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Investigating the Monophyly of *Pellaea* (Pteridaceae) in the Context of a Phylogenetic Analysis of Cheilanthoid Ferns

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ABSTRACT. Cheilanthoid ferns have a worldwide distribution and are found in rocky and seasonally dry habitats. Difficulty in deciphering natural lineages of cheilanthoids has been attributed to morphological convergence associated with adaptation to xeric environments. The goal of this study was to investigate the monophyly of the genus *Pellaea* by generating a DNA sequence-based cheilanthoid phylogeny. DNA sequences of the chloroplast *rps4* gene and *rps4-trnS* intergenic spacer (IGS) were generated from 105 exemplars; chloroplast *trnL-F* IGS sequences were also generated from 60 of these samples. Results show that *Pellaea* sensu Tryon and Tryon is polyphyletic; *Pellaea* sections *Holcochlaena* and *Ormopteris* are distant relatives of sections *Pellaea* and *Platyloma* and have closer relationships with *Doryopteris*. A monophyletic circumscription of "pellaeoid" ferns is here defined to include traditional *P.* sect. *Pellaea*, *P.* sect. *Platyloma*, *Astrolepis*, and elements of *Paragymnopteris* and *Paraceterach*, all of which form a clade sister to *Argyrochosma*. Several other novel systematic implications of cheilanthoid relationships are also presented. The distribution of base chromosome numbers across the cheilanthoid phylogeny reveals potential synapomorphies of $x = 29$ for the pellaeoid clade and $x = 27$ for *Argyrochosma*, and suggests a trend toward reduction in base number during cheilanthoid evolution. Current geographic distribution of cheilanthoid ferns suggests a history of multiple introductions into the Old World from several ancestral New World lineages.

KEYWORDS: Phylogeny, *rps4*, *rps4-trnS*, *trnL-trnF*, xeric ferns.

Cheilanthoid ferns are a fascinating component of the floras of arid regions worldwide. These unusual ferns do not live in the cool, moist, shaded habitats of "typical" ferns. Most species grow in exposed rocky habitats with an extended annual dry period. Cheilanthoid ferns belong to the subfamily Cheilanthoideae Horvat of the homosporous fern family Pteridaceae E.D.M. Kirchn. and include approximately 325 species that comprise a complex of distinctive, well-defined species-groups and ill-defined genera. The historic inability to decipher natural evolutionary lineages within the cheilanthoid ferns has been attributed to morphological convergence associated with adaptation to xeric habitats (Copeland 1947; Tryon et al. 1990; Gastony and Rollo 1995, 1998). Understanding the phylogeny of these ferns is prerequisite to investigating patterns of evolutionary change in their biogeography, morphology, physiology, and ecology associated with adaptation to xeric environments and to advance our insight into how plants respond to climate change.

The cheilanthoid genus *Pellaea* Link has long attracted the attention of North American pteridologists. The species are mainly distributed along mountain chains and occupy dry and rocky habitats. They exhibit reputed morphological and physiological adaptations to xeric environments such as an indument of protective scales, hairs, and/or farina; dissected blades of medium size with small ultimate segments; apogamy; and drought and desiccation tolerance (Pickett 1931; Hevly 1963; Tryon 1957, 1968; Tryon and Tryon 1973; Gastony 1988; Windham 1988; Gastony and Windham 1989). Smith (1981) characterized *Pellaea* as a diverse, poorly defined assemblage of xeric-adapted ferns and noted that relationships among the North American, Neotropical, and Eastern Hemisphere species were unclear. As defined by Tryon and Tryon (1982) the genus *Pellaea* (hereafter referred to as *Pellaea* s.l.) includes approximately 40 species divided among four sections. *Pellaea* sect. *Ormopteris* (J. Sm.) R. M. Tryon and A. F. Tryon comprises five to seven species in Brazil. *Pellaea* sect. *Holcochlaena* Hook. & Baker includes about 10 species in Africa and Madagascar, with three extending to India and Sri Lanka. *Pellaea* sect. *Platyloma* (J. Sm.) Hook. & Baker contains five or six species ranging from New Zealand to Tasmania, Australia, New Caledonia, New Guinea to Sri Lanka, and India. *Pellaea* sect. *Pellaea* Link comprises about 20 species, most occurring in the southwestern United States (California to Texas) and Mexico, with *P. rufa* A. F. Tryon in South Africa and *P. myrtillifolia* Mett. ex Kuhn in Chile. The most widely distributed *Pellaea* species is *P. ternifolia* (Cav.) Link of *P.* sect. *Pellaea*, which occurs in the Americas from Texas to Argentina and Hispaniola; it is the only member of the genus that occurs in Hawaii. The relationships of species in *Pellaea* s.l. with other genera of cheilanthoids, especially *Argyrochosma* (J. Sm.) Windham, *Astro-*

lepis D. M. Benham & Windham, *Cheilanthes* Sw., *Doryopteris* J. Sm., *Notholaena* R. Br., *Paraceterach* Copel., and *Paragymnopteris* K. H. Shing, are poorly understood.

The advent of DNA-based phylogenetic analyses has given systematists the opportunity to approach problems of morphological convergence with independent data sets that are presumably unaffected by the same evolutionary selective pressures. Seminal DNA sequence-based studies by Gastony and Rollo (1995, 1998) greatly advanced our understanding of relationships among cheilanthoid ferns. Sequence data from the chloroplast *rbcL* gene and nuclear rDNA internal transcribed spacer (ITS) region was used in an effort to phylogenetically test the previously described generic and sectional groupings. Their results supported many previous hypotheses of evolutionary relationships, rejected others, and generated a multitude of new questions about relationships within and among cheilanthoid lineages. Their single most parsimonious tree revealed that many traditional genera were paraphyletic or polyphyletic. For example, *Pellaea* s.l., *P.* sect. *Holcochlaena*, and *P.* sect. *Pellaea* were resolved as polyphyletic in their *rbcL* analysis, and *P.* sect. *Platyloma* nested within *P.* sect. *Pellaea*. Although they sampled broadly from the cheilanthoid group, many taxa within *Pellaea* s.l. were not included in their analyses.

Gastony and Rollo (1998) also compared their *rbcL*-based results to an analysis generated using ITS-based trees for a subset of their cheilanthoid taxa. The two data sets were congruent at shallow phylogenetic levels, but disagreed at deeper levels. For example, pairs and triplets of *Pellaea* s.l. species remained together in both data sets, but in the *rbcL*-based analysis *P.* sect. *Pellaea* was paraphyletic, with *Astrolepis* nested within it, whereas in the ITS-based tree *P.* sect. *Pellaea* was polyphyletic. Their study included 12 of the approximately 40 species of *Pellaea* s.l. These results suggested the need to sample more taxa and additional gene regions to resolve relationships between *Pellaea* s.l. and other cheilanthoid ferns.

The primary goal of this study was to investigate the monophyly of *Pellaea* s.l. as it is currently circumscribed, and to find a new monophyletic circumscription for the genus if the current circumscription is indeed non-monophyletic. To accomplish this goal, a DNA-based phylogeny using multiple gene regions was generated from a broad sampling of cheilanthoid ferns. This analysis increased the taxon sampling in *Pellaea* s.l. as compared to previous analyses and generated sequences from additional DNA regions.

Materials and Methods

Taxon Sampling. One hundred and five exemplars of *Pellaea* s.l. and related cheilanthoid ferns were analyzed in this study. Fresh and silica-dried tissues were obtained from Arizona, California, Hawaii, Kentucky, New Mexico, and the Trans-Pecos region of Texas in the U.S.; Tarija, Bolivia; the UC Botanical Garden; and fern growers in California, New York, and Washington. Vouchers of all fresh-collected material are deposited in the University Herbarium (UC) of the University of California, Berkeley, unless otherwise indicated (Appendix 1). When fresh material was not available, tissue samples were obtained from UC herbarium specimens representing worldwide distributions (Appendix 1).

In order to provide a basis for comparison, this data set was designed to include as many of the cheilanthoid species analyzed by Gastony and Rollo (1998) as possible, and expanded upon their original sampling regime. Five of their eight *Pellaea* sect. *Pellaea* species are included with an additional 12 taxa novel to this analysis; one of the two species of *P.* sect. *Platyloma* sampled by Gastony and Rollo is included with two additional species exclusive to this analysis; one of the two *Astrolepis* species sampled by Gastony and Rollo is sampled with two additional species; and one of the four *Argyrochosma* species sampled by Gastony and Rollo is included with three additional species. My analysis also included a substantial sampling of other cheilanthoids, some that were resolved by Gastony and Rollo (1998) as close to *P.* sect. *Pellaea* as well as a broader sampling across cheilanthoid species representing several of the subclades that they resolved as more distantly related to *P.* sect. *Pellaea* but broad enough to include all four sections previously regarded as composing *Pellaea* s.l.

This study included all but five (i.e., *P. cordifolia* (Sessé & Moç.) A.R.Sm., *P. glabella* Mett. ex Kuhn var. *glabella, P. myrtillifolia* Mett. ex Kuhn, *P. pringlei* Davenp., and *P. rufa* A. F. Tryon) of the 20 taxa circumscribed in the most recent monograph of *P.* sect. *Pellaea* (Tryon 1957). Of these five taxa, Gastony and Rollo (1998) examined *P. rufa*. In addition to the 20 *Pellaea* species circumscribed by Tryon (1957), six species considered part of *P.* sect. *Pellaea* are now recognized: *P. bridgesii* Hook., *P. gastonyi* Windham (FNAEC 1993), *P. lyngholmii* Windham, *P. oaxacana* Mickel & Beitel, *P. ribae* Mendoza & Windham, and *P. villosa* (Windham) Windham & Yatsk. (Mickel and Smith 2004). Only *P. bridgesii* was deliberately excluded from *P.* sect. *Pellaea* by Tryon (1957) as the other five species had not yet been described at the time of her monograph. *Pellaea bridgesii* was included in this study, while Gastony and Rollo (1998) did not include any of these six taxa, thus there is no previous hypothesis of their phylogenetic affinities. Of the five recognized species of *P.* sect. *Platyloma*, this current data set included *P. falcata, P. rotundifolia* (also included by Gastony and Rollo (1998)), and *P. nana*, and did not include *P. calidirupium* Brownsey & Lovis (included by Gastony and Rollo (1998)) and *P. paradoxa* (R. Br.) Hook. Unlike Gastony and Rollo (1998), I included exemplars of the Old World genera *Paragymnopteris* (i.e., *P. bipinnata* (Christ) K. H. Shing, *P. marantae* (L.) K. H. Shing, *P. sargentii* (Christ) K. H. Shing, and *P. vestita* (Wall. ex C. Presl) K. H. Shing) and *Paraceterach muelleri* (Hook.) Copel. *Paragymnopteris delavayi* (Bak.) K. H. Shing and *Paraceterach reynoldsii* (F. Muell.) Tindale are the remaining two species of these genera and are missing from my data set.

In various broad studies of fern phylogeny, the genera *Adiantum* L., *Bommeria* E. Fourn., *Cryptogramma* R. Br., and *Llavea* Lag. are recovered as early-diverging lineages in the Pteridaceae (Zhang et al. 2004; Gastony and Rollo 1995, 1998; Hasebe et al. 1995). Based on these studies, the following

outgroup taxa were selected: *Adiantum aleuticum* (Rupr.) C. A. Paris, two samples of *Adiantum pedatum* L., *Bommeria hispida* (Mett.) Und., *Cryptogramma acrostichoides* R. Br., and *Llavea cordifolia* Lag. (Appendix 1).

DNA Extraction, Sequencing, and Alignment. Total genomic DNA was extracted from all tissue samples using DNeasy Plant Mini Kits (Qiagen, Valencia, California) following the manufacturer's protocol. Primers *rps*5F (5′-3′: ATGTCCCGTTATCGAGGACCT) and *trn*SR (5′-3′: TACCGAGGGTTCGAATC; Nadot et al. 1995) were utilized to amplify the plastid *rps4* gene and *rps4-trnS* IGS. Primers e (5′-3′: GGTTCAAGTCCCTCTATCCC) and f (5′-3′: ATTTGAACTGGTGACACGAG) of Taberlet et al. (1991) were utilized to amplify the plastid *trnL-F* IGS. All polymerase chain reactions (PCRs) and cycle-sequencing reactions were performed in a Perkin-Elmer Applied Biosystems (Foster City, California) GeneAmp PCR System 9600 thermocycler. Bionexus (Oakland, California) premix tubes were used for PCR amplification. Reactions to amplify the plastid *rps4* gene and *rps4-trnS* IGS were carried out in a volume of 20 µl, with initial denaturation at 96°C for 1 min, followed by 40 cycles of 96°C for 30 sec, 48°C for 30 sec, and 72°C for 2 min. Amplification reactions for the plastid *trnL-F* IGS were carried out in a volume of 20 µl, with initial denaturation at 94°C for 1 min, followed by 30 cycles of 94°C for 1 minute, 50°C for 1 minute, and 72°C for 2 min, and ending with 72°C for 7 min. Amplicons were processed for cycle sequencing using BigDye-terminator chemistry following manufacturers protocols (PE Applied Biosystems). Clean-up protocols followed the USB pre-sequencing enzymatic clean-up kit (USB Corporation, Cleveland, Ohio) for PCR products and the isopropanol precipitation method for BigDye cycle-sequencing extension products. Sequence products were resolved on a Perkin Elmer model 377 automated fluorescent sequencer. Sequences were assembled, verified, and manually aligned using the program Sequence Navigator v. 1.0.1 (PE Applied Biosystems). Multiple alignments of the gene and spacer sequences were unambiguous and thus no regions were excluded from subsequent phylogenetic analyses. Most gaps were coded as missing data. However, three multi-nucleotide sequence gaps at positions 433–438, 439–447, and 448–453 in the aligned sequence file reflected potentially informative insertions/deletions (indels) and were coded as characters; each gap was treated as a single binary character regardless of length. A data set of the chloroplast *rps4* gene and non-coding *rps4-trnS* IGS were compiled for all 105 exemplars in this analysis. The chloroplast non-coding *trnL-F* IGS was additionally sequenced from 60 of the 105 exemplars. The aligned sequence data matrix was submitted to TreeBASE (study number S1721) and all individual sequences are available in GenBank (Appendix 1).

Phylogenetic Analyses. Phylogenetic analyses were performed using PAUP* 4.0b10 (Swofford 2002) alone or in combination with MacClade v. 4.06 (Maddison and Maddison 2003) or ModelTest 3.6 (Posada and Crandall 1998). Analyses followed maximum parsimony (MP) or maximum likelihood (ML) criteria with the following options: heuristic searches, all characters equally weighted and unordered, all uninformative characters excluded (only MP searches), 10,000 random addition starting trees (for MP searches), and TBR branch swapping. Branch support for each clade in MP analyses was estimated by bootstrapping (10,000 replicates (reps.)) in PAUP* 4.0b10 and by MacClade's Decay Index option (nonrandom addition and 10 reps.) for generating a PAUP* 4.0b10 command file to calculate decay indices (Bremer 1988; Donoghue et al. 1992). ML analyses were performed on the entire molecular data set ("large data set") using a GTR + I + G model of sequence evolution as chosen by ModelTest 3.6 (Posada and Crandall 1998). MP and ML analyses were also performed on a subset of the data ("small data set") that included exclusively species also analyzed by Gastony and Rollo (1998). This small data set was analyzed following ML protocols with the TVM + G model as indicated by ModelTest (Posada and Crandall 1998). Likelihood bootstrap searches of both data sets were performed with 10 reps. each using the heuristic bootstrap option in PAUP* 4.0b10 (Swofford 2002). To test the topology of Gastony and Rollo's (1998) phylogeny, MP and ML heuristic and bootstrap analyses were performed on the small data set using a constraint tree with a topology generated from Gastony and Rollo's (1998) analysis and pruned to contain only taxa similar to both studies. To simplify tree figures, clades comprising more than one exemplar of the same taxon are represented by a single terminal with the number of exemplars supporting that branch indicated in parentheses to the right of each taxon name.

Character distributions were mapped onto one of the most parsimonious reconstructions (MPR) utilizing MacClade (Maddison and Maddison 2003). Character state evolution was investigated using parsimony algorithms of MacClade that infer character states of ancestral lineages and their changes through time across a topology. Only the default DELTRAN option of character evolution was used because of multiple polytomies in the topology. Cytological, morphological, and geographic data were obtained from published literature, personal observations of live plants, herbarium specimens, and herbarium label data (Appendices 1, 2).

RESULTS

DNA Sequences. Of the 1257 aligned characters for the 105 cheilanthoid *rps4* gene and *rps4-trnS* IGS sequences, 544 basepairs (bp) were invariant, 158 bp varied but were parsimony-uninformative for this set of taxa, and 555 bp were parsimony-informative. Of the 465 aligned characters for the 60 sequences of the *trnL-F* IGS, 225 bp were invariant, 75 bp were variable but parsimony-uninformative, and 165 bp were parsimony-informative. After pruning of redundant sequences (with zero to one absolute differences at potentially informative sites compared to an included sequence), the cheilanthoid data set (heretofore referred to as the "large data set") contains 88 terminals. The small data set contains 28 sequences from exemplars representing the 19 species in common to both this and Gastony and Rollo's (1998) studies (see Fig. 2).

Phylogenetic Hypotheses. MP analysis of the large data set recovered 667 most parsimonious reconstructions (MPR) with a length (L) of 2461 steps, consistency index (CI) of 0.473, retention index (RI) of 0.781, and a rescaled consistency index (RC) of 0.370. The ML analysis of the large data set generated a tree with –ln L = 16800.79512 (evaluated in a parsimony context with only parsimony informative characters included: L = 2468, CI = 0.472, RI = 0.779, RC = 0.368). Both the MP and ML (see Fig. 1) trees consist of four major

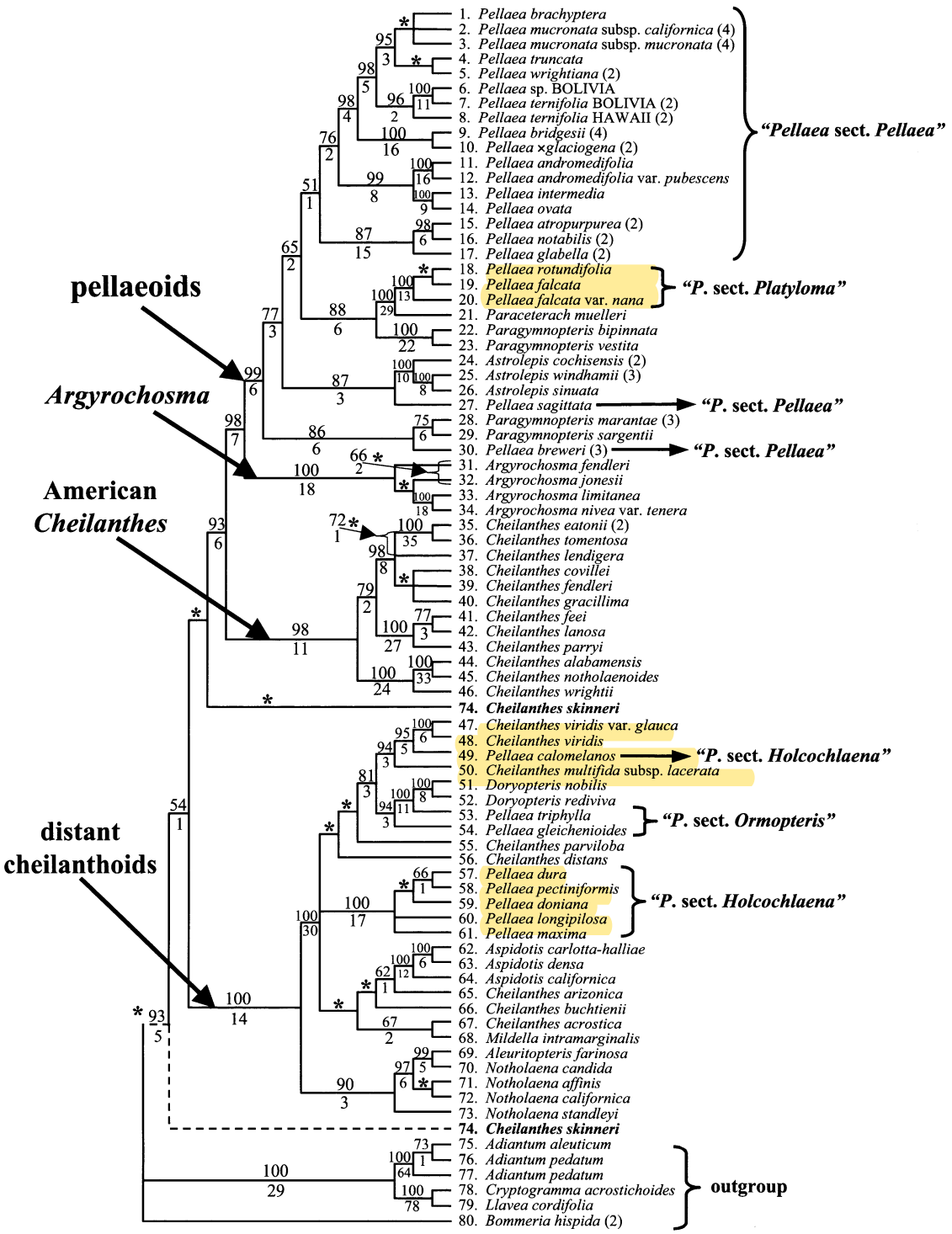

FIG. 1. The ML topology and MP strict consensus topology of 667 MPR based on chloroplast *rps4* gene and *rps4-trnS* (88 exemplars) and *trnL-F* (60 exemplars) intergenic spacers data set with terminal taxa numbered for ease of discussion (ML tree: –ln L = 16800.79512; MP tree: Length = 2461, CI = 0.473, RI = 0.781, RC = 0.370, HI = 0.527). * indicate collapsed nodes or changes as shown for MP topology, dashed line indicates location of *Cheilanthes skinneri*, in boldface, in MP topology. The numbers above the branches are MP bootstrap percentages (≥ 50%) and below branches are MP decay indices (Bremer support). Higher-level taxa indicated by quotes follow circumscriptions in Tryon and Tryon (1982).

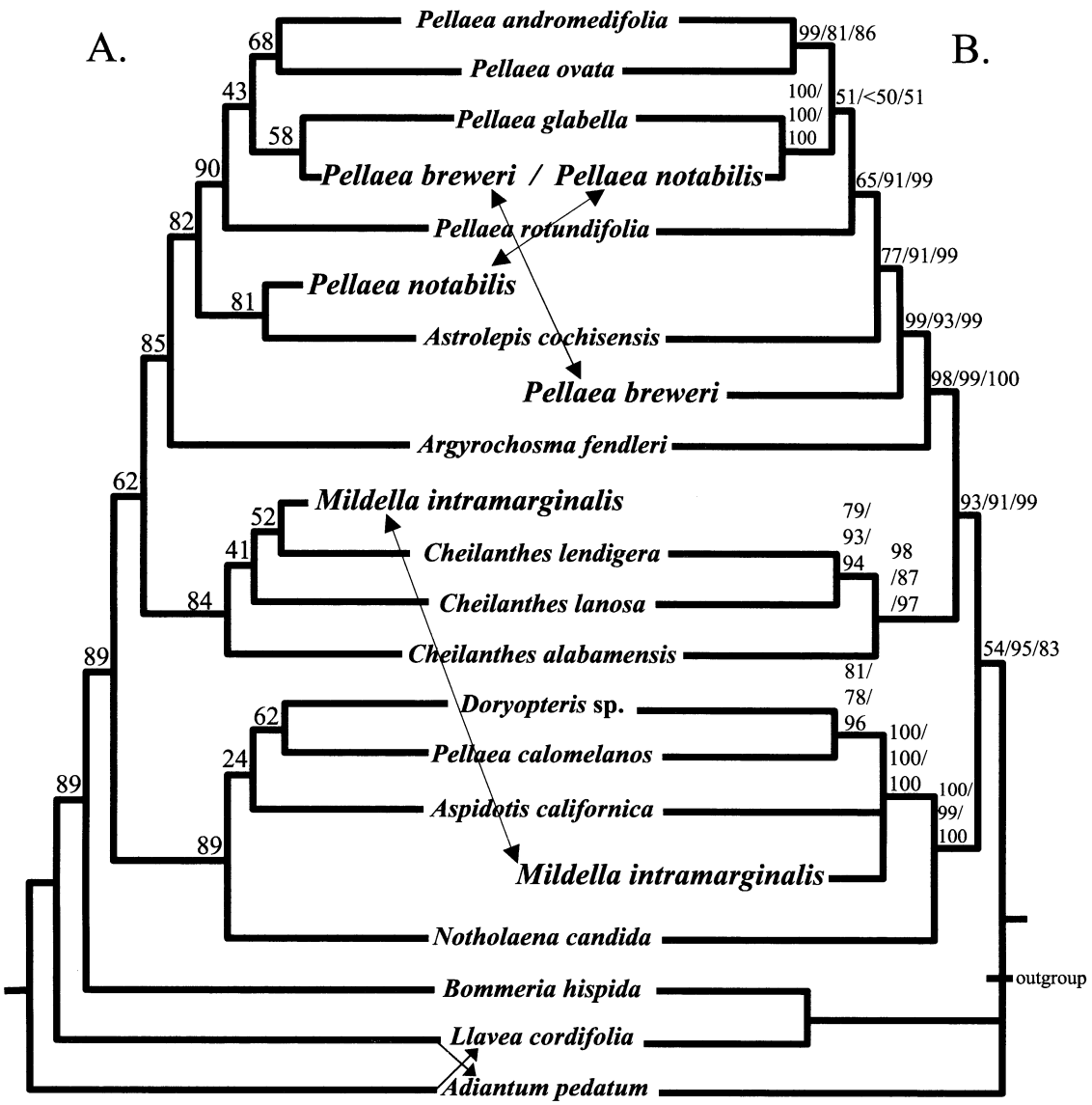

FIG. 2. A. Pruned topology of Gastony & Rollo (1998) based on *rbcL*. The numbers above the branches are bootstrap percentages as reported in Gastony and Rollo's entire *rbcL* topology. B. Pruned topology from this study based on chloroplast *rps4* gene and *rps4-trnS* and *trnL-F* intergenic spacers. The three numbers above the branches represent: large data set MP, small data set MP, and small data set ML bootstrap scores, respectively.

and well-supported clades (((pellaeoid + *Argyrochosma*) + American *Cheilanthes*) + "distant cheilanthoids") with *Cheilanthes skinneri* (Hook.) R. M. Tryon & A. F. Tryon recovered as the earliest diverging lineage in the MP tree, and is recovered as sister to (((pellaeoid + *Argyrochosma*) + American *Cheilanthes*) in the ML tree. The topology of the ML tree is largely identical to the MP strict consensus tree but shows greater resolution in certain areas, especially near the tips. For example, the polytomy of species 18, 19, and 20 in the MP tree is resolved in the ML tree with 18 and 19 sister taxa and 20 sister to them.

MP analysis of the small data set recovered 12 MPR with L = 986, CI = 0.624, RI = 0.743, and RC = 0.463, and ML analysis generated a tree with –ln L = 8204.64815 (evaluated in a parsimony context with only parsimony informative characters included: L = 987, CI = 0.623, RI = 0.742, RC = 0.462). MP analysis of the small data set, using the Gastony and Rollo (1998) pruned topology as a constraint tree (Fig. 2A), generated parsimony tree scores with L = 1085, CI = 0.567, RI = 0.674, and RC = 0.382. ML analysis of this study's small data set with the Gastony and Rollo (1998) pruned topology as a constraint tree generated a tree with

–ln L = 8446.92438 (evaluated in a parsimony context with only parsimony informative characters included: L = 1085, CI = 0.567, RI = 0.674, and RC = 0.382). A Shimodaira-Hasegawa Test, as implemented in PAUP* 4.0b10 (Swofford 2002), was performed to compare the relative likelihood of this study's ML tree topology with Gastony and Rollo's pruned topology and determined that the Gastony and Rollo pruned topology was significantly less likely (P-value = 0.000, << 0.05; one-tailed test) than the ML tree, given this study's small data set. The topologies generated from unconstrained MP and ML analyses of the small cheilanthoid data set were identical to the pruned topology generated from the large cheilanthoid data set. This topology of the small cheilanthoid data set is shown in Fig. 2B.

Discussion

Pellaea *and Cheilanthoid Phylogenies.* As shown in Fig. 1, the species represented in this analysis are arrayed in clades and subclades that are mostly congruent with previous hypotheses of relationship, but conflict with several historic taxonomic circumscriptions. *Pellaea* sect. *Platyloma*, *Aspidotis*, *Astrolepis*, *Argyrochosma*, *Doryopteris*, and a group of mostly American *Cheilanthes* are each recovered as independent monophyletic lineages. *Cheilanthes* s.l., *Notholaena*, *Paragymnopteris*, *Pellaea* s.l., and *Pellaea* sections *Pellaea*, *Holcochlaena*, and *Ormopteris* are all found to be either para- or polyphyletic. *Astrolepis* nests within *P.* sect. *Pellaea*, as was first revealed by Gastony and Rollo (1998); *P.* sect. *Holcochlaena* and *P.* sect. *Ormopteris* are recovered as distant relatives of sections *Pellaea* and *Platyloma*, supporting the hypothesis that *Pellaea* sensu Tryon and Tryon (1982) is polyphyletic (Gastony and Rollo 1995, 1998). *Cheilanthes* sensu Tryon and Tryon (1982) is also recovered as polyphyletic, as previously proposed based on both morphology (e.g., Tryon and Tryon 1973, 1982; Lellinger 1989; Gastony and Rollo 1995, 1998) and DNA sequence data (Gastony and Rollo 1995, 1998).

Results from this study provide several novel insights regarding *P.* sect. *Pellaea* in particular and relationships among cheilanthoids in general. One surprising result is the nesting of several Old World species currently assigned to the genera *Paragymnopteris* and *Paraceterach* within *P.* sect. *Pellaea* (Figs. 1, 3, and 4). The Australian species *Paraceterach muelleri* (type species for *Paraceterach*) together with Asian species *Paragymnopteris bipinnata* (H. Christ) K. H. Shing and *P. vestita* (Wall ex C. Presl) K. H. Shing form a clade with *Pellaea* sect. *Platyloma*, which has species native to Asia, Australia, Tasmania, New Zealand, and New Caledonia. *Paragymnopteris marantae* (L.) K. H. Shing (type of *Paragymnopteris*, represented by three exemplars) of Eurasia, Ethiopia, Canary Islands, and Madeira, and *P. sargentii* (H. Christ) K. H. Shing of China, are sister to the North American endemic *Pellaea breweri* D. C. Eaton (represented by three exemplars). Another novel finding is the recovery of *Pellaea breweri* in an isolated position, sister to species traditionally placed in *Paragymnopteris*, and quite distant from both samples of *P. glabella* Mett., previously considered its sister taxon (Gastony and Rollo 1998).

Exemplars of *Paraceterach* and *Paragymnopteris* were included here because of their uncertain placement within cheilanthoid ferns and controversial taxonomy. Species of *Paragymnopteris* s.l. have been placed in several other genera, including *Acrostichum* L., *Cheilanthes*, *Cincinalis* Gled., *Gymnogramma* Desv., *Gymnopteris* C. Presl, *Hemionitis* L., *Neurogramma* Ling, *Notholaena*, and *Paraceterach*. My sample of *Paragymnopteris* included four species, all of which Tryon (1986a) assigned to *Paraceterach*. Shing (1993) placed these same species in *Paragymnopteris* (distributed in cool temperate zones of the Old World) leaving just two Australian species in *Paraceterach* (*P. muelleri* and *P. reynoldsii*). My results conflict with both Tryon's and Shing's circumscriptions of these genera and with many other systematists' previous taxonomies based on morphology. This is the first molecular phylogenetic analysis of cheilanthoid ferns that has included exemplars of these genera. These findings suggest that convergent morphologies have obscured the phylogenetic placement of *Paraceterach* and *Paragymnopteris* species. Accordingly, exemplars of other potentially misplaced species need to be analyzed with both molecular and morphological data in order to test further this study's phylogenetic hypothesis and before a well-supported taxonomy of these taxa can be achieved.

These results support the polyphyly of *P.* sect. *Pellaea* as traditionally circumscribed, and emphasize the need for taxonomic revision within this clade. One revisionary option is to redefine *Pellaea* (type: *P. atropurpurea* (L.) Link) to include the entire pellaeoid clade as shown in Fig. 1 and 4, sister to the well-supported and monophyletic *Argyrochosma*. This option is supported by molecular data (99% bootstrap and 6 decay indices) and the putative synapomorphy of base chromosome number of $x = 29$ (Fig. 3B). A second option would be to divide the pellaeoid clade into four monophyletic genera, as represented by species 1–17 (*Pellaea*), 18–23 (*Platyloma*), 24–27 (*Astrolepis*), and 28–30 (*Paragymnopteris*) in Fig. 1, that form four

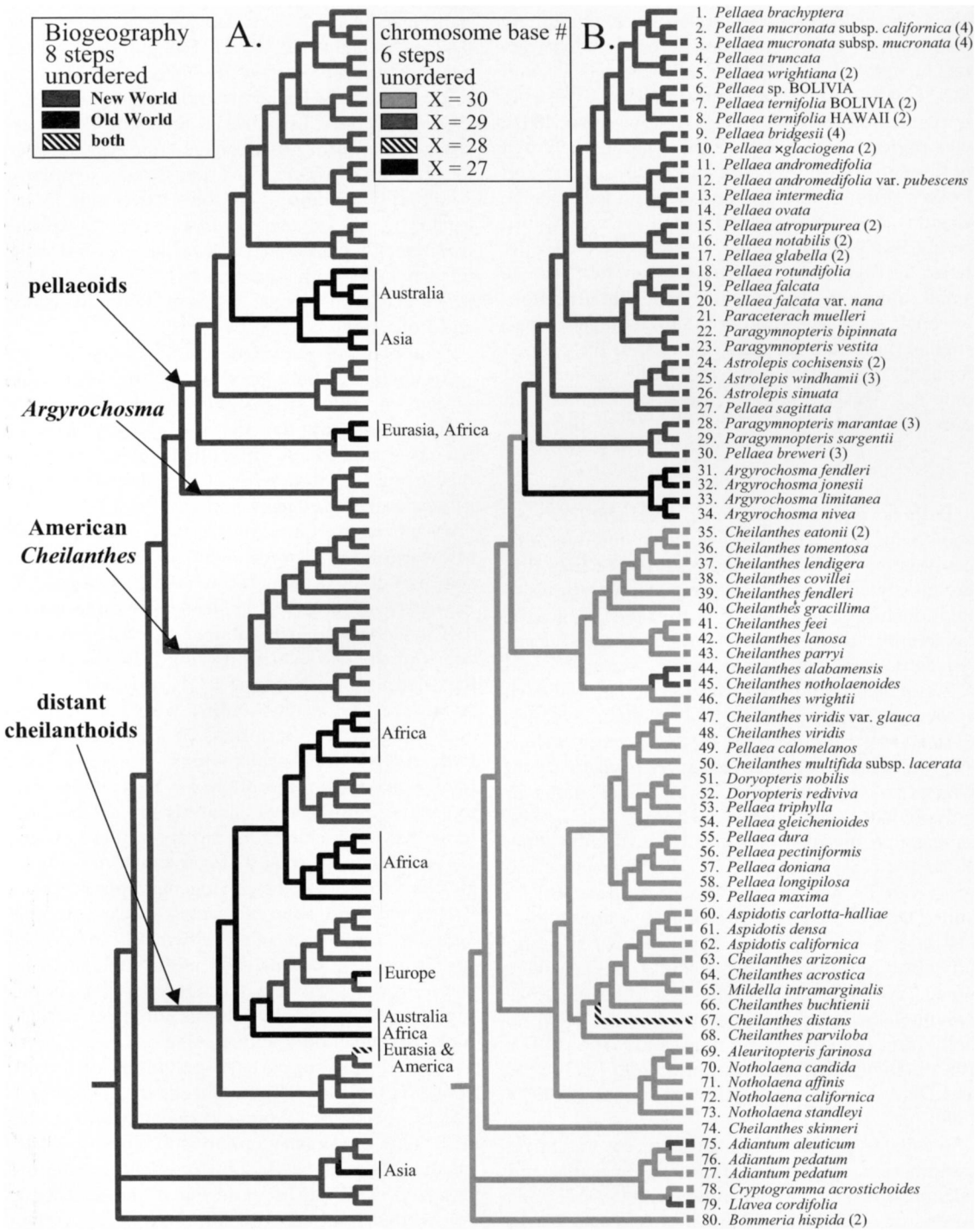

FIG. 3. A. Biogeography of cheilanthoid exemplars of this study mapped onto one of the MPR trees based on the *rps4* gene and *rps4-trnS* and *trnL-F* intergenic spacers. B. Base chromosome number of cheilanthoid exemplars of this study mapped as in A. Note: squares missing at branch tips denote chromosome counts not available (Appendix 2).

well-supported clades with many distinguishing morphological characteristics. I prefer the latter revisionary option as these four proposed genera are less disruptive to current usage, are more readily definable, and better reflect the morphological distinctions within pellaeoid ferns (Fig. 4). The pellaeoid clade of Fig. 1 represents 62% (28/45) of the species in the three genera and two

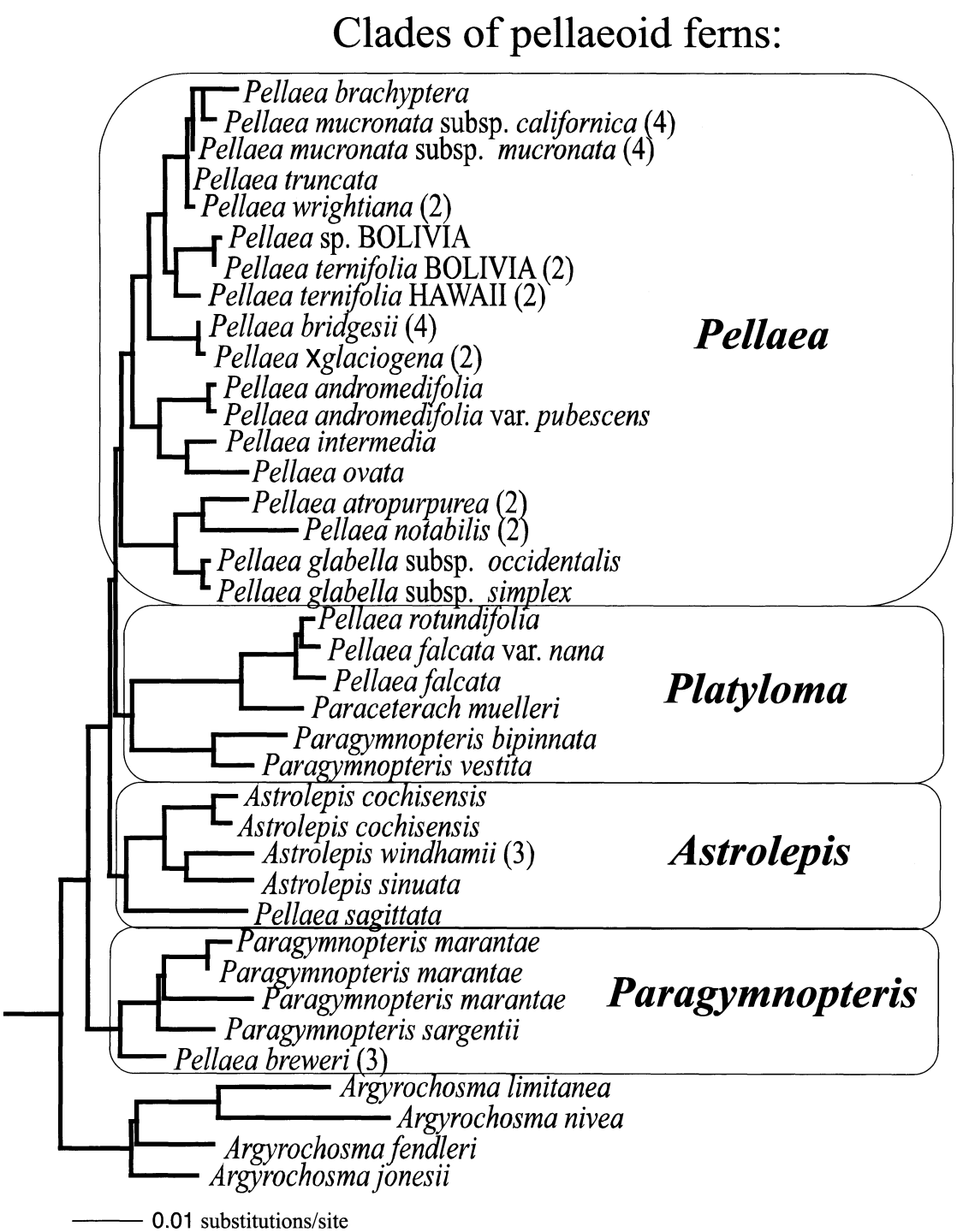

FIG. 4. ML phylogram (based on chloroplast *rps4* gene and *rps4-trnS* (88 exemplars) and *trnL-F* (60 exemplar) intergenic spacers data set) of pellaeoid and Argyrochosma clades with four pellaeoid subclades in boxes with informally proposed genus names.

sections that currently compose it (i.e., *Astrolepis* (3/6), *Paraceterach* (1/2), *Paragymnopteris* (4/5), *P.* sect. *Pellaea* (17/27), and *P.* sect. *Platyloma* (3/5)) and many of the missing species are readily assignable to a particular subclade. However, further taxon sampling and phylogenetic analysis of morphological and molecular data is needed before formal taxonomic revision.

Gastony and Rollo (1998) first identified an American *Cheilanthes* clade with molecular sequence data. This clade is strongly confirmed by results from this study (Fig. 1). Reeves (1979) recognized four subgenera of *Cheilanthes* in an unpublished monograph of *Cheilanthes* subg. *Physapteris*. Three of these subgenera (subg. *Physapteris*, subg. *Cheilanthes*, and subg. *Alabamensis*) are supported here and correspond to the three strongly supported subclades comprising species 35–40, 41–43, 44–46, respectively. The phylogenetic placement of *Cheilanthes wrightii* (46) within *C.* subg. *Alabamensis* is a new discovery of this study, as its affinities were previously uncertain (Reeves 1979). The fourth subgenus of *Cheilanthes* recognized by Reeves is *C.* subg. *Ortholonoma*, which is represented in this study by *C. arizonica* (Maxon) Mickel. This taxon is recovered as sister to a clade of all three sampled species of *Aspidotis* (Nutt. *ex* Hook. & Baker) Copel. (species 62–64) that together form a clade deep within the ''distant cheilanthoids'' clade and far from other American *Cheilanthes*. In 1968, Lellinger separated two of these species from *Cheilanthes* and placed them in *Aspidotis* (as *A. californica* and *A. carlotta-halliae*) based on the possession of elongate, distantly dentate segments, scarious indusia, and glabrous, 3–5 pinnate pentagonal blades. More evidence is needed to support a formal move but it appears that *C. arizonica* is a member of *Aspidotis*. These examples reflect the existing complexity in *Cheilanthes* s.l., its extreme diversity, and the need for further phylogenetic studies. The current study included only 14% (12/88) (FNAEC 1993, Mickel and Smith 2004) of the species hypothesized to belong to this group. Taxonomic revision of the American *Cheilanthes* awaits additional taxon sampling and analysis.

Within the ''distant cheilanthoids'' clade, represented in Fig. 1 by species 47–74, analysis of molecular sequence data revealed that *Pellaea* sect. *Holocochlaena* (species 55–59) is a well-supported clade and comprises several African species. The morphology of African *P. boivinii* Hook. (not included in this study) suggests that it may also be a member of this clade. *Pellaea doniana* Hook. is included in my analysis, and is the type of the segregate genus *Pteridella*, which could be adopted for this clade. However, additional taxon sampling and analysis is underway and prerequisite to any formal change.

Contrasting the Gastony/Rollo and Kirkpatrick Cheilanthoid Phylogenies. A topological comparison of Gastony and Rollo's *rbcL*-based cheilanthoid phylogeny with this study's *rps4* gene- and *rps4-trnS* and *trnL-F* IGS-based cheilanthoid phylogeny is shown in Fig. 2 using two pruned topologies that contain only species sampled in both studies. The Gastony/Rollo pruned topology with bootstrap scores (Fig. 2A) is based on the published results of their entire MP-analyzed data set. Because only 25 of the 57 *rbcL* gene sequences generated by Gastony and Rollo (1995, 1998) were deposited in GenBank and only seven of these were from species also analyzed in my study, I could not analyze a pruned data set of their molecular sequences, thus the bootstrap scores refer to their entire analysis not shown here and only approximate support for the represented clades. The pruned topology and bootstrap scores shown in Fig. 2B are based on MP and ML heuristic and bootstrap analyses of this study's large and small data sets, which are completely congruent. The placement of taxa in the Gastony/Rollo and Kirkpatrick trees is largely congruent. The main differences involve: 1) the phylogenetic placements of *P. breweri* D.C.Eaton, *P. notabilis* Maxon, and *Mildella intramarginalis* (Mett.) Hook. ex T. Moore and 2) the level of branch support.

The incongruence between these two cheilanthoid phylogenetic hypotheses (Fig. 2A and B) may be due to: 1) different evolutionary histories in the DNA regions utilized in each study (e.g., lineage sorting, hybridization); 2) variable amounts of historic signal within the different DNA regions employed, providing uneven support across the phylogenies; 3) relative density of taxon sampling; and 4) the relative amount of homoplasy across the two phylogenies (Wendel and Doyle 1998). DNA coding regions, such as the *rbcL* and *rps4* genes, have been found to evolve more slowly than non-coding regions, are thought to be conserved for function, and typically provide resolution among families and/or genera as exemplified in several global analyses of pteridophytes (Hasebe et al. 1995; Pryer et al. 2001). Non-coding regions, such as the *rps4-trnS* and *trnL-F* IGSs, are assumed to be under less functional constraint, evolve at a more clock-like rate, and typically provide resolution within families and genera, as demonstrated in the pteridophyte studies of Schneider et al. (2004) and Small et al. (2005). Advocates of a combined approach to phylogenetic analysis suggest that by combining independent data sets into one large data set, more characters can be considered simultaneously and combined analyses are more likely to resolve conflicts between phylogenies based on single DNA regions (Doyle and Donoghue 1987, Kluge 1989, de Queiroz et al. 1995, Nixon and Carpenter 1996, Page 1996, and Johnson and Soltis 1998). Greater density of taxon sampling provides evolutionary information along branches

of a phylogeny, breaking branches into shorter segments, and helping to avoid the problem of long-branch attraction and homoplastic similarity due to convergence (Felsenstein 1978; Wendel and Doyle 1998). A major advantage of ML, as compared to parsimony, is its attempted correction for unobserved substitutions (Swofford et al. 1996) and the associated homoplasy that, if left unchecked, can result in long-branch attraction and incorrect phylogenies.

The incongruent phylogenetic placement of *Mildella intramarginalis* in these two studies may be due to any of the reasons mentioned above, but sparse taxon sampling in the distant cheilanthoid clade is a special concern. More samples of *M. intramarginalis* and close relatives need to be included in a phylogenetic study to clarify this species relationships.

Although precise reasons for the above conflicts remain to be identified, the combination of greater taxon density, increased character number, employment of multiple cpDNA regions, and use of a variety of analytical methods and tests in this study, as well as the consistent and congruent results obtained across large- and small-scale analyses, suggest that the phylogenetic hypothesis depicted in Fig. 1 and Fig. 2B is a positive step forward toward achieving refined understanding of relationships among cheilanthoid ferns.

Character Mapping and Identification of Potential Synapomorphies. The broad cheilanthoid phylogeny produced by this study can be used to investigate the evolution of a variety of characters and suggest potential synapomorphies for the identification and definition of various lineages. The distribution of base chromosome number across the phylogeny (Fig. 3B) supports recognition of several clades hypothesized in this study. Chromosome numbers were obtained from previously published reports (see Appendix 2). Several potential synapomorphies have been proposed for some of the taxa included in this analysis (Windham 1987; Windham and Yatskievych 2003). The most parsimonious pattern of base chromosome number evolution (Fig. 3B) shows that change has been conservative throughout the evolution of the cheilanthoid ferns. The pellaeoid clade is supported by the base chromosome number of $x = 29$. *Argyrochosma* continues to be unified by the probable synapomorphy of a base chromosome number of $x = 27$. The small clade of *Cheilanthes alabamensis* and *C. notholaenoides* is supported by the potential synapomorphy of a base chromosome number of $x = 29$. The distribution of base chromosome numbers suggests that the base number has been reduced independently in several lineages from the ancestral cheilanthoid base chromosome number of $x = 30$.

Potential synapomorphies can now be recognized for several of the major pellaeoid lineages. The Mucronata Complex (species 1–10) is characterized by dark-colored stipes and rachises, bicolorous rhizome scales with dentate margins, and pinnae with mucronate tips (less prominent in species 9 and 10). Species 1–17 ("new" *Pellaea*) are characterized by having blade segments curled abaxially with drought, leaving the adaxial surface more exposed and the abaxial surface obscured. All species outside this clade appear to have ultimate segments adaxially curled, exposing the abaxial surface to a greater extent. Species 11–14 are characterized by having stramineous and flexuous rachises and stipes. Species 15–17 are characterized by having blades whose terminal pinnules are longer than sub-terminal pinnules. This character differentiates *P. glabella*, *P. atropurpurea*, and *P. notabilis* from *P. breweri*. Species 24–26 ("old" *Astrolepis*) are unequivocally characterized by the synapomorphy of two vascular strands per petiole (versus one in all other cheilanthoid exemplars of this study). Species 24–27 ("new" *Astrolepis*) are characterized by having stout, straw-colored petioles that are > 1 mm diameter, straight petioles and rachises that form an erect crown of fronds, concolorous rhizome scales with dentate margins, and spores with an echinate perispore. Most other species of pellaeoids have cristate perispores (Tryon 1972; Tryon and Tryon 1973). Species 28–30 ("new" *Paragymnopteris*) have concolorous rhizome scales with entire margins, delicate petiole bases with variably prominent articulations and that break easily, thin-textured (when dry) laminar tissue that is dark forest green in color, and varying numbers of reddish brown scales on the laminae that are concentrated along the midrib on the adaxial surface and evenly scattered on the abaxial surface. These and other characters need further study and analysis with a formal data matrix before they can be incorporated into descriptions of clades or utilized in keys.

Cheilanthoid Biogeography. Tracing current geographic distributions onto the MPR suggests a history of multiple introductions of cheilanthoid lineages into the Old World from several New World ancestral lineages (Fig. 3A). Because taxon sampling is sparse in the "distant cheilanthoids", hypotheses of ancestral origin are inconclusive for this clade. Fossil evidence suggests that ancestral lineages of Pteridaceae were rare yet widespread in cool temperate biomes of the northern hemisphere during the middle Cretaceous and later radiated into dry and montane habitats of Asia and North

America as these environments were forming in the late Cretaceous and early Cenozoic (Skog 2001; Willis and McElwain 2002). Greater taxon sampling within the "distant cheilanthoids" and further analyses are needed before a clearer picture of ancestral cheilanthoid origins can be achieved. Denser taxon sampling within the pellaeoid clade provides a more complete picture of the biogeographic history of these cheilanthoid lineages. The current distributions of species 18–23, and 28–29 suggest that spores from at least two disjunct North American ancestral lineages dispersed independently to the Australasian and Eurasian regions, respectively, where they survived and radiated. Wolf et al. (2001) explored the origins of extant homosporous fern geographic ranges and concluded that most distributions can be explained by dispersal rather than vicariance, but further evidence from individual cases is needed to determine distribution history. Tryon (1986b) and Barrington (1993) emphasized the straightforward nature of homosporous fern biogeography due to their high dispersal capability, potential for self-fertilization, and ecologies dependent on abiotic factors and independent of complicating biotic factors such as pollinators and/or seed dispersers. Smith (1972) compared the distributions of flowering plant and homosporous fern genera and species and concluded that because fern spores have high rates of dispersal, fern genera and species have broader distributions, fewer narrowly endemic species, and lower rates of evolution and extinction than angiosperm genera and species. Gradstein and van Zanten (1999) demonstrated that fern spores from widespread and alpine species could survive exposure to high levels of UV light in the jet stream. Therefore, long-distance dispersal of spores from New World ancestral pellaeoid lineages to suitable habitats in the Old World and subsequent establishment, diversification, and radiation is a reasonable explanation for the current distribution of pellaeoid ferns. The biogeography of cheilanthoid ferns examined here suggests long-distance dispersal of fern spores to suitable habitats may be more common than previously assumed (Tryon 1986b).

The phylogenetic hypotheses generated in this study improve our understanding of relationships among cheilanthoids in general, and pellaeoids in particular, and provide a new framework with which to investigate the evolutionary history of these xeric ferns. Re-examination of clade members allows for the identification of new synapomorphies that may provide useful characters for recognition of further relatives and for the generation of identification keys. The occurrence of homoplasy in a phylogenetic hypothesis suggests convergent evolution and origin of traits that may provide a functional "fit" between an organism and its environment. Detection of homoplastic morphologies, reproductive strategies, ploidy levels, habitat parameters, and physiologies can initiate investigations into adaptive scenarios and aid in the identification of correlation between traits and relevant environmental variables. Many cheilanthoid species have yet to be sampled, and many more need to be examined in a phylogenetic context before we will fully understand the evolution of these fascinating ferns.

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APPENDIX 1. List of taxa; collector, collection number; locality; herbarium voucher, botanical garden accession (if applicable); and Genbank accession numbers for *rps4* gene & *rps4-trnS* IGS (all samples) and *trnL-F* IGS (some samples). RK = Ruth Kirkpatrick, NYBG = New York Botanical Garden, UCBG = University California Botanical Garden, na = not available.

***Adiantum aleuticum* (Rupr.) C. A. Paris:** *Huiet 109*, USA, California. UC1794495; UCBG 89.1659; DQ915577. ***Adiantum pedatum* L.:** *Huiet 117*, North America, cultivated by J. Mickel, *Mickel s.n.* (UC), DQ915579. *Huiet 51*, China, *Sino Amer. Exped. 1755* (UC), DQ915578. ***Aleuritopteris farinosa* (Forssk.) Fée:** *RK 1135*; Costa Rica, Palo Verde; UC1783460; DQ914165. ***Argyrochosma fendleri* (Kunze) Windham:** *RK 1099f*; USA, New Mexico, Bernalillo Co.; UC1795046; DQ914125, DQ914209. ***Argyrochosma jonesii* (Maxon) Windham:** *RK 1145A*; USA, California, San Bernardino Co.; UC1795049; DQ914126, DQ914210. ***Argyrochosma limitanea* (Maxon) Windham:** *RK 1347*; = *Schuettpelz 463*; USA, Arizona, Cochise Co.; DUKE 391455; DQ914127, DQ914211. ***Argyrochosma nivea* (Poir.) Windham *var. tenera* (Gillies ex Hook.) Ponce:** *RK 1225*; Bolivia, Chuquisaca, Oropeza; *Huaylla 627*; GOET, LPB; DQ914128, DQ914212. ***Aspidotis californica* (Hook.) Nutt. ex Copel.:** *RK 1256*; USA, California, San Diego Co.; UC1861805; DQ914129, DQ914213. ***Aspidotis carlotta-halliae* (W. H. Wagner & E. F. Gilbert) Lellinger:** *RK 1226*; USA; UC1794523; UCBG 92.0967; DQ914130, DQ914214. ***Aspidotis densa* (Brack.) Lellinger:** *R K1177*; USA, California, Humboldt Co.; UC1795051; DQ914131. ***Astrolepis cochisensis* (Goodd.) D. M. Benham & Windham:** *RK 1146s*; USA, California, San Bernardino Co.; UC1795050; DQ914132, DQ914215. *RK 1097s*; USA, New Mexico, Socorro Co., Water Ck.; UC1795044; DQ914133. ***Astrolepis sinuata* (Lag. ex Sw.) D. M. Benham & Windham;** *RK 1194*; USA, Texas, Jeff Davis Co.; UC1795058; DQ914137, DQ914218. ***Astrolepis windhamii* D. M. Benham;** *RK 1188*; USA, Arizona, Cochise Co.; UC1861812; DQ914134, DQ914216. *RK 1189*; USA, Arizona, Cochise Co.; UC1795057; DQ914135, DQ914217. *RK 1190*; USA, Arizona, Cochise Co.; UC1861811; DQ914136. ***Bommeria hispida* (Mett.) Underw.;** *RK 1184*; USA, Arizona, Cochise Co.; UC1795053; DQ914170. *RK 1348*; = *Schuettpelz 467*; USA, Arizona, Cochise Co.; DUKE 391406; DQ914171. ***Cheilanthes acrostica* Tod.;** *RK 1227*; Portugal; UCBG 95.0028; UC1794518; DQ914142. ***Cheilanthes arizonica* (Maxon) Mickel:** *RK 1346*; = *Schuettpelz 461*; USA, Arizona, Cochise Co.; DUKE 391450; DQ914143, DQ914219. ***Cheilanthes alabamensis* Kunze;** *RK 1228*; Mexico; UCBG 94.0117; UC1794520; DQ914144, DQ914220. ***Cheilanthes buchtienii* (Rosenst.) R. M. Tryon;** *RK 1231*; Argentina; UCBG 91.1230, UC1748635; DQ914145. ***Cheilanthes covillei* Maxon;** *RK 1206*; USA, California, Riverside Co.; UC1795059; DQ914146, DQ914221. ***Cheilanthes distans* (R. Br.) Mett.;** *RK 1232*; Australia; UCBG 93.1111; UC1794522; DQ914147. ***Cheilanthes eatonii* Baker in Hook. & Baker:** *RK 1200*; USA, Texas, Jeff Davis Co.; UC1795062; DQ914148, DQ914222. *RK 1233*; USA; UCBG 92.0093, UC1794868; DQ914149, DQ914223. ***Cheilanthes feei* T. Moore:** *RK 1236*; USA; UCBG 93.0586, UC1746659; DQ914150, DQ914224. ***Cheilanthes fendleri* Hook.:** *RK 1095bs*; USA, New Mexico, Socorro Co., Water Ck.; UC1795047; DQ914151, DQ914225. ***Cheilanthes gracillima* D. C. Eaton:** *RK 1066f*; USA, California, Nevada

Co.; UC1795029; DQ914152, DQ914226. ***Cheilanthes lanosa* (Michx.) Watt:** *RK 1237*; USA; UCBG 93.1297; UC1794521: DQ914153, DQ914227. ***Cheilanthes lendigera* (Cav.) Sw.:** *RK 1251*; Costa Rica; UCBG 58.0046, UC1746655; DQ914154, DQ914228. ***Cheilanthes multifida* Sw. subsp. *lacerata* N. C. Anthony & Schelpe:** *RK 1254*; Africa, Malawi; UCBG 93.1299, UC1746703; DQ914155. ***Cheilanthes notholaenoides* (Desv.) Maxon ex Weath.:** *RK 1238*; Mexico; UCBG 94.012, UC1746466; DQ914156, DQ914229. ***Cheilanthes parryi* (D. C. Eaton) Domin:** *RK 1207*; USA, California, Riverside Co.; UC1795063; DQ914157, DQ914230. ***Cheilanthes parviloba* Sw.:** *RK 1179*; native to Africa; NYBG, 1141/96A; UC1861814; DQ914158. ***Cheilanthes skinneri* (Hook.) R. M. Tryon & A. F. Tryon:** *RK 1133*; Costa Rica, Palo Verde; UC1783461; DQ914159, DQ914231. ***Cheilanthes tomentosa* Link:** *RK 1240*; USA; UCBG 92.0104, UC1746464; DQ914160, DQ914232. ***Cheilanthes viridis* Sw.:** *RK 1287*; locality unknown, cultivated by W. Shepard; UC1861781; DQ914161. ***Cheilanthes viridis* Sw. var. *glauca* (Sim) Schelpe & N. C. Anthony:** *RK 1253*; na; UCBG 93.1300, UC1746661; DQ914162. ***Cheilanthes wrightii* Hook.:** *RK 1197*; USA, Texas, Jeff Davis Co.; UC1795060; DQ914163, DQ914233. ***Cryptogramma acrostichoides* R. Brown in Franklin:** *RK 1065*; USA, California, Nevada Co., UC1861789; DQ914172. ***Doryopteris nobilis* (T. Moore) J. Sm.:** *RK 1241*; Brazil; UC1794524; UCBG 69.0032; DQ914140. ***Doryopteris rediviva* Fée:** *RK 1242*; Brazil; UCBG 97.0581; UC1794517; DQ914141. ***Llavea cordifolia* Lag.:** *RK 1380*; cultivated by D. Swartz; UC1861791; DQ914173. ***Mildella intramarginalis* (Kaulf. ex Link) Trevis.:** *RK 1243*; Mexico; UCBG 93.1107; UC1862231; DQ914164. ***Notholaena affinis* (Mett.) T. Moore:** *RK 1134*; Costa Rica, Palo Verde; UC1783459; DQ914166. ***Notholaenacalifornica* D. C. Eaton:** *RK 1261*; USA, California, San Diego Co.; UC1795065; DQ914167. ***Notholaena candida* (M. Martens & Galeotti) Hook.:** *RK 1252*; na; UCBG 94.0205l; UC1794519; DQ914168. ***Notholaena standleyi* Maxon:** *RK 1196*; USA, Texas, Jeff Davis Co.; UC1795061; DQ914169. ***Paraceterach muelleri* (Hook.) Copel.:** *RK 1372*; Australia, Queensland, Silver Valley; UC1520478; DQ914112, DQ914203. ***Paragymnopteris bipinnata* (Christ) K. H. Shing:** *RK 1305*; China, Gansu Province; UC1765190; DQ914113, DQ914204. ***Paragymnopteris marantae* (L.) K. H. Shing:** *RK 1268*; local unknown, cultivated by D. Swartz; UC1861785; DQ914114, DQ914205. *RK 1297*; Nepal, Kyangjin, Langtang Valley; UC1747383; DQ914115, DQ914206. *RK 1303*; Bhutan, between Gang Yul & Chebesa; UC1783883; DQ914116. ***Paragymnopteris sargentii* (H. Christ) K. H. Shing:** *RK 1295*; China, Xizang, E. Tibet; UC1747398; DQ914117, DQ914207. ***Paragymnopteris vestita* (Wall. ex C.Presl) K. H. Shing:** *RK 1296*; China, Xizang, E. Tibet; UC1747397; DQ914118, DQ914208. ***Pellaea* sp. from Bolivia:** Wood 15957 = *RK 1244*; Bolivia, Tarija: Mendez. Zona del Rincon del la Victoria; UC1788706; DQ914098, DQ914192. ***Pellaea andromedifolia* (Kaulf.) Fée:** *RK 1039f*; USA, California, San Diego Co.; UC1795027; DQ914072, DQ914174. ***Pellaea andromedifolia* var. *pubescens* D. C. Eaton:** *RK 1174*; USA, California, San Luis Obispo Co.; UC1861815; DQ914073, DQ914175. ***Pellaea atropurpurea* (L.) Link:** *RK 1178*; USA, Kentucky, Lake Cumberland; UC1795052; DQ914074, DQ914176. *RK 1182*; USA, Arizona, Cochise Co.; UC1861813; DQ914075. ***Pellaea brachyptera* (T. Moore) Baker:** *RK 1068s*; USA, California, Sierra Co.; UC1795030; DQ914076, DQ914177. ***Pellaea breweri* D. C. Eaton:** *RK 1086s*; USA, California, Inyo Co.; UC1795040; DQ914077, DQ914178. *RK 1087s*; USA, California, Mono Co.; UC1795039; DQ914078, DQ914179. *RK 1089s*; USA, California, Mono Co.; UC1795038; DQ914079. ***Pellaea bridgesii* Hook.:** *RK 1063s*; USA, California, Placer Co.; USA, California, Placer Co.; UC1794514; DQ914080, DQ914180. *RK 1067s*; USA, California, Sierra Co.; UC1795031; DQ914081. *RK 1071-1s*; USA, California, Plumus Co.; UC1795032; DQ914082. *RK 1090s*; USA, California, Mariposa Co.; UC1795041; DQ914083. ***Pellaea calomelanos* Link:** *RK 1215*; Africa, Cape Provence; UC1589017; DQ914119. ***Pellaea doniana* (J. Sm.) Hook.:** *RK 1216*; Africa, Ghana; UC1620061; DQ914120. ***Pellaea dura* (Willd.) Baker:** *RK 1384*; cultivated by D. Swartz; UC1794515; DQ914121. ***Pellaea falcata* (R. Br.) Fée:** *RK 1286*; Australia, Wahalla; UC1861783; DQ914085, DQ914182. ***Pellaea falcata* var. *nana* Hook.:** *RK 1222*; na., cultivated by J. Jones; UC1861807; DQ914086, DQ914183. ***Pellaea glabella* Mett. ex Kuhn subsp. *occidentalis* (E. E. Nelson) Windham:** *RK 1319*; USA, Utah, Utah Co.; UC1861797; DQ914087, DQ914184. ***Pellaea glabella* Mett. ex Kuhn subsp. *simplex* (E. E. Nelson) Windham:** *RK 1320*; USA, Utah, Utah Co.; UC1861798; DQ914088, DQ914185. ***Pellaea gleichenioides* Gardner;** *RK 1374*; Brazil, Campos de Areias Quartzosas; UC1604873; DQ914138. ***Pellaea intermedia* Mett. ex Kuhn:** *RK 1349*; =*Schuettpelz 481*; USA, Arizona, Cochise Co.; DUKE 391444; DQ914089, DQ914186. ***Pellaea longipilosa* Bonap.:** *RK 1218*; Africa, Zambia; UC1728241; DQ914122. ***Pellaea maxima* Bonap.:** *RK 1209*; =*D. Stone 2535*; Africa, Cameroon; UC1861809; DQ914123. ***Pellaea mucronata* subsp. *californica* D. C. Eaton (Lemmon) Windham:** *RK 1082s*; USA, California, San Bernardino Co.; UC1795034; DQ914090, DQ914187. *RK 1083s*; USA, California, San Bernardino Co.; UC1795035; DQ914091. *RK 1084s*; USA, California, Inyo Co.; UC1795036; DQ914092, DQ914188. *RK 1085s*; USA, California, Inyo Co.; UC1795037; DQ914093. ***Pellaea mucronata* subsp. *mucronata* (D. C. Eaton) D. C. Eaton:** *RK 1057s*; USA, California, Lake Co.; UC1795026; DQ914094, DQ914189. *RK 1078as*; USA, California, Plumus Co.; UC1861788, DQ914095. *RK 1079bs*; USA, California, Los Angeles Co.; UC1795033; DQ914096, DQ914190. *RK 1091s*; USA, California, Tuolumne Co.; UC1861787; DQ914097, DQ914191. ***Pellaea notabilis* Maxon:** *RK 1282*; Mexico, Tamaulipas; UC1738599; DQ914099, DQ914193. *RK 1289*; Mexico, Nuevo Leon; UC1861780, DQ914100, DQ914194. ***Pellaea ovata* (Desv.) Weath.:** *RK 1267*; local unknown, cultivated by R. Halley; UC1795069; DQ914101, DQ914195. ***Pellaea pectiniformis* Baker:** *RK 1219*; Africa, Madagascar, Prov. Fianarantsoa; UC1749813; DQ914124. ***Pellaea rotundifolia* (G. Forst.) Hook.:** *RK 1246*; houseplant; UC1795064; DQ914084, DQ914181. ***Pellaea sagittata* Link:** *RK 1265*; local unknown, cultivated by R. Halley; UC1795068; DQ914101, DQ914196. ***Pellaea ternifolia* (Cav.) Link:** *RK 1224*; Bolivia, Chuquisaca, Oropeza, Cajamarca; GOET, *Huaylla, H. 623*; DQ914103, DQ914197. *RK 1210*; Bolivia, Cochabamba; LPB, *Ivan Jimenez 1341*; DQ914104. *A. Smith 2898*= *RK 1245*; USA, Hawaii, Maui, Haleakala; UC1861808; DQ914105, DQ914198. *Tom Ranker 1997*= *RK 1273*; USA, Hawaii, Hawaii; UC1788357; DQ914106. ***Pellaea triphylla* Kaulf.;** *M.Sundue 585*= *RK 1248*; Bolivia, Santa Cruz; UC1780942; DQ914139. ***Pellaea truncata* Goodd.:** *RK 1102f*; USA, New Mexico, Bernalillo Co.; UC1795048; DQ914107, DQ914199. ***Pellaea wrightiana* Hook.:** *RK 1187*; USA, Arizona, Cochise Co.; UC1795056; DQ914108, DQ914200. *RK 1192*; USA, Arizona, Cochise Co.; UC1861810; DQ914109. ***Pellaea* × *glaciogena* W. H. Wagner, Pray, & A. R. Sm.:** *RK 1092s*; USA, California, Tuolumne Co.; UC1795043; DQ914110, DQ914201. *RK 1093s*; USA, California, Tuolumne Co.; UC1862330, DQ914111, DQ914202.

APPENDIX 2. List of taxa: species, 2*n* chromosome number, and reference (na = not available).

Adiantum aleuticum* (Rupr.) C. A. Paris**, 2*n* = 58, FNAEC, 1993. ***Adiantum pedatum* L.**, 2*n* = 58, FNAEC, 1993. ***Aleuritopteris farinosa* Fée**, 2*n* = 60, Vasudeva & Bir, 1983; Srivastava, 1985. ***Argyrochosma fendleri* (Kunze) Windham**, 2*n* = 54, Windham & Yatskievych, 2003. ***Argyrochosma

***jonesii* (Maxon) Windham**, 2*n* = 54, 108, Windham & Yatskievych, 2003. ***Argyrochosma limitanea* (Maxon) Windham**, 2*n* = 81, Windham & Yatskievych, 2003. ***Argyrochosma nivea* (Poir.) Windham var. *tenera* (Gillies ex Hook.) Ponce**, na. ***Aspidotis californica* (Hook.) Nutt. ex Copel.**, 2*n* = 60, 120, Smith, 1975; Windham & Yatskievych, 2003. ***Aspidotis carlotta-halliae* (W. H. Wagner & E. F. Gilbert) Lellinger**, 2*n* = 120, Smith, 1975; Windham & Yatskievych, 2003. ***Aspidotis densa* (Brack.) Lellinger**, 2*n* = 60, Smith, 1975; Windham & Yatskievych, 2003. ***Astrolepis cochisensis* (Goodd.) D. M. Benham & Windham**, 2*n* = 58, 87, 116, Benham & Windham, 1992; Windham & Yatskievych, 2003. ***Astrolepis sinuata* (Lag. ex Sw.) D. M. Benham & Windham**, 2*n* = 58, 87, Benham & Windham, 1992; Windham & Yatskievych, 2003. ***Astrolepis windhamii* D. M. Benham**, 2*n* = 87, Windham & Yatskievych, 2003. ***Bommeria hispida* (Mett.) Underw.**, 2*n* = 60, Smith, 1974; Gastony & Haufler, 1976. ***Cheilanthes acrostica* Tod.**, na. ***Cheilanthes alabamensis* Kunze**, 2*n* = 58, Windham & Yatskievych, 2003. ***Cheilanthes arizonica* (Maxon) Mickel**, 2n = 90, Windham & Yatskievych, 2003. ***Cheilanthes buchtienii* (Rosenst.) R. M. Tryon**, na. ***Cheilanthes covillei* Maxon**, 2*n* = 60, Smith, 1974; Windham & Yatskievych, 2003. ***Cheilanthes distans* (R. Br.) Mett.**, 2*n* = 84, Tindale & Roy, 2002. ***Cheilanthes eatonii* Baker in Hook. & Baker**, 2*n* = 90, Benham & Schaack, 1988; Windham & Yatskievych, 2003. ***Cheilanthes feei* Moore**, 2*n* = 90, Windham & Yatskievych, 2003. ***Cheilanthes fendleri* Hook.**, 2*n* = 60, Windham, 1983; Windham & Schaack, 1983; Windham & Yatskievych, 2003. ***Cheilanthes gracillima* D. C. Eaton**, na. ***Cheilanthes lanosa* (Michx.) Watt**, 2*n* = 60, Britton (in Fabbri, 1963). ***Cheilanthes lendigera* (Cav.) Sw.**, 2*n* = 120, Windham & Yatskievych, 2003. ***Cheilanthes multifida* Sw. subsp. *lacerata* N. C. Anthony & Schelpe**, na. ***Cheilanthes notholaenoides* (Desv.) Maxon ex Weath.**, 2*n* = 87, Smith & Mickel, 1977. ***Cheilanthes parryi* (D. C. Eaton) Domin**, 2*n* = 60, Schaack, et al., 1984. ***Cheilanthes parviloba* Sw.**, na. ***Cheilanthes skinneri* (Hook.) R. M. Tryon & A. F. Tryon**, na. ***Cheilanthes tomentosa* Link**, 2*n* = 90, Knobloch et al., 1975. ***Cheilanthes viridis* Sw.**, na. ***Cheilanthes viridis* Sw. var. *glauca* (Sim) Schelpe & N. C. Anthony**, na. ***Cheilanthes wrightii* Hook.**, 2*n* = 60, Windham & Yatskievych, 2003. ***Cryptogramma acrostichoides* R. Br.**, 2*n* = 60, FNAEC, 1993. ***Doryopteris nobilis* (Moore) J. Sm.**, na. ***Doryopteris rediviva* Fée**, na. ***Llavea cordifolia* Lag.**, 2*n* = 58, Mickel & Smith, 2004. ***Mildella intramarginalis* (Link) Trevis.**, 2*n* = 60, 90, Mickel & Smith, 2004; Windham & Yatskievych, 2003. ***Notholaena affinis* (Mett.) Moore**, na. ***Notholaena californica* D. C. Eaton**, 2*n* = 150, Windham & Yatskievych, 2003. ***Notholaena candida* (Mart. & Galeotti) Hook.**, 2*n* = 60, Windham & Yatskievych, 2003. ***Notholaena standleyi* Maxon**, 2*n* = 60, Benham & Schaack, 1988. ***Paraceterach muelleri* (Hook.) Copel.**, na. ***Paragymnopteris bipinnata* (H. Christ) K. H. Shing**, na. ***Paragymnopteris marantae* (L.) K. H. Shing**, 2*n* = 58, Ivanova, 1998. ***Paragymnopteris sargentii* (H. Christ) K. H. Shing**, na. ***Paragymnopteris vestita* (Wall. ex C. Presl) K. H. Shing**, 2*n* = 58, Lin et al. 1996. ***Pellaea* sp. (from Bolivia)**, 2*n* = 58, Smith, A.R., unpublished data. ***Pellaea andromedifolia* (Kaulf.) Fée**, 2*n* = 58, 87, 116, Tryon, A. F. (in Fabbri, 1965); Tryon, A. F., 1968; Smith, A. R., 1974. ***Pellaea atropurpurea* (L.) Link**, 2*n* = 87, Cody & Mulligan, 1982. ***Pellaea brachyptera* (Moore) Baker**, na. ***Pellaea breweri* D. C. Eaton**, 2*n* = 58, Britton (in Tryon, A. F. 1957); Tryon & Britton, 1958; Windham & Yatskievych, 2003. ***Pellaea bridgesii* Hook.**, 2*n* = 58, Wagner et al., 1983. ***Pellaea calomelanos* Link**, na. ***Pellaea doniana* (J.Sm.) Hook.**, na. ***Pellaea dura* (Willd.) Baker**, na. ***Pellaea falcata* (R. Br.) Fée**, 2*n* = 58, Tindale & Roy, 2002; 2*n* = 116, Brownlie, 1961. ***Pellaea falcata* var. *nana* Hook.**, 2*n* = 58, 116, Tindale & Roy, 2002. ***Pellaea glabella* Mett. ex Kuhn subsp. *occidentalis* (E. E. Nelson) Windham**, 2*n* = 58, FNAEC, 1993. ***Pellaea glabella* Mett. ex Kuhn subsp. *simplex* (E. E. Nelson) Windham**, 2*n* = 116, Tryon & Britton 1958. ***Pellaea gleichenioides* Gardner**, na. ***Pellaea intermedia* Mett. ex Kuhn**, 2*n* = 87, 116, Tryon, A. F., 1968; Windham & Yatskievych, 2003. ***Pellaea longipilosa* Bonap.**, na. ***Pellaea maxima* Bonap.**, na. ***Pellaea mucronata* D. C. Eaton subsp. *californica* (Lemmon) Windham**, na. ***Pellaea mucronata* subsp. *mucronata* (D. C. Eaton) D. C. Eaton**, 2*n* = 58, Wagner et al., 1983. ***Pellaea notabilis* Maxon**, 2*n* = 58, Tryon, A. F. (in Fabbri, 1965). ***Pellaea ovata* (Desv.) Weath.**, 2*n* = 58, Britton (in Tryon, A. F., 1957). ***Pellaea pectiniformis* Baker**, na. ***Pellaea rotundifolia* (G. Forst.) Hook.**, 2*n* = 87, 116, Kurita (in Fabbri, 1965). ***Pellaea sagittata* Link**, 2*n* = 58, 116, Britton (in Tryon, A. F. 1957). ***Pellaea ternifolia* (Cav.) Link**, 2*n* = 58, 116, Tryon & Britton 1958; Windham, 1988. ***Pellaea triphylla* Kaulf.**, na. ***Pellaea truncata* Goodd.**, 2*n* = 58, Windham, 1983, 1988. ***Pellaea wrightiana* Hook.**, 2*n* = 58, Benham & Schaack, 1988; Windham, 1983, 1988. ***Pellaea* × *glaciogena* W. H. Wagner, Pray, & A. R. Sm.**, 2*n* = 58I, Wagner et al., 1983.