris likiangensis*** Ching [-/Si]: *Zhang 278* (PE); China; DQ432645, NA, NA (Zhang & al., 2007). ***Aleuritopteris mairei*** (Brause) Windham & Schuettp., *Oeosporangium mairei* (Brause) Fraser-Jenk. [CP/Si]: *Zhang 254* (MO); China; PQ417505, PQ417643, PQ412433 (this study). ***Aleuritopteris mexicana*** Fée [CP/MeAn]: *Yatskievych 07-101* (DUKE); Mexico; PQ417435, PQ417552, PQ412362 (this study). ***Aleuritopteris niphobola*** (C.Chr.) Ching [C/Si]: *Zhang 258* (PE); China; AY266409, NA, NA (Zhang & al., 2003). ***Aleuritopteris nitidula*** (Wall. ex Hook.) Windham & Schuettp., *Mildella nitidula* (Wall. ex Hook.) C.C.Hall & Lellinger [CP/Si]: *Kuo 105* (TAIF); Taiwan; PQ417506, PQ417644, PQ412434 (this study). ***Aleuritopteris papuana*** (C.Chr.) H.Schneid. [C/Si]: *Johns 9463* (K); Indonesia; PQ417436, NA, NA (this study). ***Aleuritopteris parishii*** Fraser-Jenk. [-/Si]: *Fraser-Jenkins 32114* (MO); Myanmar; PQ417437, PQ417553, PQ412363 (this study). ***Aleuritopteris patula*** (Baker) Windham & Schuettp., *Oeosporangium patulum* (Baker) Fraser-Jenk. [CP/Si]: *Zhang 228* (PE); China; DQ432641, NA, NA (Zhang & al., 2007). ***Aleuritopteris paupercula*** (Christ) Windham & Schuettp., *Oeosporangium pauperculum* (Christ) Fraser-Jenk. & Pariyar [CP/Si]: *Zhang 260* (PE); China; DQ432640, NA, NA (Zhang & al., 2007). ***Aleuritopteris persica*** (Bory) Windham & Schuettp., *Oeosporangium persica* (Bory) Vis. [CN/AfSi]: *Kurbanov 993* (MO); Turkmenistan; PQ417507, PQ417645, PQ412435 (this study). ***Aleuritopteris pteridioides*** (Reichard) Windham & Schuettp., *Oeosporangium pteridioides* (Reichard) Fraser-Jenk. & Pariyar [C/Af]: *Gastony 90-4* (IND); Spain; PQ417508, PQ417646, PQ412436 (this study). ***Aleuritopteris pulchella*** (Bory ex Willd.) Windham & Schuettp., *Oeosporangium pulchellum* (Bory ex Willd.) Fraser-Jenk. & Pariyar [C/Af]: *Unknown s.n.* (HBG); Spain; GU935503, NA, NA (Eiserhardt & al., 2011). ***Aleuritopteris rosulata*** (C.Chr.) Ching [C/Si]: *Zhang 263* (PE); China; PQ417438, PQ417554, PQ412364 (this study). ***Aleuritopteris rufa*** (D.Don) Ching [C/Si]: *Yatskievych 09-060* (MO); Nepal; PQ417439, PQ417555, PQ412365 (this study). ***Aleuritopteris scioana*** (Chiov.) Fraser-Jenk. & Dulawat [C/AfSi]: *Wieland 4713* (MO); Somalia; PQ417440, PQ417556, PQ412366 (this study). ***Aleuritopteris smithii*** (C.Chr.) Windham & Schuettp., *Oeosporangium smithii* (C.Chr.) Fraser-Jenk. & Pariyar [CP/Si]: *Mao M2012072003* (BJFC); China; KP126963, NA, NA (Wang & al., 2015a). ***Aleuritopteris squamosa*** (C.Hope & Wright) Ching [CP/Si]: *Dong 28* (PE); China; PQ417441, PQ417557, PQ412367 (this study). ***Aleuritopteris straminea*** (Ching) Windham & Schuettp., *Oeosporangium stramineum* (Ching) Fraser-Jenk. [CP/Si]: *Rothfels 5314* (DUKE); China; PQ417509, NA, NA (this study). ***Aleuritopteris subargentea*** Ching [C/Si]: *Schneider 50* (no voucher); Unknown; PQ417442, PQ417558, PQ412368 (this study). ***Aleuritopteris subdimorpha*** (C.B.Clarke & Baker) Fraser-Jenk. [C/Si]: *Wu WS-2270* (MO); Laos; PQ417443, PQ417559, PQ412369 (this study). ***Aleuritopteris subvillosa*** (Hook.) Ching, *Oeosporangium subvillosum* (Hook.) Fraser-Jenk. & Pariyar [C/Si]: *Sundue 1028* (DUKE); China; PQ417510, PQ417647, PQ412437 (this study). ***Aleuritopteris tamburii*** (Hook.) Ching [CP/Si]: *Yatskievych 09-091* (MO); Nepal; PQ417444, PQ417560, PQ412370 (this study). ***Aleuritopteris trichophylla*** (Baker) Windham & Schuettp., *Oeosporangium trichophyllum* (Baker) Fraser-Jenk. [CP/Si]: *Zhang 266* (PE); China; DQ432639, NA, NA (Zhang & al., 2007). ***Aleuritopteris veitchii*** (Christ) Ching [C/Si]: *Unknown 2417* (PE); China; PQ417445, PQ417561, NA (this study). ***Aleuritopteris welwitschii*** (Hook. ex Baker) Ching [C/Af]: *Chapman 7050* (MO); Malawi; PQ417446, PQ417562, PQ412371 (this study). ***Anthonya bergiana*** (Schltdl.) Windham & Pryer, *Cheilanthes bergiana* Schltdl. [CN/Af]: *Festo 810* (DUKE); Tanzania; MH170412, PQ417566, PQ412373 (Sosa & al., 2021; this study). ***Anthonya ceterachoides*** (A.W.Klopper & Klopper) Windham & Pryer, *Cheilanthes ceterachoides* A.W.Klopper & Klopper [C/Af]: *Klopper 422* (PRE); South Africa; PQ417451, PQ417571, PQ412378 (this study). ***Anthonya contracta*** (Kunze) Windham & Pryer, *Cheilanthes contracta* (Kunze) Mett. ex Kuhn [CP/Af]: *Eiserhardt WE-065* (HBG); South Africa; GU935519, GU935478, GU935570 (Eiserhardt & al., 2011). ***Anthonya depauperata*** (Baker) Windham & Pryer, *Cheilanthes depauperata* Baker [C/Af]: *Eiserhardt WE-200734* (HBG); South Africa; GU935516, GU935476, NA (Eiserhardt & al., 2011). ***Anthonya dinteri*** (Brause) Windham & Pryer, *Cheilanthes dinteri* Brause [C/Af]: *BIOTA s.n.* (HBG); Namibia; GU935506, GU935461, GU935558 (Eiserhardt & al., 2011). ***Anthonya eckloniana*** (Kunze) Windham & Pryer, *Cheilanthes eckloniana* (Kunze) Mett. [CN/Af]: *Turner 620* (BM); South Africa; GU935513, GU935473, NA (Eiserhardt & al., 2011). ***Anthonya hirta*** (Sw.) Windham & Pryer, *Cheilanthes hirta* Sw. [CN/Af]: *Schelpe 3120* (BM); South Africa; GU935515, GU935474, NA (Eiserhardt & al., 2011). ***Anthonya marlothii*** (Hieron.) Windham & Pryer, *Cheilanthes marlothii* (Hieron.) Domin [CN/Af]: *BIOTA s.n.* (HBG); Namibia; GU935514, GU935472, GU935569 (Eiserhardt & al., 2011). ***Anthonya parviloba*** (Sw.) Windham & Pryer, *Cheilanthes parviloba* (Sw.) Sw. [C/Af]: *Roux 4163* (NBG); South Africa; GU935517, GU935475, GU935571 (Eiserhardt & al., 2011). ***Aspidotis californica*** (Nutt. ex Hook.) Nutt. ex Copel. [C/Me]: *Metzgar 178* (DUKE); U.S.A.; JX313525, PQ417563, JX313445 (Li & al., 2012; this study). ***Aspidotis densa*** (Brack.) Lellinger [CP/Me]: *Pryer 06-02* (DUKE); U.S.A.; EU268773, EU268723, EU268669 (Rothfels & al., 2008). ***Aspidotis meifolia*** (D.C.Eaton) Pic.Serm. [C/Me]: *Yatskievych 89-219* (IND); Mexico; JX313527, PQ417564, JX313447 (Li & al., 2012; this study). ***Brasiliopteris pohliana*** (Mett.) J.Prado, Schuettp. & Yatsk., *Cheilanthes pohliana* Mett. [CN/Br]: *Schuettpelz 1372* (SP); Brazil; MH170421, MH170432, MH170457 (Sosa & al., 2021). ***Brasiliopteris regnelliana*** (Mett.) J.Prado, Schuettp. & Yatsk., *Cheilanthes regnelliana* Mett. [CP/Br]: *Schuettpelz 1466* (SP); Brazil; PQ417469, PQ417590, PQ412396 (this study). ***Carlottahallia poeppigiana*** (Mett. ex Kuhn) Windham, *Cheilanthes poeppigiana* Mett. ex Kuhn [C/An]: *Huaylla 1876* (MO); Bolivia; PQ417466, PQ417586, PQ412392 (this study). ***Cheilanthes arequipensis*** (Maxon) R.M.Tryon & A.F.Tryon [CN/An]: *van der Werff 20479* (MO); Peru; MH170411, PQ417565, PQ412372 (Sosa & al., 2021; this study). ***Cheilanthes brownii*** (Desv.) Domin [CN/Au]: *van der Werff 22406* (MO); Australia; PQ417447, PQ417567, PQ412374 (this study). ***Cheilanthes caudata*** R.Br. [C/Au]: *Kemp TH444* (NSW); Australia; PQ417450, PQ417570, PQ412377 (this study). ***Cheilanthes distans*** (R.Br.) Mett. [CN/SiAu]: *Nagalingum 23* (DUKE); Australia; EU268783, EU268734, EU268680 (Rothfels & al., 2008). ***Cheilanthes ecuadorensis*** Windham & K.Sosa [C/An]: *Madsen 7940* (MO); Ecuador; MH170415, MH170433, NA (Sosa & al., 2021). ***Cheilanthes fractifera*** R.M.Tryon [C/An]: *Saunders 353* (UC); Peru; MK020118, MK020109, MK020128 (George & al., 2019). ***Cheilanthes fragillima*** F.Muell. [CN/Au]: *Dunlop 8625* (NSW); Australia; PQ417453, NA, NA (this study). ***Cheilanthes hieronymi*** Herter [C/Br]: *Arana s.n.* (SI); Argentina; MG593090, NA, NA (Ponce & Scataglini, 2018). ***Cheilanthes incarum*** Maxon [C/An]: *Lehnert 340* (UC); Peru; PQ417458, PQ417577, PQ412384 (this

Appendix 1. Continued.

study). ***Cheilanthes lasiophylla*** Pic.Serm. [CN/Au]: *Greuter 20743* (NSW); Australia; HM003032, HM003028, HM003036 (Pryer & al., 2010). ***Cheilanthes lonchophylla*** (R.M.Tryon) R.M.Tryon & A.F.Tryon [CN/An]: *Sagástegui 15319* (UC); Peru; PQ417460, PQ417579, PQ412385 (this study). ***Cheilanthes micropteris*** Sw. [CN/AnBr]: *Prado 2132* (DUKE); Brazil; MH173078, MH173078, MH173078 (Robison & al., 2018). ***Cheilanthes nitida*** (R.Br.) P.S.Green [CP/Au]: *Dunlop 8612* (NSW); Australia; PQ417462, PQ417581, PQ412387 (this study). ***Cheilanthes nudiuscula*** (R.Br.) Moore [CNP/SiAu]: *Kuo 211* (TAIF); Taiwan; PQ417463, PQ417582, PQ412388 (this study). ***Cheilanthes obducta*** Mett. ex Kuhn [CN/AnBr]: *Nee 51199* (MO); Bolivia; MH170418, PQ417583, PQ412389 (Sosa & al., 2021; this study). ***Cheilanthes pantanalensis*** E.L.M.Assis, Ponce & Labiak [C/Br]: *Assis 364* (UPCB); Brazil; PQ417464, NA, NA (this study). ***Cheilanthes praetermissa*** D.L.Jones [C/Au]: *Dixon 1373* (MO); Australia; PQ417467, PQ417587, PQ412393 (this study). ***Cheilanthes pumilio*** (R.Br.) F.Muell. [CN/Au]: *Walsh 4451* (MEL); Australia; PQ417468, PQ417589, PQ412395 (this study). ***Cheilanthes sarmientoi*** Ponce [C/An]: *Ponce 112* (SI); Argentina; MG593098, NA, NA (Ponce & Scataglini, 2018). ***Cheilanthes scariosa*** (Sw.) C.Presl [C/An]: *Linneo 824* (LPB); Bolivia; MG593099, NA, NA (Ponce & Scataglini, 2018). ***Cheilanthes sieberi*** Kunze [C/Au]: *Nagalingum 22* (DUKE); Australia; PQ417471, PQ417593, PQ412399 (this study). ***Cheilanthes squamosa*** Gill. ex Hook. & Grev. [CNP/An]: *Huaylla 1920* (MO); Bolivia; MH170424, PQ417594, PQ412400 (Sosa & al., 2021; this study). ***Cheilanthes tenuifolia*** (Burm.f.) Sw. [CNP/SiAu]: *Wu 314* (MO); Laos; PQ417472, PQ417595, PQ412401 (this study). ***Choristosoria calomelanos*** (Sw.) Windham & Schuettp., *Pellaea calomelanos* (Sw.) Link [NP/AfSi]: *BIOTA s.n.* (HBG); Namibia; GU935497, GU935483, GU935565 (Eiserhardt & al., 2011). ***Choristosoria induta*** (Kunze) Windham & Schuettp., *Cheilanthes induta* Kunze [C/Af]: *Eiserhardt WE-200731* (HBG); South Africa; GU935501, GU935465, GU935563 (Eiserhardt & al., 2011). ***Choristosoria multifida*** (Sw.) Windham & Schuettp., *Cheilanthes multifida* (Sw.) Sw. [C/Af]: *Eiserhardt WE-064* (HBG); South Africa; GU935500, GU935464, GU935562 (Eiserhardt & al., 2011). ***Choristosoria namaquensis*** (Baker) Windham & Schuettp., *Cheilanthes namaquensis* (Baker) Schelpe & N.C.Anthony [CP/Af]: *Esterhuysen 22946* (BM); South Africa; GU935491, GU935482, GU935560 (Eiserhardt & al., 2011). ***Choristosoria pteroides*** (L.) Mett. ex Kuhn, *Pellaea pteroides* (L.) Prantl [CP/Af]: *Eiserhardt WE-062a* (HBG); South Africa; GU935502, GU935479, GU935564 (Eiserhardt & al., 2011). ***Choristosoria quadripinnata*** (Forssk.) Windham & Schuettp., *Cheilanthes quadripinnata* (Forssk.) Kuhn [CP/Af]: *Schelpe 5926* (BM); South Africa; GU935496, GU935484, GU935566 (Eiserhardt & al., 2011). ***Choristosoria viridis*** (Forssk.) Windham & Schuettp., *Cheilanthes viridis* (Forssk.) Sw. [CP/BrAf]: *Schelpe 2525* (BM); South Africa; GU935494, GU935485, GU935567 (Eiserhardt & al., 2011). ***Christenhuszia cantangensis*** (R.M.Tryon) Schuettp. & J.Prado, *Cheilanthes cantangensis* (R.M.Tryon) R.M.Tryon [CN/An]: *van der Werff 17020* (MO); Peru; PQ417449, PQ417569, PQ412376 (this study). ***Christenhuszia hassleri*** (Weath.) Schuettp. & J.Prado, *Cheilanthes hassleri* (Weath.) Ponce [CN/Br]: *Damasceno 4196* (SI); Brazil; MG593089, NA, NA (Ponce & Scataglini, 2018). ***Doryopteris collina*** (Raddi) J.Sm. [P/Br]: *Abbott 16375* (UC); Bolivia; PQ417473, PQ417596, PQ412402 (this study). ***Doryopteris concolor*** (Langsd. & Fisch.) Kuhn [CP/MeAnBrAfSiAu]: *Dunlop 8472* (NSW); Australia; PQ417474, PQ417597, PQ412403 (this study). ***Doryopteris decora*** Brack. [C/-]: *Flynn s.n.* (IND); U.S.A.; U27446, PQ417599, PQ412404 (Gastony & Rollo, 1995; this study). ***Doryopteris incisa*** (Kunze ex Mett.) J.Prado & Schuettp., *Cheilanthes incisa* Kunze ex Mett. [C/Br]: *Mynssen 1524* (SP); Brazil; PQ417459, PQ417578, NA (this study). ***Doryopteris kirkii*** (Hook.) Alston [CP/Af]: *Festo 1558* (DUKE); Tanzania; PQ417476, PQ417600, PQ412405 (this study). ***Doryopteris lorentzii*** (Hieron.) Diels [P/AnBr]: *Prado 2118* (DUKE); Brazil; PQ417477, NA, PQ412406 (this study). ***Doryopteris nobilis*** (Moore) J.Sm. [-/Br]: *Yesilyurt 542* (BM); Brazil; KP407204, NA, NA (Yesilyurt & al., 2015). ***Doryopteris palmata*** (Willd.) J.Sm. [-/MeAn]: *Huamantupa 4545* (UC); Peru; PQ417479, PQ417602, PQ412408 (this study). ***Doryopteris patula*** (Fée) Fée [P/AnBr]: *Schuettpelz 1458* (SP); Brazil; PQ417480, PQ417603, PQ412409 (this study). ***Doryopteris pentagona*** Pic.Serm. [-/AnBr]: *Cayola 2416* (MO); Bolivia; PQ417481, PQ417604, PQ412410 (this study). ***Doryopteris rediviva*** Fée [-/Br]: *Schuettpelz 1437* (SP); Brazil; PQ417483, PQ417606, NA (this study). ***Doryopteris rivalis*** Sehnem [-/Br]: *Schuettpelz 1370* (SP); Brazil; PQ417484, PQ417607, PQ412412 (this study). ***Doryopteris sagittifolia*** (Raddi) J.Sm. [P/Br]: *Schuettpelz 1438* (SP); Brazil; PQ417485, PQ417608, PQ412413 (this study). ***Doryopteris surinamensis*** Yesilyurt [-/-]: *Schulz 10262* (GH); Suriname; KP407215, NA, NA (Yesilyurt & al., 2015). ***Doryopteris triphylla*** (Lam.) Christ [P/AnBr]: *Antezana 558* (MO); Bolivia; PQ417486, PQ417609, PQ412414 (this study). ***Doryopteris varians*** (Raddi) J.Sm. [P/Br]: *Prado 1104* (UC); Brazil; PQ417487, PQ417610, PQ412415 (this study). ***Estrella mollis*** (Kunze) Windham, *Cheilanthes mollis* (Kunze) C.Presl [CN/An]: *Billiet 5546* (MO); Chile; PQ417461, PQ417580, PQ412386 (this study). ***Gaga angustifolia*** (Kunth) Fay W.Li & Windham [CP/Me]: *van Devender 97-1244* (MO); Mexico; JN647777, PQ417611, JX313452 (Li & al., 2012; this study). ***Gaga apiacea*** (Mickel) Fay W.Li & Windham [C/Me]: *Webster 18* (TEX); Mexico; JX313539, PQ417612, JX313505 (Li & al., 2012; this study). ***Gaga arizonica*** (Maxon) Fay W.Li & Windham [C/Me]: *Schuettpelz 461* (DUKE); U.S.A.; EU268776, EU268727, EU268673 (Rothfels & al., 2008). ***Gaga chaerophylla*** (M.Martens & Galeotti) Fay W.Li & Windham [C/Me]: *Steinmann 4721* (MO); Mexico; JN647788, PQ417613, JX313463 (Li & al., 2012; this study). ***Gaga complanata*** (A.R.Sm.) Fay W.Li & Windham [C/Me]: *Lloyd 4040a* (DUKE); Guatemala; JX313533, NA, JX313468 (Li & al., 2012). ***Gaga cuneata*** (Link) Fay W.Li & Windham [CP/MeAn]: *Rothfels 3288* (DUKE); Mexico; JN647794, PQ417614, JX313472 (Li & al., 2012; this study). ***Gaga decomposita*** (M.Martens & Galeotti) Fay W.Li & Windham [CP/Me]: *Rothfels 3183* (DUKE); Mexico; JN647797, PQ417615, JX313475 (Li & al., 2012; this study). ***Gaga germanotta*** Fay W.Li & Windham [-/Me]: *Rothfels 2618* (DUKE); Costa Rica; JX313546, PQ417616, JX313522 (Li & al., 2012; this study). ***Gaga harrisii*** (Maxon) Fay W.Li & Windham [C/Me]: *Rothfels 2628* (DUKE); Costa Rica; PQ417488, PQ417617, PQ412416 (this study). ***Gaga hintoniorum*** (Mendenh. & Nesom) Fay W.Li & Windham [C/Me]: *Hinton 22695* (NY); Mexico; JN647804, PQ417618, JX313482 (Li & al., 2012; this study). ***Gaga hirsuta*** (Link) Fay W.Li & Windham [CP/Me]: *van Devender 2008-457* (MO); Mexico; PQ417489, PQ417619, PQ412417 (this study). ***Gaga kaulfussii*** (Kunze) Fay W.Li & Windham [C/MeAn]: *Windham 519* (DUKE); Mexico; JN647807, JQ855918, JX313485 (Johnson & al., 2012; Li & al., 2012). ***Gaga lerstenii*** (Mickel & Beitel) Fay W.Li & Windham [-/Me]: *Mickel 6238b* (UC); Mexico; JX313536, PQ417620, JX313490 (Li & al., 2012; this study). ***Gaga marginata*** (Kunth) Fay W.Li & Windham [CP/MeAn]: *Rothfels 2688* (DUKE); Costa Rica; PQ417490, PQ417621, PQ412418 (this study). ***Gaga membranacea*** (Davenp.) Fay W.Li & Windham [CP/Me]: *Mickel 7431* (NY); Mexico; JN647821, NA, JX313501 (Li & al., 2012). ***Gaga monstraparva*** Fay W.Li & Windham [-/Me]: *Beck 1229* (DUKE); Mexico; JX313547, PQ417622, JX313523 (Li & al., 2012; this study). ***Gaga pellaeopsis*** (Mickel) Fay W.Li & Windham [C/Me]: *Iltis 29543* (NY); Mexico; JX313541, PQ417623, JX313508 (Li & al., 2012; this study). ***Gaga purpusii*** (T.Reeves) Fay W.Li & Windham [C/Me]: *Steinmann 2528* (MO); Mexico; JN647825, PQ417624, JX313509 (Li & al., 2012; this study). ***Hemionitis levyi*** E.Fourn. [-/Me]: *Yatskievych 89-253* (IND); Mexico; U27725, NA, NA (Gastony & Rollo, 1995). ***Hemionitis palmata*** L. [-/MeAn]: *Rothfels 08-184* (DUKE); Costa Rica; MK632712, MK632500, MK632821 (Kao & al., 2019). ***Hemionitis rufa*** (L.) Sw. [-/MeAn]: *Jansen-Jacobs 5838* (UC); Guyana; PQ417491, PQ417625, PQ412419 (this study). ***Hemionitis tomentosa*** (Lam.) Raddi [-/AnBr]: *Carretero 809* (UC); Bolivia; PQ417492, PQ417626, PQ412420 (this study). ***Lytoneuron acutilobum*** (Prantl) Yesilyurt [P/Br]: *Yesilyurt 715* (BM); Brazil; KP407206, NA, NA (Yesilyurt & al., 2015). ***Lytoneuron crenulans*** (Fée) Yesilyurt [P/AnBr]: *Schuettpelz 1465* (SP); Brazil; PQ417493, PQ417627, PQ412421 (this study). ***Lytoneuron feei*** (Brade) Yesilyurt [-/Br]: *Schuettpelz 1442* (SP); Brazil; PQ417494, PQ417628, NA (this study). ***Lytoneuron itatiaiense*** (Fée) Yesilyurt [P/Br]: *Prado 1121* (UC); Brazil; PQ417495, PQ417629, PQ412422 (this study). ***Lytoneuron lomariaceum*** (Kunze ex Klotzsch) Yesilyurt [P/AnBr]: *Schuettpelz 1462* (SP); Brazil; PQ417496, PQ417630, PQ412423 (this study). ***Lytoneuron ornithopus*** (Mett. ex Hook. & Baker) Yesilyurt [P/Br]: *Schuettpelz 1367* (SP); Brazil; PQ417497, PQ417631, PQ412424 (this study). ***Mineirella geraniifolia*** (St.-Hil. ex Weath.) Ponce & Scataglini [CN/Br]: *Almeida 1340* (BHCB); Brazil; MG593086, NA, NA (Ponce & Scataglini, 2018). ***Mineirella goyazensis*** (Taub.) Ponce & Scataglini [CN/Br]: *Schuettpelz 1405* (SP); Brazil; PQ417498, PQ417635, NA (this study). ***Mineirella venusta*** (Brade) Ponce & Scataglini [CN/Br]: *Schuettpelz 1425* (SP); Brazil; PQ417499, PQ417636, NA (this study). ***Namaquapteris capensis*** (Thunb.) Windham & Pryer, *Cheilanthes capensis* (Thunb.) Sw. [C/Af]: *Mothogoane 734* (US); South Africa; MK020116, MK020107, MK020126 (George & al., 2019). ***Namaquapteris deltoidea*** (Kunze) Windham & Pryer, *Cheilanthes deltoidea* Kunze [CP/Af]: *BIOTA 127.270* (HBG); South Africa; GU935512, GU935467, GU935572 (Eiserhardt & al., 2011). ***Namaquapteris hastata*** (L.f.) Windham & Pryer, *Cheilanthes hastata* (L.f.) Kunze [CP/Af]: *Eiserhardt WE-063* (HBG); South Africa; GU935510, GU935469, GU935574 (Eiserhardt & al., 2011). ***Namaquapteris kunzei*** (Mett.) Windham & Pryer, *Cheilanthes kunzei* Mett. [CNP/Af]: *BIOTA 127.273* (HBG); South Africa; GU935508, GU935470, GU935575 (Eiserhardt & al., 2011). ***Namaquapteris robusta*** (Kunze) Windham & Pryer, *Cheilanthes robusta* (Kunze) R.M.Tryon [CP/Af]: *BIOTA 127.478* (HBG);

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South Africa; GU935507, GU935466, GU935573 (Eiserhardt & al., 2011). ***Namaquapteris schimperi*** (Kunze) Windham & Pryer, *Cheilanthes schimperi* Kunze [C/Af]: *Luwiika 637* (MO); Zambia; MH170410, PQ417592, PQ412398 (Sosa & al., 2021; this study). ***Ormopteris crenata*** (R.M.Tryon) T.Barbará [P/Br]: *Schuettpelz 1377* (SP); Brazil; PQ417511, PQ417648, PQ412438 (this study). ***Ormopteris cymbiformis*** (J.Prado) T.Barbará [P/Br]: *Schuettpelz 1384* (SP); Brazil; PQ417512, PQ417649, PQ412439 (this study). ***Ormopteris gleichenioides*** (Gardner) J.Sm. [P/Br]: *Prado 1406* (UC); Brazil; PQ417513, PQ417650, PQ412440 (this study). ***Ormopteris pinnata*** (Kaulf.) Lellinger [P/AnBr]: *Prado 1407* (SP); Brazil; EF473699, NA, NA (Prado & al., 2007). ***Ormopteris riedelii*** (Baker) T. Barbará [P/Br]: *Schuettpelz 1382* (SP); Brazil; PQ417514, PQ417651, PQ412441 (this study). ***Parahemionitis arifolia*** (Burm.f.) Panigrahi [-/Si]: *Wu WS-296* (MO); Laos; JX313529, PQ417632, JX313449 (Li & al., 2012; this study). ***Parahemionitis cordifolia*** (Baker) Windham & Schuettp., *Doryopteris cordifolia* (Baker) Diels [-/Af]: *Nusbaumer 1315* (MO); Madagascar; PQ417475, PQ417598, NA (this study). ***Pellaeopsis angulosa*** (Bory ex Willd.) Windham, *Pellaea angulosa* (Bory ex Willd.) Baker [P/Af]: *Grangaud s.n.* (DUKE); France; PQ417515, NA, NA (this study). ***Pellaeopsis boivinii*** (Hook.) Windham, *Pellaea boivinii* Hook. [P/AfSi]: *Jarrett 637* (US); India; PQ417516, PQ417652, PQ412442 (this study). ***Pellaeopsis deboeri*** (Verdc.) Windham, *Cheilanthes deboeri* Verdc. [C/Af]: *Mlangwa 1360* (MO); Tanzania; PQ417452, PQ417572, PQ412379 (this study). ***Pellaeopsis doniana*** (J.Sm.) Windham, *Pellaea doniana* J.Sm. [P/Af]: *Festo 1580* (DUKE); Tanzania; PQ417517, PQ417653, PQ412443 (this study). ***Pellaeopsis dura*** (Willd.) Windham, *Pellaea dura* (Willd.) Hook. [CP/Af]: *Rwaburindore 4600* (MO); Uganda; PQ417518, PQ417654, PQ412444 (this study). ***Pellaeopsis inaequalis*** (Kunze) Windham, *Cheilanthes inaequalis* (Kunze) Mett. [CN/Af]: *Bidgood 5801* (MO); Tanzania; PQ417457, PQ417576, PQ412383 (this study). ***Pellaeopsis lanceolata*** (Bonap.) Windham, *Cheilanthes perrieri* J.P.Roux [CN/Af]: *Rakotondrainibe 3259* (MO); Madagascar; PQ417465, PQ417584, PQ412390 (this study). ***Pellaeopsis longipilosa*** (Bonap.) Windham, *Pellaea longipilosa* Bonap. [P/Af]: *Luwiika 639* (UC); Zambia; PQ417519, PQ417655, PQ412445 (this study). ***Pellaeopsis madagascariensis*** (Tardieu) Windham, *Doryopteris madagascariensis* Tardieu [-/Af]: *Phillipson 2946* (MO); Madagascar; PQ417478, PQ417601, PQ412407 (this study). ***Pellaeopsis pedatoides*** (Desv.) Windham, *Doryopteris pedatoides* (Desv.) Kuhn [-/Af]: *Hennequin R9* (BM); France; KF992477, NA, NA (Hennequin & al., 2014). ***Pellaeopsis pilosa*** (Poir.) Windham, *Doryopteris pilosa* (Poir.) Kuhn [CP/Af]: *Machol s.n.* (MO); Cultivated; PQ417482, PQ417605, PQ412411 (this study). ***Pellaeopsis schippersii*** (Verdc.) Windham, *Pellaea schippersii* Verdc. [P/Af]: *Simon 433* (MO); Tanzania; PQ417520, NA, NA (this study). ***Pellaeopsis schweinfurthii*** (Hieron. ex Diels) Windham, *Pellaea schweinfurthii* Hieron. ex Diels [P/Af]: *Drummond 2042* (US); Tanzania; PQ417521, PQ417656, PQ412446 (this study). ***Pellaeopsis tomentosa*** (Bonap.) Windham, *Pellaea tomentosa* Bonap. [P/Af]: *Stone 2640* (UC); Madagascar; PQ417522, PQ417657, PQ412447 (this study). ***Pentagramma glanduloviscida*** Schuettp. & Windham [-/Me]: *Schuettpelz 1264* (DUKE); U.S.A.; PQ417523, KR066354, KR132633 (Schuettpelz & al., 2015; this study). ***Pentagramma maxonii*** (Weath.) Schuettp. & Windham [-/Me]: *Schuettpelz 445* (DUKE); U.S.A.; EF452165, EF452111, EU268716 (Schuettpelz & al., 2007; Rothfels & al., 2008). ***Pentagramma pallida*** (Weath.) Yatsk., Windham & E.Wollenw. [-/Me]: *Windham 3433* (DUKE); U.S.A.; PQ417524, PQ417658, PQ412448 (this study). ***Pentagramma rebmanii*** (Winner & M.G.Simpson) Schuettp. & Windham [-/Me]: *Rebman 8919* (MO); U.S.A.; PQ417525, PQ417659, PQ412449 (this study). ***Pentagramma triangularis*** (Kaulf.) Yatsk., Windham & E.Wollenw. [-/Me]: *Windham 3431* (DUKE); U.S.A.; PQ417526, KR066381, KR132660 (Schuettpelz & al., 2015; this study). ***Pentagramma viscosa*** (Nutt. ex D.C.Eaton) Schuettp. & Windham [-/Me]: *Metzgar 172* (DUKE); U.S.A.; PQ417527, PQ417660, PQ412450 (this study). ***Quechuapteris buchtienii*** (Rosenst.) Windham, *Cheilanthes buchtienii* (Rosenst.) R.M.Tryon [CN/An]: *Schuettpelz 316* (DUKE); Cultivated; PQ417448, PQ417568, PQ412375 (this study). ***Quechuapteris fraseri*** (Mett. ex Kuhn) Windham, *Cheilanthes fraseri* Mett. ex Kuhn [CN/An]: *Galiano 5034* (MO); Peru; MH170416, PQ417573, PQ412380 (Sosa & al., 2021; this study). ***Quechuapteris glauca*** (Cav.) Windham, *Cheilanthes glauca* (Cav.) Mett. [CP/An]: *Hammel 5851* (MO); Chile; PQ417454, NA, NA (this study). ***Quechuapteris glutinosa*** (M.Kessler & A.R.Sm.) Windham, *Cheilanthes glutinosa* M.Kessler & A.R.Sm. [C/An]: *Jimenez 1928* (MO); Bolivia; PQ417455, PQ417574, PQ412381 (this study). ***Quechuapteris hypoleuca*** (Kunze) Windham, *Cheilanthes hypoleuca* (Kunze) Mett. [CN/An]: *Taylor 11013* (MO); Chile; PQ417456, PQ417575, PQ412382 (this study). ***Quechuapteris pilosa*** (Goldm.) Windham, *Cheilanthes pilosa* Goldm. [C/An]: *Fuentes 10353* (UC); Bolivia; MH170420, PQ417585, PQ412391 (Sosa & al., 2021; this study). ***Quechuapteris pruinata*** (Kaulf.) Windham, *Cheilanthes pruinata* Kaulf. [CN/An]: *Valenzuela 2058* (MO); Peru; MH170422, PQ417588, PQ412394 (Sosa & al., 2021; this study). ***Quechuapteris rufopunctata*** (Rosenst.) Windham, *Cheilanthes rufopunctata* Rosenst. [C/An]: *Sundue 613* (UC); Bolivia; PQ417470, PQ417591, PQ412397 (this study). ***Trachypteris induta*** (Maxon) R.M.Tryon & A.F.Tryon [-/An]: *Sagástegui 15199* (UC); Peru; PQ417528, PQ417661, PQ412451 (this study). ***Trachypteris pinnata*** (Hook.f.) C.Chr. [-/An]: *Windisch 6088* (SJRP); Bolivia; PQ417529, PQ417662, PQ412452 (this study).

Appendix 2. Hemionitid fern species not included in our three-gene dataset. Species are listed by currently accepted name (following the classification presented herein), but we also provide the name most commonly used prior to this study (if different), as well as a summary of current or historical combinations and the biogeographic centers occupied (see Appendix 1 for abbreviations) in brackets. The information included in this appendix also appears in a combined machine-readable suppl. Appendix S1.

Adiantopsis asplenioides Maxon [-/-]. ***Adiantopsis cheilanthoides*** R.M.Senna [-/Br]. ***Adiantopsis crinoidea*** Link-Pérez & Hickey [-/-]. ***Adiantopsis luetzelburgii*** Rosenst. [-/Br]. ***Adiantopsis occulta*** Sehnem [-/Br]. ***Adiantopsis propinqua*** (Mett.) Prantl [C/An]. ***Adiantopsis recurvata*** (Baker) Ponce & Scataglini [C/Br]. ***Adiantopsis scalariformis*** Link-Pérez, Seabolt & Ledford [-/-]. ***Aleuritopteris agetae*** Saiki [C/-]. ***Aleuritopteris belensis*** (Weath. ex Copel.) H.Schneid. [C/-]. ***Aleuritopteris ×confundans*** Fraser-Jenk. [-/Si]. ***Aleuritopteris delicatula*** (Tagawa & K.Iwats.) Windham & Schuettp., *Oeosporangium delicatulum* (Tagawa & K.Iwats.) Fraser-Jenk. & Pariyar [C/Si]. ***Aleuritopteris ×duriensis*** (Mendonça & Vasc.) Windham & Schuettp., "*Oeosporangium ×duriense*" (Mendonça & Vasc.) comb. ined. [C/-]. ***Aleuritopteris erythraea*** (Pic.Serm.) E.A.Hooper, *Cheilanthes erythraea* Pic.Serm. [C/Af]. ***Aleuritopteris ×fraser-jenkinsii*** (Thapa) Fraser-Jenk. & Khullar [C/Si]. ***Aleuritopteris ×gardneri*** Fraser-Jenk. [-/Si]. ***Aleuritopteris ×godavariensis*** Fraser-Jenk. & Khullar [-/Si]. ***Aleuritopteris ×hamiltonii*** Fraser-Jenk. [-/Si]. ***Aleuritopteris hispanica*** (Mett.) Windham & Schuettp., *Oeosporangium hispanicum* (Mett.) Fraser-Jenk. & Pariyar [C/-]. ***Aleuritopteris ×iberica*** (Rasbach & Reichst.) Windham & Schuettp., *Oeosporangium ×ibericum* (Rasbach & Reichst.) Arana & Mor.-Saiz [C/-]. ***Aleuritopteris ×insularis*** (Rasbach & Reichst.) Windham & Schuettp., *Oeosporangium ×insulare* (Rasbach & Reichst.) Arana & Mor.-Saiz [C/-]. ***Aleuritopteris ×khasiana*** Fraser-Jenk. [-/Si]. ***Aleuritopteris ×kochiana*** (Rasbach, Reichst. & Schneller) Windham & Schuettp., *Oeosporangium ×kochianum* (Rasbach, Reichst. & Schneller) L. Sáez & Aymerich [C/-]. ***Aleuritopteris ×kurdica*** (Rasbach & Reichst.) Windham & Schuettp., *Oeosporangium ×kurdicum* (Rasbach & Reichst.) Fraser-Jenk. & Pariyar [C/-]. ***Aleuritopteris leonardii*** (Maxon) Windham & Schuettp., *Mildella leonardii* (Maxon) C.C.Hall & Lellinger [C/-]. ***Aleuritopteris ×malacitensis*** (Rasbach & Reichst.) Windham & Schuettp., *Oeosporangium ×malacitense* (Rasbach & Reichst.) Arana & Mor.-Saiz [C/-]. ***Aleuritopteris ×marchettiana*** (Rasbach, Reichst. & Schneller) Windham & Schuettp., *Oeosporangium ×marchettianum* (Rasbach, Reichst. & Schneller) Arana & Mor.-Saiz [C/-]. ***Aleuritopteris ×meridionalis*** (F.M.Vazquez) Windham & Schuettp., "*Oeosporangium ×meridionale*" (F.M.Vazquez) comb. ined. [-/-]. ***Aleuritopteris ×nepalensis*** Fraser-Jenk. [-/Si]. ***Aleuritopteris ×pangteyi*** Fraser-Jenk. & E.Wollenw. [-/Si]. ***Aleuritopteris pentagona*** Saiki [-/Si]. ***Aleuritopteris pseudoargentea*** S.K.Wu [C/Si]. ***Aleuritopteris pygmaea*** Ching [-/Si]. ***Aleuritopteris rouxii*** Fraser-Jenk. & E.Wollenw. [-/-]. ***Aleuritopteris siamensis*** S.K.Wu [C/Si]. ***Aleuritopteris sichouensis*** Ching & S.K.Wu [-/Si]. ***Aleuritopteris speciosa*** Ching & S.K.Wu [-/Si]. ***Aleuritopteris stenochlamys*** Ching [-/Si]. ***Aleuritopteris ×teneriffae*** (Rasbach & Reichst.) Windham & Schuettp., *Oeosporangium ×teneriffae* (Rasbach & Reichst.) Arana & Mor.-Saiz [C/-]. ***Aleuritopteris thwaitesii*** (Mett.) Saiki, *Oeosporangium thwaitesii* (Mett.) Fraser-Jenk. [C/Si]. ***Aleuritopteris tinaei*** (Tod.) Windham & Schuettp., *Oeosporangium tinaei* (Tod.) Fraser-Jenk. [C/-]. ***Aleuritopteris tirajanae*** (T.S.Velázquez) Windham & Schuettp., "*Oeosporangium tirajanae*" (T.S.Velázquez) comb. ined. [C/-]. ***Aleuritopteris ×tolocensis*** (Rasbach, Reichst. & Schneller) Windham & Schuettp., *Oeosporangium ×tolocense* (Rasbach, Reichst. & Schneller) Arana & Mor.-Saiz [C/-]. ***Aleuritopteris ×unicolor*** Fraser-Jenk. & Khullar [-/Si]. ***Aleuritopteris velutina*** (Tardieu & C.Chr.) Windham & Schuettp., *Oeosporangium velutinum* (Tardieu & C.Chr.) Fraser-Jenk. [CN/Si]. ***Aleuritopteris ×vermae*** (Fraser-Jenk. & Viane) Fraser-Jenk. & Khullar [C/Si]. ***Aleuritopteris ×wallichiana*** Fraser-Jenk. [-/Si].

Appendix 2. Continued.

Aleuritopteris wollenweberi Fraser-Jenk. [-/Si]. ***Aleuritopteris yalungensis*** H.S.Kung [-/Si]. ***Aleuritopteris yunnanensis*** (Ching) Windham & Schuettp., *Oeosporangium yunnanense* (Ching) Fraser-Jenk. & Pariyar [CP/Si]. ***Anthonya hyaloglandulosa*** (W.Jacobsen & N.H.G.Jacobsen) Windham & Pryer, *Cheilanthes hyaloglandulosa* W.Jacobsen & N.H.G.Jacobsen [C/Af]. ***Anthonya nielsii*** (W.Jacobsen) Windham & Pryer, *Cheilanthes nielsii* W.Jacobsen [C/Af]. ***Aspidotis carlotta-halliae*** (W.H.Wagner & E.F.Gilbert) Lellinger [C/Me]. ***Cheilanthes adiantoides*** T.C.Chambers & P.A.Farrant [C/Au]. ***Cheilanthes austrotenuifolia*** H.Quirk & T.C.Chambers [C/Au]. ***Cheilanthes contigua*** Baker [C/Au]. ***Cheilanthes juergensii*** Rosenst. [C/Br]. ***Cheilanthes peruviana*** (Desv.) Moore [N/An]. ***Cheilanthes prenticei*** Luerss. [CN/Au]. ***Choristosoria botswanae*** (Schelpe & N.C.Anthony) Windham & Schuettp., *Cheilanthes botswanae* Schelpe & N.C. Anthony [C/Af]. ***Choristosoria dolomiticola*** (Schelpe) Windham & Schuettp., *Cheilanthes dolomiticola* (Schelpe) Schelpe & N.C.Anthony [CP/Af]. ***Choristosoria glauca*** (Sim) Windham & Schuettp., *Cheilanthes viridis* (Forssk.) Sw. [CP/Af]. ***Choristosoria involuta*** (Sw.) Windham & Schuettp., *Cheilanthes involuta* (Sw.) Schelpe & N.C.Anthony [CP/Af]. ***Choristosoria lacerata*** (N.C.Anthony & Schelpe) Windham & Schuettp., *Cheilanthes multifida* (Sw.) Sw. [C/Af]. ***Choristosoria leucomelas*** (Mett. ex Kuhn) Windham & Schuettp., *Pellaea leucomelas* (Mett. ex Kuhn) Baker [P/Af]. ***Choristosoria pentagona*** (Schelpe & N.C.Anthony) Windham & Schuettp., *Cheilanthes pentagona* Schelpe & N.C.Anthony [C/Af]. ***Doryopteris adornata*** Yesilyurt [-/Br]. ***Doryopteris alata*** A.G.S.Oliveira & Schwartsb. [-/Br]. ***Doryopteris angelica*** K.Wood & W.H.Wagner [-/Br]. ***Doryopteris angustata*** Sehnem [-/Br]. ***Doryopteris apparicioi*** Brade [-/Br]. ***Doryopteris campos-portoi*** Brade [-/Br]. ***Doryopteris conformis*** K.U.Kramer & R.M.Tryon [-/-]. ***Doryopteris crispatula*** (Baker) C.Chr. [P/Br]. ***Doryopteris cyclophylla*** A.R.Sm. [-/-]. ***Doryopteris davidsei*** A.R.Sm. [-/-]. ***Doryopteris decipiens*** (Hook.) J.Sm. [-/-]. ***Doryopteris ×excisa*** Sehnem [-/Br]. ***Doryopteris ×hybrida*** Brade & Rosenst. [-/Br]. ***Doryopteris ×intermedia*** Sehnem [-/Br]. ***Doryopteris jequitinhonhensis*** Salino [-/Br]. ***Doryopteris lonchophora*** (Mett.) J.Sm. [P/Br]. ***Doryopteris pedata*** (L.) Fée [P/-]. ***Doryopteris ×procera*** Sehnem [-/Br]. ***Doryopteris raddiana*** (Raddi) Fée [P/Br]. ***Doryopteris ×scalaris*** Sehnem [-/Br]. ***Doryopteris spiritu-sanctensis*** A.G.S.Oliveira & Schwartsb. [-/Br]. ***Doryopteris stieri*** Rosenst. [-/Br]. ***Doryopteris ×subdecipiens*** W.H.Wagner [-/-]. ***Doryopteris takeuchii*** (W.H.Wagner) W.H.Wagner [C/-]. ***Doryopteris trilobata*** J.Prado [-/Br]. ***Gaga decurrens*** (Mickel) Fay W.Li & Windham [C/Me]. ***Hemionitis ×smithii*** (Trevis.) C.Chr. [-/-]. ***Hemionitis pinnatifida*** Baker [-/Me]. ***Hemionitis umbrosa*** R.Y.Hirai & J.Prado [-/Br]. ***Lytoneuron bradei*** (Rosenst.) Yesilyurt [-/Br]. ***Lytoneuron columbinum*** (Hook.) Smith-Braga & Schwartsburd [P/Br]. ***Lytoneuron microphyllum*** (Christ) Yesilyurt [P/Br]. ***Lytoneuron paradoxum*** (Fée) Yesilyurt [P/Br]. ***Lytoneuron poseidonii*** Smith-Braga & Schwartsburd [-/Br]. ***Lytoneuron quinquelobatum*** (Fée) Yesilyurt [P/Br]. ***Lytoneuron rosenstockii*** (Brade) Yesilyurt [-/Br]. ***Lytoneuron rufum*** (Brade) Yesilyurt [-/Br]. ***Lytoneuron subsimplex*** (Fée) Yesilyurt [-/Br]. ***Lytoneuron tijucanum*** (Brade) Yesilyurt [-/Br]. ***Mineirella eriophora*** (Fée) Ponce & Scataglini [CN/Br]. ***Mineirella steyermarkii*** (Vareschi) Ponce & Scataglini [N/-]. ***Parahemionitis humbertii*** (Tardieu) Windham & Schuettp., *Doryopteris humbertii* Tardieu [-/Af]. ***Pellaeopsis buchananii*** (Baker) Windham, *Cheilanthes buchananii* (Baker) Domin [CN/Af]. ***Pellaeopsis leachii*** (Schelpe) Windham, *Cheilanthes leachii* (Schelpe) Schelpe [CN/Af]. ***Pellaeopsis pectiniformis*** (Baker) Windham, *Pellaea pectiniformis* Baker [P/Af]. ***Pellaeopsis similis*** (F.Ballard) Windham, *Cheilanthes similis* F.Ballard [CN/Af]. ***Quechuapteris andina*** (Hook.) Windham, *Cheilanthes andina* Hook. [C/An]. ***Trachypteris gilliana*** (Baker) Svenson [-/Br]. INCERTAE SEDIS. ***Cheilanthes angustifrondosa*** Alston [C/Af]. ***Cheilanthes boivinii*** Mett. ex Kuhn [C/Af]. ***Cheilanthes boliviana*** C.Chr. [C/An]. ***Cheilanthes bonapartei*** J.P.Roux [C/Af]. ***Cheilanthes laciniata*** Sodiro [C/An]. ***Cheilanthes madagascariensis*** Baker [C/Af]. ***Cheilanthes perlanata*** (Pic.Serm.) Kornas [CN/Af]. ***Cheilanthes valdiviana*** Phil. [C/An]. ***Cheilanthes volcanensis*** de la Sota [C/An]. ***Doryopteris kitchingii*** (Baker) Bonap. [P/Af]. ***Doryopteris latiloba*** C.Chr. [-/Af]. ***Notholaena solitaria*** R.M.Tryon [N/-]. ***Pellaea angolensis*** Schelpe [P/Af]. ***Pellaea prolifera*** Schelpe [P/Af]. ***Pellaea striata*** (Desv.) C.Chr. [P/Af]. ***Pellaea tripinnata*** Baker [P/Af]. ***Trachypteris drakeana*** C.Chr. [-/Af].

Appendix 3. Replicate hemionitid fern samples included in our all-samples dataset. Species are listed by currently accepted name (following the classification presented herein). For each sample, we then include: voucher information including collector and collection number (plus herbarium code), country of origin, and *rbcL* GenBank accession number (with corresponding citation; * = sequence edited). The information included in this appendix also appears in a combined machine-readable suppl. Appendix S1.

Adiantopsis alata Prantl: *Salino 8133* (UPCB), Brazil, KY020079 (Link-Pérez & al., 2016). ***Adiantopsis ×australopedata*** Hickey, M.S.Barker & Ponce: *Zuloaga 8873* (MU), Argentina, JN709746 (Link-Pérez & al., 2011). ***Adiantopsis chlorophylla*** (Sw.) Fée: *Jimenez 2409* (UC), Bolivia, JN709742 (Link-Pérez & al., 2011); *Link-Pérez 193* (MU), Argentina, JN709737 (Link-Pérez & al., 2011); *Link-Pérez 201* (MU), Argentina, JN709743 (Link-Pérez & al., 2011); *Link-Pérez 221* (MU), Argentina, JN709738 (Link-Pérez & al., 2011); *Link-Pérez 356* (MU), Bolivia, JN709739 (Link-Pérez & al., 2011); *Link-Pérez 357* (MU), Bolivia, JN709744 (Link-Pérez & al., 2011); *Link-Pérez s.n.* (MU), Cultivated, JN709740 (Link-Pérez & al., 2011); *Prado 1047* (SP), Brazil, EF473684 (Prado & al., 2007). ***Adiantopsis dichotoma*** (Cav.) T.Moore: *Múlgura 3819* (SI), Argentina, MG593078 (Ponce & Scataglini, 2018); *Romero 3819* (MU), Argentina, JN709728 (Link-Pérez & al., 2011). ***Adiantopsis flexuosa*** (Kunze) Link-Pérez & Hickey: *Forza 1503* (SP), Brazil, EF473686 (Prado & al., 2007); *Mello-Silva 2566* (SP), Brazil, JN717154 (Link-Pérez & al., 2011); *Pirani 5059* (SP), Brazil, JN709722 (Link-Pérez & al., 2011); *Schuettpelz 1368* (SP), Brazil, PQ463088 (this study); *Schuettpelz 1428* (SP), Brazil, PQ463089 (this study); *Thomas 9680* (NY), Brazil, JN709723 (Link-Pérez & al., 2011). ***Adiantopsis hickeyi*** Link-Pérez, Seabolt & Ledford: *Granville 15476* (NY), France, JN709763 (Link-Pérez & al., 2011). ***Adiantopsis orbignyana*** (Mett. ex Kuhn) Ponce & Scataglini: *Sagástegui 11235* (F), Peru, MG593080 (Ponce & Scataglini, 2018). ***Adiantopsis radiata*** (L.) Fée: *Cremers 5049* (NY), France, JN709761 (Link-Pérez & al., 2011); *Link-Pérez 183* (MU), Argentina, JN709760 (Link-Pérez & al., 2011); *Link-Pérez 327* (MU), Bolivia, JN717156 (Link-Pérez & al., 2011); *Link-Pérez 355* (MU), Bolivia, JN717155 (Link-Pérez & al., 2011); *Márquez 19* (LP), Argentina, MG593079 (Ponce & Scataglini, 2018); *Prado 1046* (SP), Brazil, EF473685 (Prado & al., 2007). ***Adiantopsis regularis*** (Mett.) Moore: *Prado 2019* (SP), Brazil, PQ463091 (this study); *Schuettpelz 1468* (SP), Brazil, PQ463090 (this study); *Silva 3001* (UC), Brazil, JN709726 (Link-Pérez & al., 2011). ***Adiantopsis seemannii*** (Hook.) Maxon: *Reina 2008-726* (MO), Mexico, JN709731 (Link-Pérez & al., 2011). ***Adiantopsis senae*** (Baker) Schuettp. & A.Davila: *Hirai 714* (SP), Brazil, KF800703 (Schuettpelz & al., 2014). ***Adiantopsis timida*** Link-Pérez & Hickey: *Santos 249* (NY), Brazil, JN709758 (Link-Pérez & al., 2011). ***Adiantopsis trifurcata*** (Baker) Link-Pérez & Hickey: *Jimenez 2685* (NY), Bolivia, JN709767 (Link-Pérez & al., 2011); *Pirani 1314* (NY), Brazil, JN709768 (Link-Pérez & al., 2011). ***Adiantopsis tweediana*** (Hook.) Link-Pérez & Hickey: *Biganzoli 2068* (SI), Argentina, MG593081 (Ponce & Scataglini, 2018); *Link-Pérez 213* (MU), Argentina, JN709725 (Link-Pérez & al., 2011); *Zardini 6640* (MO), Paraguay, JN709724 (Link-Pérez & al., 2011). ***Adiantopsis vincentii*** M.S.Barker & Hickey: *Morton 10389* (US), Cuba, JN709752 (Link-Pérez & al., 2011). ***Aleuritopteris acrostica*** (Balb.) Windham & Schuettp.: *Rothfels 2735* (DUKE), Oman, MK632705 (Kao & al., 2019). ***Aleuritopteris albofusca*** (Baker) Pic.Serm.: *Li S-4L* (IND), China, U19498 (Gastony & Rollo, 1998); *Mao 080612* (BJFC), China, KP085561* (Wang & al., 2015a). ***Aleuritopteris albomarginata*** (C.B.Clarke) Ching: *Yatskievych 01-31* (MO), China, PQ463092 (this study); *Yatskievych 09-092* (MO), Nepal, PQ463093 (this study); *Zhang 457* (PE), India, AY266411 (Zhang & al., 2003). ***Aleuritopteris anceps*** (Blanf.) Panigrahi: *Zhang 481* (MO), China, PQ463094 (this study). ***Aleuritopteris argentea*** (S.G.Gmel.) Fée: *s.coll. 765868* (TNS), Japan, AB574806 (Ebihara & al., 2010); *Zhang 460* (PE), China, AY266410 (Zhang & al., 2003). ***Aleuritopteris argyrophylla*** (Sw.) Fée: *Carvalho 3656* (MO), Equatorial Guinea, PQ463095 (this study); *Hennequin R175* (BM), France, KF992450 (Hennequin & al., 2014); *Kamau 491* (MO), Kenya, PQ463096 (this study); *Kamau 500* (MO), Kenya, PQ463097 (this study). ***Aleuritopteris belangeri*** (Bory) Windham & Schuettp.: *Wu WS-313* (MO), Laos, PQ463180 (this study). ***Aleuritopteris bicolor*** (Roxb.) Fraser-Jenk.: *Yatskievych 09-097* (MO), Nepal, PQ463098 (this study). ***Aleuritopteris chinensis*** (Baker) Windham & Schuettp.: *Zhang 227* (PE), China, DQ432651 (Zhang & al., 2007). ***Aleuritopteris chrysophylla*** (Hook.) Ching: *Zhang s.n.* (BJFC), China, KP126955* (Wang & al., 2015b); *Zhang s.n.* (PE), China, KP126956* (Wang & al., 2015b). ***Aleuritopteris chusana*** (Hook.) Windham & Schuettp.: *s.coll. 764374* (TNS), Japan, AB574808 (Ebihara & al., 2010); *Zhang 641* (PE), China, DQ432650 (Zhang & al., 2007). ***Aleuritopteris dealbata*** (C.Presl) Fée: *Mikage 9682426* (MO), Nepal, PQ463099 (this study); *Yatskievych 09-075* (MO), Nepal, PQ463100 (this study). ***Aleuritopteris dubia*** (C.Hope) Ching: *MEG-18Y-90* (HITBC), China, LC496742 (Fujiwara & al., 2023); *Yatskievych 09-079* (MO), Nepal, PQ463101 (this study). ***Aleuritopteris duclouxii*** (Christ) Ching: *Li S-18L* (IND), China, U27447 (Gastony

Appendix 3. Continued.

& Rollo, 1995); *Mao 2013080411* (BJFC), China, KP126961* (Wang & al., 2015b); *Mao M2012071804* (BJFC), China, KP085550* (Wang & al., 2015a); *Rothfels 5347* (DUKE), China, PQ463102 (this study). ***Aleuritopteris farinosa*** (Forssk.) Fée: *Gereau 6448* (MO), Tanzania, PQ463103 (this study); *Kamau 531* (MO), Kenya, PQ463108 (this study); *Kamau 532* (MO), Kenya, PQ463105 (this study); *Kamau 538* (MO), Kenya, PQ463107 (this study); *Kamau 564* (MO), Kenya, PQ463106 (this study); *Kayombo 5677* (MO), Tanzania, PQ463104 (this study). ***Aleuritopteris formosana*** (Hayata) Tagawa: *Schuettpelz 1025A* (DUKE), Taiwan, PQ463109 (this study); *Yatskievych 09-076* (MO), Nepal, PQ463110 (this study); *Zhang 458* (PE), India, DQ432643 (Zhang & al., 2007). ***Aleuritopteris grisea*** (Blanf.) Panigrahi: *Boufford 28883* (MO), China, PQ463111 (this study); *Zhang 326* (PE), China, AY299653 (Zhang & al., 2003); *Zhang 437* (PE), China, PQ463112 (this study). ***Aleuritopteris intramarginalis*** (Kaulf. ex Link) Windham & Schuettp.: *Schneider s.n.* (GOET), Cultivated, EF452146 (Schuettpelz & al., 2007). ***Aleuritopteris krameri*** (Franch. & Sav.) Ching: *Wu 1275* (MO), Taiwan, PQ463114 (this study); *Yatskievych 04-77* (MO), China, PQ463113 (this study); *Yatskievych 09-055* (MO), Nepal, PQ463115 (this study). ***Aleuritopteris kuhnii*** (Milde) Ching: *s.coll. 765116* (TNS), Japan, AB574807 (Ebihara & al., 2010); *Mao 080904* (BJFC), China, KP085549* (Wang & al., 2015a); *Schneider s.n.* (no voucher), Unknown, PQ463181 (this study); *Zhang 461* (PE), China, AY266412 (Zhang & al., 2003). ***Aleuritopteris leptolepis*** (Fraser-Jenk.) Fraser-Jenk.: *Zhang 328* (PE), China, DQ432646 (Zhang & al., 2007). ***Aleuritopteris mairei*** (Brause) Windham & Schuettp.: *Mao 2013082904* (BJFC), China, KP085560* (Wang & al., 2015a); *Zhang 314* (MO), China, PQ463182 (this study). ***Aleuritopteris mexicana*** Fée: *Rothfels 08-021* (DUKE), Costa Rica, PQ463116 (this study); *Steinmann 2359* (MO), Mexico, PQ463118 (this study); *van der Werff 16806* (MO), Peru, PQ463117 (this study); *Veliz 10000* (MO), Guatemala, PQ463119 (this study); *Windham 541* (DUKE), Mexico, EU268770 (Rothfels & al., 2008). ***Aleuritopteris niphobola*** (C.Chr.) Ching: *Mao M2012072009* (BJFC), China, KP085548* (Wang & al., 2015a). ***Aleuritopteris nitidula*** (Wall. ex Hook.) Windham & Schuettp.: *Liu 20080805-10* (TAIF), Taiwan, KF289628 (Chao & al., 2014); *Mao M2012071801* (BJFC), China, KP085555* (Wang & al., 2015a); *Zhang 244* (PE), China, DQ432638 (Zhang & al., 2007). ***Aleuritopteris patula*** (Baker) Windham & Schuettp.: *Mao 072309* (BJFC), China, KP085557* (Wang & al., 2015a). ***Aleuritopteris paupercula*** (Christ) Windham & Schuettp.: *Mao M2012071803* (BJFC), China, KP085554* (Wang & al., 2015a). ***Aleuritopteris pteridioides*** (Reichard) Windham & Schuettp.: *Vogel CHEI-23* (BM), Italy, GU935505 (Eiserhardt & al., 2011). ***Aleuritopteris rufa*** (D.Don) Ching: *Mao 2013082915* (BJFC), China, KP126962* (Wang & al., 2015b); *Sundue 1016* (DUKE), China, PQ463120 (this study); *Yatskievych 09-073* (MO), Nepal, PQ463121 (this study). ***Aleuritopteris scioana*** (Chiov.) Fraser-Jenk. & Dulawat: *Rothfels 4287* (DUKE), Oman, MK632714 (Kao & al., 2019). ***Aleuritopteris straminea*** (Ching) Windham & Schuettp.: *Mao M2012071807* (BJFC), China, KP085559* (Wang & al., 2015a). ***Aleuritopteris subargentea*** Ching: *Mao M2012072007* (BJFC), China, KP126960* (Wang & al., 2015b). ***Aleuritopteris subdimorpha*** (C.B.Clarke & Baker) Fraser-Jenk.: *Zhou 721* (PE), China, PQ463122 (this study). ***Aleuritopteris subvillosa*** (Hook.) Ching: *Anderson 22* (MO), China, JQ855926 (Johnson & al., 2012); *Mao 2013090303* (BJFC), China, KP126964 (Wang & al., 2015c). ***Aleuritopteris tamburii*** (Hook.) Ching: *Zhang 434* (PE), China, DQ432644 (Zhang & al., 2007). ***Aleuritopteris trichophylla*** (Baker) Windham & Schuettp.: *Mao 080101* (BJFC), China, KP085556* (Wang & al., 2015a). ***Aleuritopteris veitchii*** (Christ) Ching: *Mao M2012070708* (BJFC), China, KP126959 (Wang & al., 2015b). ***Anthonya bergiana*** (Schltdl.) Windham & Pryer: *Rothfels 4697* (UC), South Africa, PQ463125 (this study). ***Anthonya contracta*** (Kunze) Windham & Pryer: *Eiserhardt WE-200732* (HBG), South Africa, GU935518 (Eiserhardt & al., 2011); *Rothfels 4634* (UC), South Africa, PQ463127 (this study). ***Anthonya depauperata*** (Baker) Windham & Pryer: *Mothogoane 719* (US), South Africa, PQ463128 (this study). ***Anthonya dinteri*** (Brause) Windham & Pryer: *Seydel 3112* (US), Namibia, MH170414 (Sosa & al., 2021). ***Anthonya eckloniana*** (Kunze) Windham & Pryer: *Huiet 126* (DUKE), Cultivated, PQ463129 (this study); *Rothfels 4641* (UC), South Africa, PQ463130 (this study); *Wen 10088* (US), South Africa, JF935343 (Lu & al., 2012). ***Anthonya hirta*** (Sw.) Windham & Pryer: *Hennequin R8* (BM), France, KF992451 (Hennequin & al., 2014); *Huiet 125* (DUKE), Cultivated, PQ463140 (this study); *Huiet 128* (DUKE), Cultivated, PQ463141 (this study); *Rothfels 4644* (UC), South Africa, PQ463138 (this study); *Rothfels 4649* (UC), South Africa, PQ463139 (this study). ***Anthonya marlothii*** (Hieron.) Windham & Pryer: *Seydel 3189* (UC), Namibia, PQ463147 (this study). ***Anthonya parviloba*** (Sw.) Windham & Pryer: *Smith s.n.* (UC), Cultivated, MH170419 (Sosa & al., 2021). ***Aspidotis californica*** (Nutt. ex Hook.) Nutt. ex Copel.: *Kirkpatrick s.n.* (IND), U.S.A., AF336101 (Gastony & Johnson, 2001); *Windham 98-110* (DUKE), U.S.A., PQ463123 (this study). ***Aspidotis densa*** (Brack.) Lellinger: *Schuettpelz 1359A* (DUKE), U.S.A., PQ463124 (this study). ***Brasiliopteris pohliana*** (Mett.) J.Prado, Schuettp. & Yatsk.: *Schuettpelz 1373* (SP), Brazil, PQ463155 (this study). ***Carlottahallia poeppigiana*** (Mett. ex Kuhn) Windham: *Lewis 3282* (MO), Ecuador, PQ463154 (this study); *Ponce 88* (SI), Argentina, KT932741 (Ponce & Scataglini, 2016); *Ponce 88* (SI), Argentina, MG593095 (Ponce & Scataglini, 2018). ***Cheilanthes distans*** (R.Br.) Mett.: *s.coll. P022566* (WELT), New Zealand, GU136791 (Bouma & al., 2010); *Schuettpelz 320* (DUKE), Cultivated, HM003029 (Pryer & al., 2010). ***Cheilanthes fragillima*** F.Muell.: *Dunlop 10039* (MEL), Australia, PQ463131 (this study). ***Cheilanthes hieronymi*** Herter: *Arana s.n.* (SI), Argentina, KT932742 (Ponce & Scataglini, 2016); *de la Sota s.n.* (MO), Argentina, PQ463137 (this study). ***Cheilanthes incarum*** Maxon: *Galiano 5703* (UC), Peru, PQ463143 (this study). ***Cheilanthes lasiophylla*** Pic.Serm.: *Barritt 30* (NSW), Australia, PQ463145 (this study); *Latz 17080* (MEL), Australia, PQ463146 (this study). ***Cheilanthes micropteris*** Sw.: *Deginani 1363* (MO), Argentina, EF452145 (Schuettpelz & al., 2007); *Huaylla 69* (MO), Bolivia, MH170408 (Sosa & al., 2021); *Zavala-Gallo 7* (SI), Argentina, MG593092 (Ponce & Scataglini, 2018). ***Cheilanthes nudiuscula*** (R.Br.) Moore: *Bostock 1407* (NSW), Australia, PQ463151 (this study); *Mao M2013010503* (BJFC), China, KP126968* (Wang & al., 2015c); *Nitta 619* (UC), France, KY099780 (Nitta & al., 2017); *van der Werff 11780* (UC), Australia, PQ463152 (this study). ***Cheilanthes pumilio*** (R.Br.) F.Muell.: *Duretto 1038* (MEL), Australia, PQ463156 (this study). ***Cheilanthes sieberi*** Kunze: *Fraser 281* (NSW), Australia, PQ463158 (this study); *Nagalingum 20* (DUKE), Australia, MH170423 (Sosa & al., 2021); *s.coll. P022565* (WELT), New Zealand, GU136792 (Bouma & al., 2010). ***Cheilanthes squamosa*** Gill. ex Hook. & Grev.: *Biganzoli 2102* (SI), Argentina, MG593100 (Ponce & Scataglini, 2018). ***Cheilanthes tenuifolia*** (Burm.f.) Sw.: *Grusz 1* (DUKE), Malaysia, MH170425 (Sosa & al., 2021); *Kuo 394* (TAIF), Taiwan, MK632709 (Kao & al., 2019); *Mao M2013010501* (BJFC), China, KP126965* (Wang & al., 2015c); *Yatskievych 09-094* (MO), Nepal, PQ463159 (this study). ***Choristosoria calomelanos*** (Sw.) Windham & Schuettp.: *Harder 3784* (MO), Zimbabwe, PQ463190 (this study); *Hennequin R15* (BM), France, KF992508 (Hennequin & al., 2014); *Mao 081501* (BJFC), China, KP085558* (Wang & al., 2015a); *Polunin 3322* (US), Nepal, PQ463191 (this study); *Rothfels 4682* (UC), South Africa, PQ463189 (this study); *Wen 10082* (US), South Africa, JF935346 (Lu & al., 2012). ***Choristosoria induta*** (Kunze) Windham & Schuettp.: *Esterhuysen 23413* (US), South Africa, PQ463144 (this study). ***Choristosoria multifida*** (Sw.) Windham & Schuettp.: *DeMarie s.n.* (UC), Malawi, PQ463150 (this study); *Eiserhardt WE-200730* (HBG), South Africa, GU935499 (Eiserhardt & al., 2011); *Gereau 6409* (MO), Tanzania, JN709734 (Link-Pérez & al., 2011); *Lampinen s.n.* (BM), Tanzania, GU935498 (Eiserhardt & al., 2011); *Rothfels 4627* (UC), South Africa, PQ463149 (this study). ***Choristosoria namaquensis*** (Baker) Windham & Schuettp.: *Eiserhardt WE-200735* (HBG), South Africa, GU935492 (Eiserhardt & al., 2011); *Eiserhardt WE-200737* (HBG), South Africa, GU935493 (Eiserhardt & al., 2011). ***Choristosoria pteroides*** (L.) Mett. ex Kuhn: *Price s.n.* (no voucher), South Africa, PQ463193 (this study); *Rothfels 4626* (UC), South Africa, PQ463192 (this study). ***Choristosoria quadripinnata*** (Forssk.) Windham & Schuettp.: *Brand 1248* (NY), Unknown, KF724190 (Little, 2014); *Luke 10983* (MO), Tanzania, PQ463157 (this study). ***Choristosoria viridis*** (Forssk.) Windham & Schuettp.: *Janssen 2701* (P), France, EF452147 (Schuettpelz & al., 2007); *Mlangwa 1533* (DUKE), Tanzania, PQ463161 (this study); *Prado 2036* (SP), Brazil, JX455163 (Prado & al., 2013); *Rothfels 4681* (UC), South Africa, PQ463160 (this study); *Schelpe 2959* (BM), South Africa, GU935495 (Eiserhardt & al., 2011). ***Doryopteris collina*** (Raddi) J.Sm.: *Prado 1402* (SP), Brazil, EF473688 (Prado & al., 2007); *Schuettpelz 1403* (SP), Brazil, PQ463162 (this study); *Schuettpelz 1453* (SP), Brazil, PQ463163 (this study); *Schuettpelz 1454* (SP), Brazil, PQ463164 (this study); *Yesilyurt 552* (BM), Brazil, KP407199 (Yesilyurt & al., 2015). ***Doryopteris concolor*** (Langsd. & Fisch.) Kuhn: *Dong 178* (PE), China, AY266414 (Zhang & al., 2003); *Hasebe 27609* (TI), Taiwan, U05621 (Hasebe & al., 1995); *Ranker 1939* (COLO), France, KY099797 (Nitta & al., 2017); *Yesilyurt 557* (BM), Brazil, KP407197 (Yesilyurt & al., 2015). ***Doryopteris lorentzii*** (Hieron.) Diels: *Hernández 757* (LIL), Argentina, MG593101 (Ponce & Scataglini, 2018); *Lliully 38* (MO), Bolivia, PQ463165 (this study); *Yesilyurt 527* (BM), Brazil, KP407213 (Yesilyurt & al., 2015); *Yesilyurt 527* (BM), Brazil, JN122015 (Eiserhardt & al., 2011). ***Doryopteris nobilis*** (Moore) J.Sm.: *Prado 1119* (SP), Brazil, EF473690 (Prado & al., 2007). ***Doryopteris palmata*** (Willd.) J.Sm.: *Riba 1746* (IND), Mexico, U27206 (Gastony & Rollo, 1995). ***Doryopteris patula*** (Fée) Fée: *Silva 3708* (UC), Brazil, PQ463168 (this study); *Zardini 49059* (MO), Paraguay, PQ463167 (this study). ***Doryopteris pentagona*** Pic.Serm.: *Múlgura 3906* (SI), Argentina, MG593102 (Ponce

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& Scataglini, 2018); *Prado 1100* (SP), Brazil, EF473693 (Prado & al., 2007). ***Doryopteris rediviva*** Fée: *Prado 1107* (SP), Brazil, EF473694 (Prado & al., 2007); *Yesilyurt 732* (BM), Brazil, KP407200 (Yesilyurt & al., 2015). ***Doryopteris sagittifolia*** (Raddi) J.Sm.: *Prado 1108* (SP), Brazil, EF473695 (Prado & al., 2007); *Schuettpelz 562* (GOET), Cultivated, EF452151 (Schuettpelz & al., 2007); *Yesilyurt 733* (BM), Brazil, KP407205 (Yesilyurt & al., 2015). ***Doryopteris triphylla*** (Lam.) Christ: *Morrone 5881* (SI), Argentina, MG593103 (Ponce & Scataglini, 2018); *Schuettpelz 340* (DUKE), Cultivated, PQ463169 (this study); *Yesilyurt 519* (BM), Brazil, KP407214 (Yesilyurt & al., 2015). ***Doryopteris varians*** (Raddi) J.Sm.: *Yesilyurt 563* (BM), Brazil, KP407201 (Yesilyurt & al., 2015). ***Estrella mollis*** (Kunze) Windham: *Ramirez 361* (ULS), Chile, PQ463148 (this study). ***Gaga angustifolia*** (Kunth) Fay W.Li & Windham: *Anderson 12567* (NY), Mexico, JN647780 (Li & al., 2012); *Breedlove 20549* (CAS), Mexico, JN647782 (Li & al., 2012); *McVaugh 17184* (NY), Mexico, JN647781 (Li & al., 2012); *Rothfels 3109* (DUKE), Mexico, JN647778 (Li & al., 2012); *Rothfels 3116* (DUKE), Mexico, JN647779 (Li & al., 2012). ***Gaga apiacea*** (Mickel) Fay W.Li & Windham: *Diggs 2378* (F), Mexico, JX313540 (Li & al., 2012); *Hinton 23441* (TEX), Mexico, JN647783 (Li & al., 2012). ***Gaga arizonica*** (Maxon) Fay W.Li & Windham: *Breedlove 18570* (NY), Mexico, JN647786 (Li & al., 2012); *Koch 89200* (NY), Mexico, JN647785 (Li & al., 2012); *Tejero-Diez 2839* (NY), Mexico, JN647787 (Li & al., 2012). ***Gaga chaerophylla*** (M.Martens & Galeotti) Fay W.Li & Windham: *Bartholomew 2516* (NY), Mexico, JN647791 (Li & al., 2012); *McVaugh 16108* (NY), Mexico, JN647790 (Li & al., 2012); *Rothfels 3110* (DUKE), Mexico, JN647789 (Li & al., 2012). ***Gaga complanata*** (A.R.Sm.) Fay W.Li & Windham: *Breedlove 40335* (CAS), Mexico, JN647793 (Li & al., 2012); *Breedlove 55870* (NY), Mexico, JN647792 (Li & al., 2012); *Millan 149* (NY), Mexico, JX313535 (Li & al., 2012). ***Gaga cuneata*** (Link) Fay W.Li & Windham: *Mickel 4881* (NY), Mexico, JN647795 (Li & al., 2012); *Montoya 53* (MO), Honduras, JX313532 (Li & al., 2012). ***Gaga decomposita*** (M.Martens & Galeotti) Fay W.Li & Windham: *McVaugh 16427* (NY), Mexico, JN647799 (Li & al., 2012); *Mickel 6064* (NY), Mexico, JN647798 (Li & al., 2012); *Rothfels 3119A* (DUKE), Mexico, JN647796 (Li & al., 2012). ***Gaga harrisii*** (Maxon) Fay W.Li & Windham: *Grusz 105* (DUKE), Costa Rica, JN647803 (Li & al., 2012); *Rothfels 2689* (DUKE), Costa Rica, JN647802 (Li & al., 2012). ***Gaga hintoniorum*** (Mendenh. & Nesom) Fay W.Li & Windham: *Hinton 20157* (TEX), Mexico, JN647805 (Li & al., 2012); *Hinton 28587* (TEX), Mexico, JN647806 (Li & al., 2012). ***Gaga hirsuta*** (Link) Fay W.Li & Windham: *Breedlove 22395* (NY), Mexico, JN647832 (Li & al., 2012); *Hinton 6837* (LL), Mexico, JN647834 (Li & al., 2012); *Leon de la Luz 9704* (MO), Mexico, PQ463170 (this study); *Mickel 3891* (NY), Mexico, JN647833 (Li & al., 2012); *Rothfels 2696* (DUKE), Costa Rica, JN647827 (Li & al., 2012); *Rothfels 3023* (DUKE), Mexico, JN647828 (Li & al., 2012); *Rothfels 3032* (DUKE), Mexico, JN647829 (Li & al., 2012); *Rothfels 3154* (DUKE), Mexico, JN647830 (Li & al., 2012); *Rothfels 3212* (DUKE), Mexico, JN647831 (Li & al., 2012). ***Gaga kaulfussii*** (Kunze) Fay W.Li & Windham: *Larsson 109* (DUKE), Mexico, JN647811 (Li & al., 2012); *Rothfels 08-022* (DUKE), Costa Rica, JN647809 (Li & al., 2012); *Rothfels 2988* (DUKE), Mexico, JN647810 (Li & al., 2012); *Yatskievych 89-286* (MO), Mexico, JN647808 (Li & al., 2012). ***Gaga marginata*** (Kunth) Fay W.Li & Windham: *Boutin & Brandt 2306* (NY), Mexico, JN647820 (Li & al., 2012); *Mickel 7432* (NY), Mexico, JN647819 (Li & al., 2012); *Moran 2361* (MO), Costa Rica, JX313537 (Li & al., 2012); *Ponce 95* (SI), Argentina, MG593104 (Ponce & Scataglini, 2018); *Rothfels 08-023* (DUKE), Costa Rica, JN647813 (Li & al., 2012); *Rothfels 2692* (DUKE), Costa Rica, JN647815 (Li & al., 2012); *Rothfels 2693* (DUKE), Costa Rica, JN647814 (Li & al., 2012); *Rothfels 3137* (DUKE), Mexico, JN647816 (Li & al., 2012); *Rothfels 3731* (DUKE), Ecuador, JN647817 (Li & al., 2012); *Serrano 6089* (MO), Bolivia, JN647812 (Li & al., 2012); *Ventura 1393* (NY), Mexico, JN647818 (Li & al., 2012). ***Gaga membranacea*** (Davenp.) Fay W.Li & Windham: *Davidse 24959* (MO), Costa Rica, JX313538 (Li & al., 2012); *Mickel 7057* (NY), Mexico, JN647822 (Li & al., 2012). ***Gaga pellaeopsis*** (Mickel) Fay W.Li & Windham: *Anderson 4394* (NY), Mexico, JN647823 (Li & al., 2012); *Breedlove 59767* (CAS), Mexico, JN647824 (Li & al., 2012). ***Gaga purpusii*** (T.Reeves) Fay W.Li & Windham: *Barriga 6598* (NY), Mexico, JX313544 (Li & al., 2012); *Purpus 4881* (UC), Mexico, JX313545 (Li & al., 2012); *Ventura 9059* (NY), Mexico, JX313543 (Li & al., 2012). ***Hemionitis palmata*** L.: *Ranker s.n.* (no voucher), Unknown, AY357708 (Ranker & Geiger, unpublished); *Schuettpelz 297* (DUKE), Cultivated, KC984525 (Rothfels & Schuettpelz, 2014). ***Hemionitis rufa*** (L.) Sw.: *Ranker s.n.* (no voucher), Unknown, AY357707 (Ranker & Geiger, unpublished). ***Hemionitis tomentosa*** (Lam.) Raddi: *Prado 2147* (SP), Brazil, PQ463171 (this study); *Márquez 73* (LP), Argentina, MG593105 (Ponce & Scataglini, 2018); *Ranker s.n.* (no voucher), Unknown, AY357709 (Ranker & Geiger, unpublished). ***Lytoneuron crenulans*** (Fée) Yesilyurt: *Schuettpelz 1460* (SP), Brazil, PQ463173 (this study); *Serrano 6982* (UC), Bolivia, PQ463172 (this study); *Yesilyurt 555* (BM), Brazil, KP407207 (Yesilyurt & al., 2015). ***Lytoneuron feei*** (Brade) Yesilyurt: *Yesilyurt 738* (BM), Brazil, KP407210 (Yesilyurt & al., 2015). ***Lytoneuron itatiaiense*** (Fée) Yesilyurt: *Schuettpelz 1443* (SP), Brazil, PQ463174 (this study); *Schuettpelz 1463* (SP), Brazil, PQ463175 (this study); *Yesilyurt 739* (BM), Brazil, KP407208 (Yesilyurt & al., 2015). ***Lytoneuron lomariaceum*** (Kunze ex Klotzsch) Yesilyurt: *Prado 1045* (SP), Brazil, EF473689 (Prado & al., 2007); *Yesilyurt 547* (BM), Brazil, KP407209 (Yesilyurt & al., 2015). ***Lytoneuron ornithopus*** (Mett. ex Hook. & Baker) Yesilyurt: *Prado 1399* (SP), Brazil, EF473691 (Prado & al., 2007); *Schuettpelz 1408* (SP), Brazil, PQ463176 (this study); *Schuettpelz 1419* (SP), Brazil, PQ463177 (this study); *Schuettpelz 1426* (SP), Brazil, PQ463178 (this study); *Schuettpelz 1432* (SP), Brazil, PQ463179 (this study); *Yesilyurt 548* (BM), Brazil, KP407212 (Yesilyurt & al., 2015). ***Mineirella goyazensis*** (Taub.) Ponce & Scataglini: *Prado 1403* (SP), Brazil, EF473687 (Prado & al., 2007). ***Mineirella venusta*** (Brade) Ponce & Scataglini: *Yesilyurt 549* (BM), Brazil, JN122014 (Eiserhardt & al., 2011). ***Namaquapteris capensis*** (Thunb.) Windham & Pryer: *Eiserhardt WE-062d* (HBG), South Africa, GU935511 (Eiserhardt & al., 2011); *Rothfels 4635* (UC), South Africa, PQ463126 (this study). ***Namaquapteris deltoidea*** (Kunze) Windham & Pryer: *Rodin 2187* (UC), South Africa, MK020117 (George & al., 2019). ***Namaquapteris hastata*** (L.f.) Windham & Pryer: *Eiserhardt WE-200733* (HBG), South Africa, GU935509 (Eiserhardt & al., 2011); *Rodin 1442* (UC), South Africa, PQ463134 (this study); *Rothfels 4631* (UC), South Africa, PQ463135 (this study); *Rothfels 4639* (UC), South Africa, PQ463136 (this study). ***Ormopteris crenata*** (R.M.Tryon) T.Barbará: *Prado 1409* (SP), Brazil, KM081636 (Yesilyurt & al., 2015); *Schuettpelz 1381* (SP), Brazil, PQ463183 (this study); *Schuettpelz 1423* (SP), Brazil, PQ463184 (this study); *Schuettpelz 1435* (SP), Brazil, PQ463185 (this study). ***Ormopteris cymbiformis*** (J.Prado) T.Barbará: *Prado 1404* (SP), Brazil, EF473697 (Prado & al., 2007). ***Ormopteris gleichenioides*** (Gardner) J.Sm.: *Prado 1398* (SP), Brazil, EF473698 (Prado & al., 2007); *Prado 1406* (SP), Brazil, KM081638 (Yesilyurt & al., 2015); *Schuettpelz 1374* (SP), Brazil, PQ463186 (this study). ***Ormopteris riedelii*** (Baker) T.Barbará: *Forza 1515* (SP), Brazil, EF473700 (Prado & al., 2007); *Prado 1408* (SP), Brazil, PQ463187 (this study); *Schuettpelz 1383* (SP), Brazil, PQ463188 (this study). ***Parahemionitis arifolia*** (Burm.f.) Panigrahi: *Mo 20070903-26* (TAIF), Taiwan, KF289629 (Chao & al., 2014); *Ranker s.n.* (no voucher), Unknown, AY357706 (Ranker & Geiger, unpublished); *Unknown s.n.* (no voucher), Unknown, MK573828 (Morajkar, unpublished); *Zhang 3530* (unknown), China, FJ628168 (Zhang & al., 2009). ***Pellaeopsis angulosa*** (Bory ex Willd.) Windham: *Hennequin R6* (BM), France, KF992507 (Hennequin & al., 2014). ***Pellaeopsis dura*** (Willd.) Windham: *Kayombo 2654* (MO), Tanzania, JX313530 (Li & al., 2012). ***Pellaeopsis madagascariensis*** (Tardieu) Windham: *Rakotondrainibe 3261* (MO), Madagascar, PQ463166 (this study). ***Pellaeopsis pilosa*** (Poir.) Windham: *Gibby s.n.* (RBGE), Mauritius, JN122017 (Eiserhardt & al., 2011); *Lindsay s.n.* (E), Mauritius, KF992478 (Hennequin & al., 2014). ***Pentagramma maxonii*** (Weath.) Schuettp. & Windham: *Rothfels 2570* (DUKE), U.S.A., MK632740 (Kao & al., 2019); *Schuettpelz 473* (DUKE), U.S.A., PQ463194 (this study). ***Pentagramma pallida*** (Weath.) Yatsk., Windham & E.Wollenw.: *Schuettpelz 1350A* (DUKE), U.S.A., PQ463195 (this study). ***Pentagramma rebmanii*** (Winner & M.G.Simpson) Schuettp. & Windham: *Rothfels 2553* (DUKE), U.S.A., MK632741 (Kao & al., 2019); *Schuettpelz 1257A* (DUKE), U.S.A., PQ463196 (this study). ***Pentagramma triangularis*** (Kaulf.) Yatsk., Windham & E.Wollenw.: *Metzgar 179* (DUKE), U.S.A., PQ463197 (this study); *Pryer 06-01* (DUKE), U.S.A., JX313531 (Li & al., 2012). ***Pentagramma viscosa*** (Nutt. ex D.C.Eaton) Schuettp. & Windham: *Schuettpelz 1287A* (DUKE), U.S.A., PQ463198 (this study). ***Quechuapteris buchtienii*** (Rosenst.) Windham: *Ponce 95* (SI), Argentina, MG593084 (Ponce & Scataglini, 2018). ***Quechuapteris fraseri*** (Mett. ex Kuhn) Windham: *Biganzoli 2195* (SI), Peru, MG593085 (Ponce & Scataglini, 2018); *PE-0-BONN-29933* (no voucher), Cultivated, KU744807 (Zumkeller & al., 2016); *Rothfels 3592* (DUKE), Ecuador, PQ463132 (this study). ***Quechuapteris glauca*** (Cav.) Windham: *Ramirez 360* (ULS), Chile, PQ463133 (this study). ***Quechuapteris glutinosa*** (M.Kessler & A.R.Sm.) Windham: *Jimenez 1928* (LPB), Bolivia, MG593088 (Ponce & Scataglini, 2018). ***Quechuapteris hypoleuca*** (Kunze) Windham: *Ponce 116* (SI), Chile, MG593091 (Ponce & Scataglini, 2018); *Ramirez 362* (ULS), Chile, PQ463142 (this study). ***Quechuapteris pilosa*** (Goldm.) Windham: *Wood 13393A* (UC), Bolivia, PQ463153 (this study); *Zuloaga 9453* (SI), Argentina, MG593094 (Ponce & Scataglini, 2018). ***Quechuapteris pruinata*** (Kaulf.) Windham: *Forbes s.n.* (UC), Cultivated, MK632708 (Kao & al., 2019); *Zuloaga 9234* (SI), Argentina, MG593096 (Ponce

Appendix 3. Continued.

& Scataglini, 2018). ***Quechuapteris rufopunctata*** (Rosenst.) Windham: *Sundue 613* (US), Bolivia, JX313528 (Li & al., 2012); *Wood 14579* (LPB), Bolivia, MG593097 (Ponce & Scataglini, 2018). ***Trachypteris pinnata*** (Hook.f.) C.Chr.: *Aldaz s.n.* (MO), Ecuador, MH170428 (Sosa & al., 2021).

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