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A molecular phylogeny of the fern family Pteridaceae: Assessing overall relationships and the affinities of previously unsampled genera

Eric Schuettpelz [a,*], Harald Schneider [b,1], Layne Huiet [c], Michael D. Windham [d,a], Kathleen M. Pryer [a]

[a] *Department of Biology, Duke University, Durham, NC 27708, USA*
[b] *Albrecht-von-Haller Institute für Pflanzenwissenschaften, Georg-August-Universität, 37073 Göttingen, Germany*
[c] *University Herbarium, University of California, Berkeley, CA 94720, USA*
[d] *Utah Museum of Natural History, University of Utah, Salt Lake City, UT 84112, USA*

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Abstract

The monophyletic Pteridaceae accounts for roughly 10% of extant fern diversity and occupies an unusually broad range of ecological niches, including terrestrial, epiphytic, xeric-adapted rupestral, and even aquatic species. In this study, we present the results of the first broad-scale and multi-gene phylogenetic analyses of these ferns, and determine the affinities of several previously unsampled genera. Our analyses of two newly assembled data sets (including 169 newly obtained sequences) resolve five major clades within the Pteridaceae: cryptogrammoids, ceratopteridoids, pteridoids, adiantoids, and cheilanthoids. Although the composition of these clades is in general agreement with earlier phylogenetic studies, it is very much at odds with the most recent subfamilial classification. Of the previously unsampled genera, two (*Neurocallis* and *Ochropteris*) are nested within the genus *Pteris*; two others (*Monogramma* and *Rheopteris*) are early diverging vittarioid ferns, with *Monogramma* resolved as polyphyletic; the last previously unsampled genus (*Adiantopsis*) occupies a rather derived position among cheilanthoids. Interestingly, some clades resolved within the Pteridaceae can be characterized by their ecological preferences, suggesting that the initial diversification in this family was tied to ecological innovation and specialization. These processes may well be the basis for the diversity and success of the Pteridaceae today.

Keywords: *atpA*; *atpB*; *Ceratopteris*; Fern systematics; Molecular phylogenetics; Pteridaceae; *rbcL*

1. Introduction

Pteridaceae, as circumscribed in the most recent familial classification (Smith et al., 2006), comprises over 50 genera and more than 1000 species, accounting for roughly 10% of extant leptosporangiate fern diversity. Clearly monophyletic in earlier phylogenetic analyses (Gastony and Johnson, 2001; Hasebe et al., 1995; Pryer et al., 1995; Schneider et al., 2004), this family is characterized by sporangia borne along veins or in marginal coenosori, often protected by reflexed segment margins (pseudoindusia), and chromosome numbers predominantly based on $x = 29$ or 30 (Kramer, 1990a; Tryon et al., 1990). Pteridaceae has a cosmopolitan distribution concentrated in wet tropical and arid regions and occupies an unusually broad range of ecological niches. It differs notably from most other fern families by encompassing terrestrial, epiphytic, xeric-adapted rupestral, and even aquatic species.

As might be expected given their ecological—as well as morphological—disparity, the classification of these ferns has been controversial. Historically, many taxa were segregated and variously recognized as tribes, subfamilies, or even as distinct families (Ching, 1940; Copeland, 1947; Holttum, 1949; Nayar, 1970; Pichi Sermolli, 1977). In the most recent classification that formally addressed

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[*] Corresponding author. Fax: +1 919 660 7293.
E-mail address: ejs7@duke.edu (E. Schuettpelz).
[1] Present address: Department of Botany, Natural History Museum, London SW7 5BD, UK.

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subfamilial taxa, the Pteridaceae (*sensu* Smith et al., 2006) was divided into two families, the Pteridaceae and Vittariaceae (Kramer, 1990b), with the Pteridaceae (*sensu* Kramer, 1990b) subsequently segregated into six subfamilies (Adiantoideae, Ceratopteridoideae, Cheilanthoideae, Platyzomatoideae, Pteridoideae, and Taenitidoideae; Tryon et al., 1990).

Molecular phylogenetic studies of the Pteridaceae, to date, have primarily focused on the relationships within a few segregates (Crane et al., 1995; Gastony and Rollo, 1995, 1998; Nakazato and Gastony, 2003; Sánchez-Baracaldo, 2004; Zhang et al., 2005). Our current understanding of overall Pteridaceae phylogeny mostly stems from these results combined with those from analyses aimed at leptosporangiate ferns as a whole, generally with only a few Pteridaceae exemplars and based on a single gene (Gastony and Johnson, 2001; Hasebe et al., 1995; Pryer et al., 1995). Although these studies together established that Vittariaceae is nested within Pteridaceae and that many of the previously recognized subfamilies most likely do not represent natural (i.e., monophyletic) groups, they were not adequate to fully resolve all parts of the Pteridaceae phylogeny.

Broad-scale and multi-gene analyses to explicitly determine what major clades are present within the Pteridaceae, and the relationships of these lineages to one another, have not yet been conducted. Furthermore, there are several genera assigned to this family—among them *Adiantopsis*, *Monogramma*, *Neurocallis*, *Ochropteris*, and the enigmatic *Rheopteris* (Kramer, 1990a; Schneider, 1996; Tryon et al., 1990; Tryon and Lugardon, 1991)—that have not been included in any molecular phylogenetic analysis (*Rheopteris* was included in two cladistic analyses of morphological data; Schneider, 1996; Stevenson and Loconte, 1996). In this study, the affinities of these previously unsampled genera are assessed and the overall phylogeny of the Pteridaceae is more fully examined through analyses of two newly assembled data sets: (1) a three-gene (plastid *rbcL*, *atpB*, and *atpA*) data set including 55 Pteridaceae exemplars from 37 genera; and (2) a taxonomically expanded single-gene (plastid *rbcL*) data set including 135 Pteridaceae species from 47 genera.

2. Materials and methods

2.1. Taxonomic sampling

For the three-gene data set, 55 exemplars were selected from the Pteridaceae, representing all previously recognized major subgroups. Twelve additional species were selected from the related dennstaedtioid and eupolypod fern clades (Schneider et al., 2004) to serve as outgroups (55 ingroup and 12 outgroup species, for a total of 67 species; Appendix A). For the taxonomically expanded single-gene data set, 80 additional Pteridaceae species were included (55 ingroup and 12 outgroup species from the three-gene data set, plus an additional 80 ingroup species, for a total of 147 species; Appendix A).

2.2. DNA isolation, amplification, sequencing, and alignment

Protocols for the extraction of genomic DNA, and for the amplification and sequencing of the plastid genes *rbcL* and *atpB*, were as described in Pryer et al. (2004). The plastid *atpA* region was amplified and sequenced using newly designed primers (Schuettpelz et al., 2006), but established protocols (Pryer et al., 2004). Manual alignments of the *rbcL*, *atpB*, and *atpA* sequences were performed using MacClade 4.08 (Maddison and Maddison, 2005).

2.3. Phylogenetic analysis

To determine phylogenetic relationships within the Pteridaceae and assess whether conflict was present among the sequenced genes, a total of five data sets was analyzed: a 67-taxon combined three-gene (plastid *rbcL*, *atpB*, and *atpA*) data set, a 147-taxon single-gene (plastid *rbcL*) data set, and the three 67-taxon single-gene data sets that together composed the combined data set. For each of these, the best-fitting model of sequence evolution was identified with the Akaike Information Criterion (AIC) in Modeltest 3.7 (Posada and Crandall, 1998; best-fitting models for each data set are given in Table 1). The five data sets were then analyzed using a Bayesian Markov chain Monte Carlo (B/MCMC) approach, as implemented in MrBayes 3.1.1 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). For each of the four single-gene B/MCMC analyses, the appropriate model of sequence evolution was employed; for the combined three-gene analysis, each gene was assigned its own model of sequence evolution. When a best-fitting model, as identified by Modeltest, could not be implemented, the next more complex model was used (Table 1). All B/MCMC analyses comprised four independent runs, each with four chains (one cold and three heated). Default (i.e., flat) priors were used, with the exception of the rate prior that was set to allow rates of evolution to vary among the partitions (ratepr = variable) in the combined analysis. Chains were run for 10 million generations and trees were sampled from the cold chain every 1000 generations. To identify when analyses had reached stationarity (i.e., were yielding a representative sample from the posterior probability distribution) the standard deviation of the split frequencies among the independent runs (as calculated by MrBayes) was examined, and the output parameter estimates were plotted using Tracer 1.2.1 (Rambaut and Drummond, 2005). Based on these convergence diagnostics, the first 2.5 million generations were (very conservatively) excluded from each analysis before obtaining a consensus phylogeny and clade posterior probabilities with the “sumt” command (contype = allcompat).

For each of the five data sets, branch support was also assessed using a maximum likelihood bootstrap (MLBS) approach. MLBS analyses (1000 replicates) were conducted using PHYML 2.4.4 (Guindon and Gascuel, 2003), employing the model of sequence evolution

Table 1
Statistics for the five data sets analyzed in this study of Pteridaceae phylogeny

Data set	Characters		Missing data (%)	Best-fitting model	Bipartitions receiving good support from various measures		
	Total	Variable			MLBS $\geqslant$ 70	BPP $\geqslant$ 0.95	MLBS $\geqslant$ 70 and BPP $\geqslant$ 0.95
rbcL (67 species)	1308	567	1	GTR + I + G	41 (64%)	42 (66%)	38 (59%)
atpB (67 species)	1278	532	3	TVM + I + G[a]	37 (58%)	35 (55%)	32 (50%)
atpA (67 species)	1506	707	1	GTR + I + G	42 (66%)	39 (61%)	38 (59%)
Combined (67 species)	4092	1806	2	GTR + I + G	51 (80%)	51 (80%)	48 (75%)
rbcL (147 species)	1308	673	1	GTR + I + G	92 (64%)	95 (66%)	86 (60%)

[a] Model could not be implemented in MrBayes or PHYML; GTR + I + G model was used.

identified by Modeltest (when a best-fitting model could not be implemented, the next more complex model was used; Table 1). A BIONJ starting tree was employed, and parameter values were estimated by PHYML.

3. Results

3.1. Data

All gene sequences used in this study, including the 169 newly obtained sequences, were deposited in GenBank (Appendix A). The portions of the *rbcL*, *atpB*, and *atpA* genes utilized were without codon insertions or deletions; therefore, sequence alignment was straightforward with no areas of ambiguous alignment. Statistics for the three 67-taxon single-gene data sets, the 67-taxon combined three-gene data set, and the 147-taxon *rbcL* data set are presented in Table 1.

3.2. Phylogeny

Analyses of the three 67-taxon single-gene data sets resulted in phylogenetic hypotheses with similar levels of branch support (Table 1). The topologies were also largely congruent, with differences never well supported by both maximum likelihood bootstrap (MLBS $\geqslant$ 70) and Bayesian posterior probability (BPP $\geqslant$ 0.95) values (trees not shown). Analyses of the 67-taxon combined three-gene data set resulted in a considerably more robust phylogeny, with improved MLBS and BPP support (Table 1 and Fig. 1). The phylogeny resulting from analyses of the expanded 147-taxon *rbcL* data set was largely in agreement with that from the combined three-gene analyses; however, the level of branch support was similar to that from the 67-taxon *rbcL* data set (Table 1 and Figs. 2–4).

4. Discussion

4.1. Overall Pteridaceae phylogeny

The results of our analyses are in general agreement with earlier phylogenetic studies (Gastony and Johnson, 2001; Hasebe et al., 1995; Pryer et al., 1995; Sánchez-Baracaldo, 2004; Zhang et al., 2005), but very much at odds with the most recent subfamilial classification (Kramer, 1990b; Tryon et al., 1990). The vittarioid ferns (Vittariaceae *sensu* Kramer, 1990b; vi in Figs. 1 and 3) are sister to (or perhaps even embedded within) the monogeneric subfamily Adiantoideae (*sensu* Tryon et al., 1990; ad in Figs. 1 and 3), rendering the Pteridaceae (*sensu* Kramer, 1990b) paraphyletic. Subfamilies Cheilanthoideae, Pteridoideae, and Taenitidoideae, as defined by Tryon et al. (1990; ch, pt, and ta in Figs. 1, 2, and 4), are also not monophyletic; instead, the genera assigned to these groups are somewhat intermixed. Recognizing the monogeneric Ceratopteridoideae and Platyzomatoideae (*sensu* Tryon et al., 1990; ce and pl in Figs. 1 and 2) exacerbates this problem, as these smaller subfamilies are sister to, or nested within, portions of the larger subfamilies of Tryon et al. (1990).

In our phylogenetic analyses, five major clades are resolved, and (mostly) well-supported as monophyletic (Figs. 1–4): the *cryptogrammoid* clade (CR) is sister to the remainder of the Pteridaceae; a small—but no longer monogeneric—*ceratopteridoid* clade (CE) is sister to a much-expanded *pteridoid* clade (PT); and a re-circumscribed *adiantoid* clade (AD) is sister to a somewhat more exclusive *cheilanthoid* clade (CH).

4.2. Cryptogrammoid clade (CR)

The well-supported cryptogrammoid ferns (CR in Figs. 1 and 2) comprise three genera (*Coniogramme*, *Cryptogramma*, and *Llavea*) and approximately 23 species. The morphology is highly variable in this group, and a clear morphological synapomorphy is lacking. Although all three genera display sterile-fertile leaf dimorphism, this character is widespread throughout the Pteridaceae.

A family Cryptogrammaceae has been proposed previously (Pichi Sermolli, 1963); however, that circumscription included only two of the three genera in this clade (*Cryptogramma* and *Llavea*), as well as the genus *Onychium*, which has affinities to pteridoid ferns (Gastony and Johnson, 2001; Hasebe et al., 1995; Zhang et al., 2005; PT in Figs. 1 and 2). A relationship between *Coniogramme* and the genera *Cryptogramma* and *Llavea* was never suggested based on morphology alone.

4.3. Ceratopteridoid clade (CE)

Although the ceratopteridoid ferns (CE in Figs. 1 and 2) include just two genera (*Acrostichum* and *Ceratopteris*) and six species, this well-supported clade is home to *Ceratopteris*

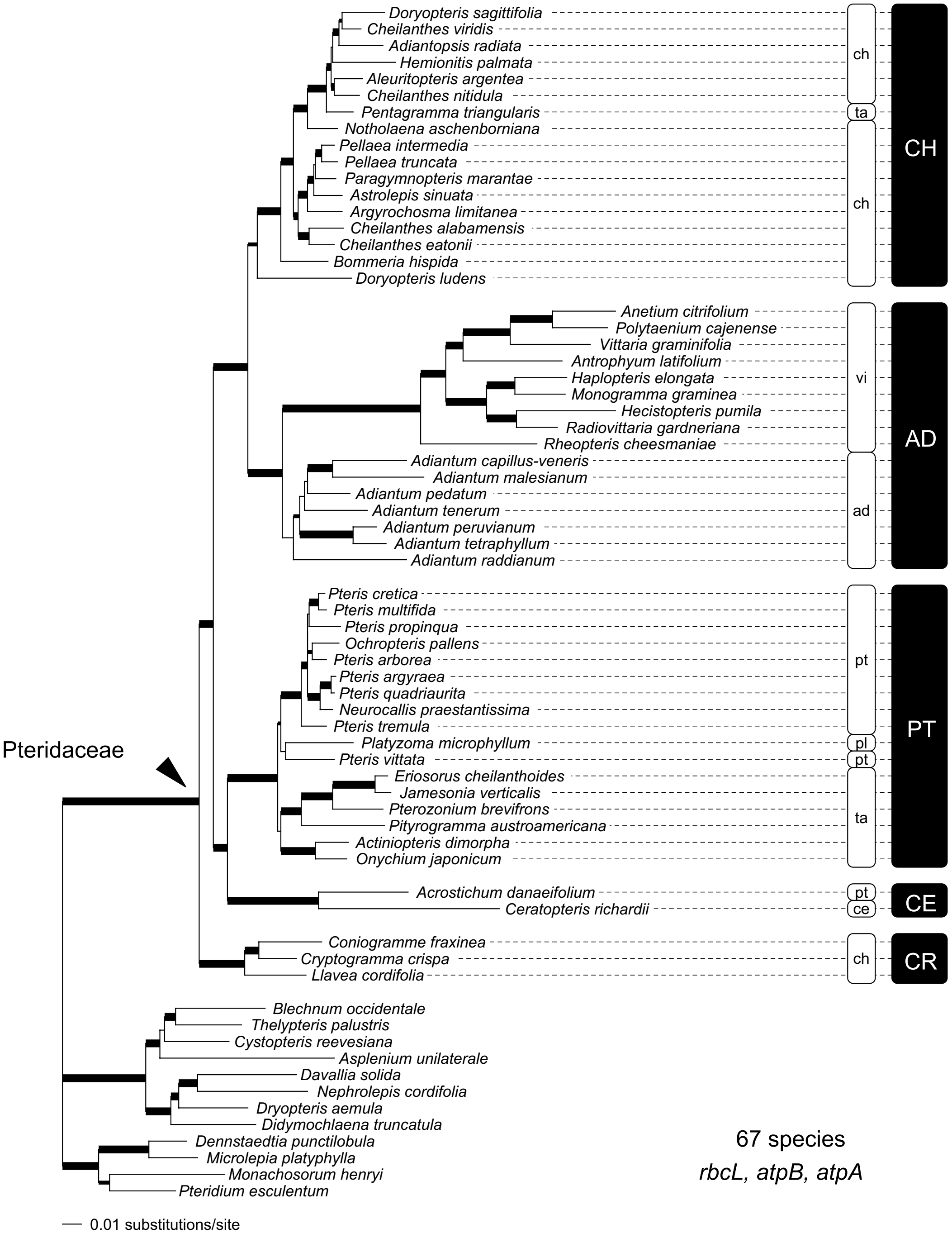

Fig. 1. Plurality consensus phylogeny (with average branch lengths) of the Pteridaceae resulting from Bayesian analysis of three plastid genes (*rbcL*, *atpB*, *atpA*) for 67 species. Five major clades recognized in this study are indicated (black boxes): cryptogrammoids (CR); ceratopteridoids (CE); pteridoids (PT); adiantoids (AD); and cheilanthoids (CH). Taxa as circumscribed in the most recent subfamilial classification (Kramer, 1990b; Tryon et al., 1990) are also indicated (white boxes): Adiantoideae (ad); Ceratopteridoideae (ce); Cheilanthoideae (ch); Platyzomatoideae (pl); Pteridoideae (pt); Taenitidoideae (ta); and Vittariaceae (vi). Heavily thickened branches (most bipartitions) indicate good posterior probability (⩾0.95) *and* maximum likelihood (⩾70) support; thickened branches indicate good support from only one of these two measures.

richardii—a model system for the investigation of developmental and genetic questions in "seed-free" vascular plants (Banks et al., 1993; Chatterjee and Roux, 2000; Hickok et al., 1995; Hill, 2001; Hou and Hill, 2004). Tryon et al. (1990) treated *Ceratopteris* as the sole member of subfamily Ceratopteridoideae, and this genus is sometimes placed in its own family (Parkeriaceae; Copeland, 1947; Pichi Sermolli, 1977). It is now clear, however, that *Ceratopteris* is sister to *Acrostichum* and well nested within the Pteridaceae (Hasebe et al., 1995; Pryer et al., 1995; Schneider et al., 2004; and Figs. 1 and 2). *Ceratopteris* (a freshwater genus) and *Acrostichum* (a mangrove genus) are the only aquatic members of the Pteridaceae, and both genera have morphological features that have been interpreted as adaptations to an

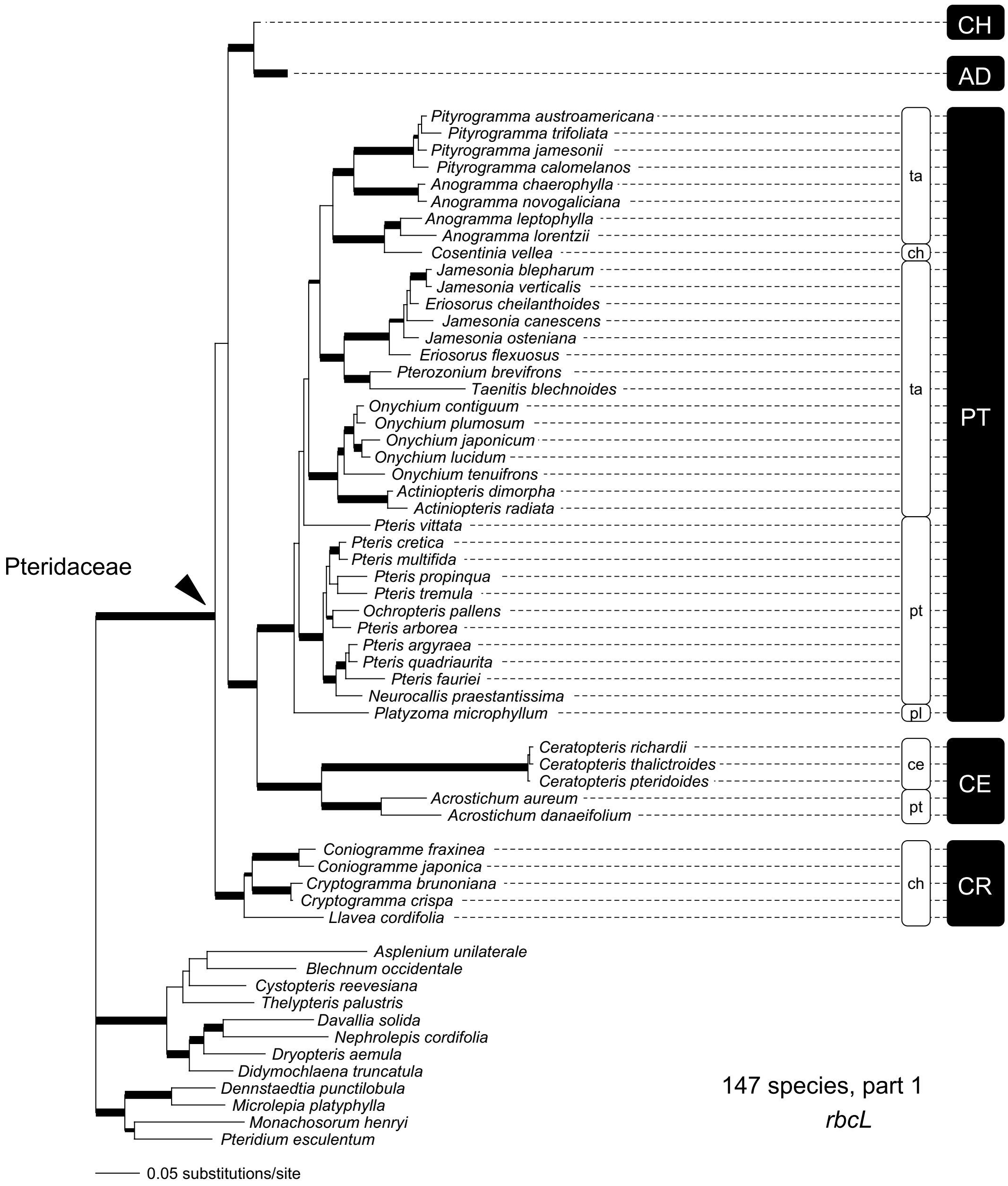

Fig. 2. Plurality consensus phylogeny (with average branch lengths) of the Pteridaceae resulting from Bayesian analysis of the plastid *rbcL* gene for 147 species. Five major clades recognized in this study are indicated, but only relationships within cryptogrammoids (CR), ceratopteridoids (CE), and pteridoids (PT) are shown here; relationships within adiantoids (AD) and cheilanthoids (CH) are shown in Figs. 3 and 4. Taxa as circumscribed in the most recent subfamilial classification are also indicated (see Fig. 1 legend). Branch thickening follows Fig. 1.

aquatic lifestyle, including the formation of aerenchyma (Schneider, 1996).

4.4. Pteridoid clade (PT)

The well-supported pteridoid ferns (PT in Figs. 1 and 2) comprise about 17 genera and 400 species. This clade is characterized by cingulate spores (Tryon and Lugardon, 1991) and contains most of the genera assigned to subfamilies Platyzomatoideae (pl), Pteridoideae (pt), and Taenitidoideae (ta) by Tryon et al. (1990; Figs. 1 and 2). In both the combined three-gene analyses and the expanded *rbcL* analyses, the remnants of these subfamilies did at least partially segregate within the pteridoid clade. However, the Pteridoideae (pt) was never fully resolved as monophyletic and the Taenitidoideae (ta) was not well supported by either MLBS or BPP (Figs. 1 and 2).

The monophyly of *Pteris* was seriously called into question by our analyses, principally because *Pteris vittata* was never resolved as closely allied to the remainder of the genus (Figs. 1 and 2). Instead, this species appeared in two different, unsupported positions in our trees: either

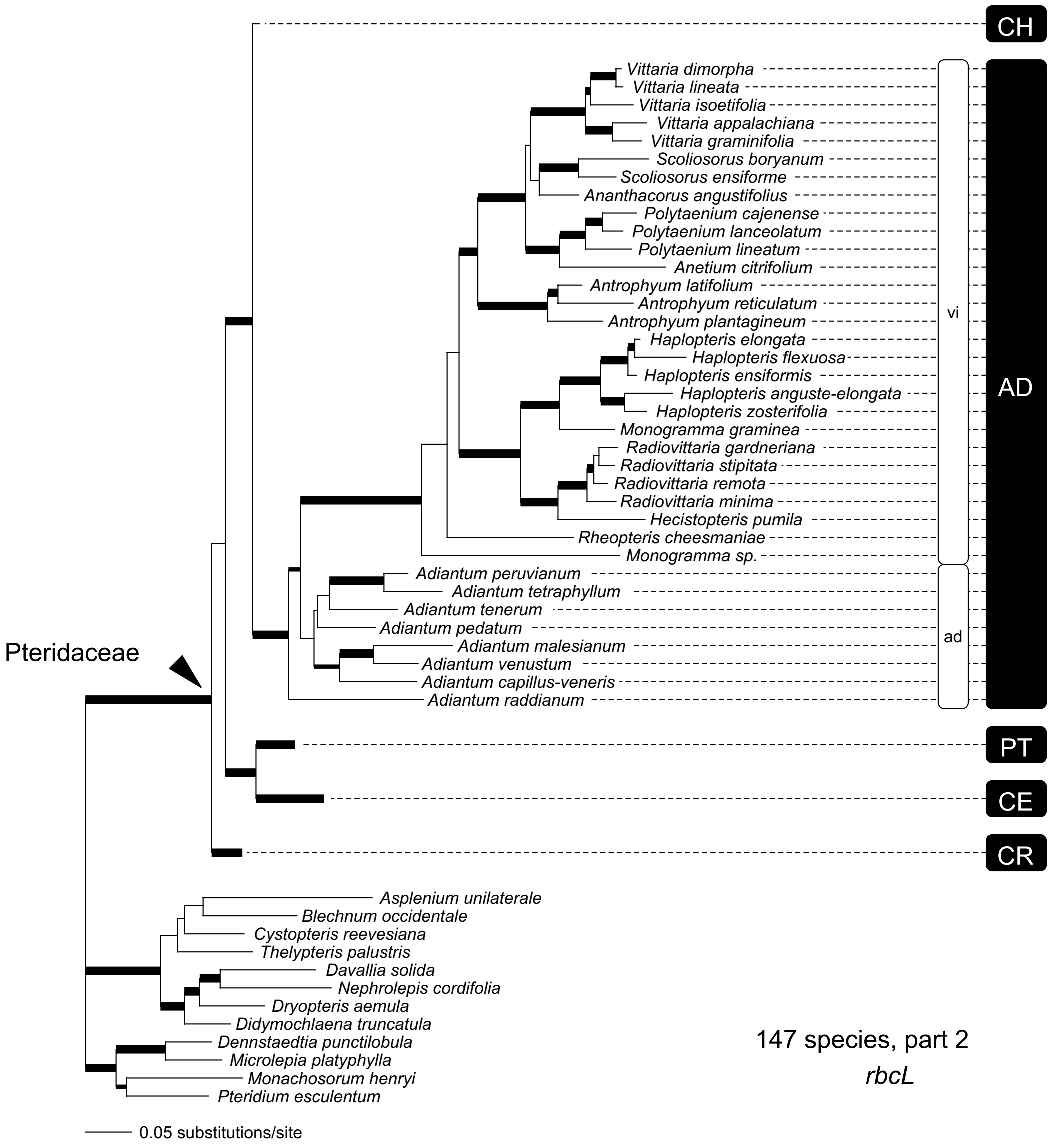

Fig. 3. Plurality consensus phylogeny (with average branch lengths) of the Pteridaceae resulting from Bayesian analysis of the plastid *rbcL* gene for 147 species. Five major clades recognized in this study are indicated, but only relationships within adiantoids (AD) are shown here; relationships within cryptogrammoids (CR), ceratopteridoids (CE), pteridoids (PT), and cheilanthoids (CH) are shown in Figs. 2 and 4. Taxa as circumscribed in the most recent subfamilial classification are also indicated (see Fig. 1 legend). Branch thickening follows Fig. 1.

sister to the isolated genus *Platyzoma* (pl in Fig. 1) or sister to a clade largely corresponding to the Taenitidoideae of Tryon et al. (ta in Fig. 2). Although the species allied to *Pteris vittata* are probably few, *Pteris longifolia* (the type of the genus; not sampled here) is almost certainly among them (Mickel and Smith, 2004). Thus, to maintain the monophyly of the genus, the definition of *Pteris* would either need to be expanded to include the entire pteridoid clade (PT in Figs. 1 and 2) or—perhaps more tenably—restricted to the small clade of *P. longifolia*, *P. vittata*, and their close allies. The remaining members of the genus *Pteris*, as currently circumscribed, do fall together within a large well-supported clade (Figs. 1 and 2), to which the generic names *Litobrochia* C. Presl or *Campteria* C. Presl could be applied. However, two small, previously unsampled genera (*Neurocallis* and *Ochropteris*) also fall within this clade. This result supports further disintegration of *Pteris* or, alternatively, the inclusion of *Neurocallis* and *Ochropteris* within a larger *Litobrochia* or *Campteria*.

Six additional genera—all comprising one or a few species—that were assigned to the Pteridoideae (pt) or Taenitidoideae (ta) by Tryon et al. (1990) were not included in our study due to a lack of suitable material for extraction. Three of these (*Anopteris*, *Cerosora*, and *Nephopteris*) have yet to be included in any phylogenetic study, but the three others (*Afropteris*, *Austrogramme*, and *Syngramma*) were included in an earlier molecular study focused specifically on subfamily Taenitidoideae (Sánchez-Baracaldo, 2004). In that study, *Austrogramme* and *Syngramma* formed a clade sister to *Taenitis*, whereas *Afropteris* was allied to *Pteris*. All other genera included by Sánchez-Baracaldo (2004) were included here, and the resulting phylogenies

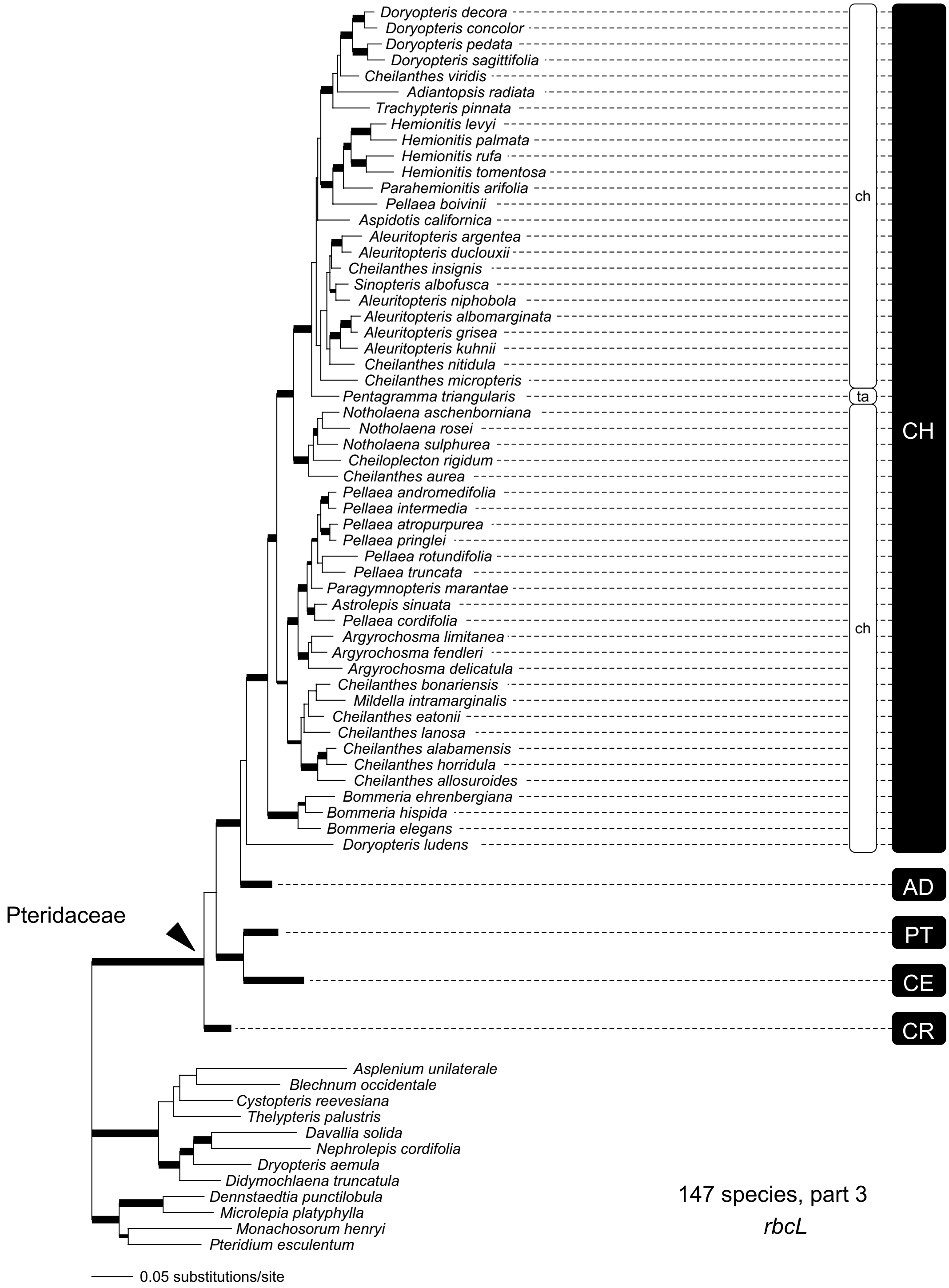

Fig. 4. Plurality consensus phylogeny (with average branch lengths) of the Pteridaceae resulting from Bayesian analysis of the plastid *rbcL* gene for 147 species. Five major clades recognized in this study are indicated, but only relationships within cheilanthoids (CH) are shown here; relationships within cryptogrammoids (CR), ceratopteridoids (CE), pteridoids (PT), and adiantoids (AD) are shown in Figs. 2 and 3. Taxa as circumscribed in the most recent subfamilial classification are also indicated (see Fig. 1 legend). Branch thickening follows Fig. 1.

are essentially congruent. While the relationships resolved in this part of the phylogeny are somewhat consistent with those suggested by morphology (Schneider, 1996; Tryon et al., 1990; Tryon and Lugardon, 1991), further work is needed to assess the affinities of the remaining unsampled genera and also a few putative segregates of *Pteris* not sampled here (e.g., *Copelandiopteris* and *Idiopteris*).

The phylogenetic relationships within the pteridoid clade are of broader interest especially due to the presence in this clade of several species that have been shown to hyperaccumulate arsenic (Ma et al., 2001; Meharg, 2003). These species—and probably also their close relatives—have the potential to remediate arsenic-contaminated soils. An improved understanding of pteridoid phylogeny will provide a framework in which to examine the evolution of this trait and will also help to identify candidate species for additional screening.

4.5. Adiantoid clade (AD)

The genus *Adiantum* (ad) and the vittarioid ferns (vi) together form a well-supported adiantoid fern clade (AD in Figs. 1 and 3), comprising about 12 genera and 300 species. A close relationship among these ferns has been suggested previously (Gastony and Johnson, 2001; Hasebe et al., 1995; Pryer et al., 1995; Schneider et al., 2004). However, the lack of support in our study for the monophyly of *Adiantum* is somewhat surprising. In the combined three-gene analysis, this genus is resolved as monophyletic, but without either MLBS or BPP support (Fig. 1). In the expanded *rbcL* analysis, *Adiantum* is supported as paraphyletic by BPP (Fig. 3), suggesting that the vittarioids may actually be derived from within the genus *Adiantum* as it is currently circumscribed. This result certainly warrants further scrutiny, and additional data will be required to make a solid assessment of the monophyly of *Adiantum*.

The extremely rare (collected only three times) and enigmatic fern genus *Rheopteris* was generally thought to be allied to the vittarioid ferns (Kramer, 1990a; Lindsay, 2003; Schneider, 1996; Tryon and Lugardon, 1991). However, its unique suite of morphological and anatomical characteristics (roots lacking sclerenchyma; outer root cortex cells with spiral wall thickenings; rhizomes with clathrate scales; leaves pinnate with dimidiate pinnae, free veins, and spicular cells in the epidermis; sporangia arranged in sorus-like groups with glandular paraphyses; spores tetrahedral and psilate to finely granulate) did not unequivocally place it in this group. Based on the results of our analyses, *Rheopteris* is indeed a vittarioid fern, but is among the earliest diverging genera in that clade (Figs. 1 and 3). This phylogenetic position suggests that the unique combination of morphological and anatomical traits observed in *Rheopteris* resulted from the retention of some plesiomorphic states (found in the common ancestor of *Adiantum* and vittarioid ferns) and the acquisition of other apomorphic states that now characterize the vittarioids.

Another previously unsampled genus, *Monogramma*, is also confirmed to be a vittarioid fern (Figs. 1 and 3). Although the alliance itself is not surprising (Kramer, 1990a), it is interesting to note that the two species sampled (from about seven total in the genus) fall out in very different places within the vittarioid phylogeny (Fig. 3). One (*M. sp.*) is resolved as sister to all other vittarioids (including *Rheopteris*); the other (*M. graminea*, the type species for the genus) is sister to *Haplopteris*. Species assigned to *Monogramma* are characterized by their extreme morphological simplification and, based on our results, this reduction occurred independently in at least two distinct lineages. Further sampling of species assigned to this already unnatural genus will be required to detect whether or not this evolutionary simplification has occurred in parallel in other vittarioid clades.

A second look at the phylogeny presented in Fig. 3 reveals a rather striking *rbcL* branch length discrepancy between the vittarioid ferns and *Adiantum*. This difference holds between the vittarioids and all other clades of the Pteridaceae and is also consistent across all three plastid genes—vittarioid branches are always substantially longer (Fig. 1). This molecular rate heterogeneity requires further study to assess its significance and identify its underlying causal mechanisms. Are there correlates in the morphology, ecology, and life history of vittarioid ferns that could be identified as contributing to a seemingly faster rate of molecular evolution?

4.6. Cheilanthoid clade (CH)

The cheilanthoid ferns (CH in Figs. 1 and 4) comprise about 20 genera and 400 species. Although this group largely corresponds to subfamily Cheilanthoideae of Tryon et al. (1990), three genera included in that subfamily (*Coniogramme*, *Cryptogramma*, and *Llavea*) are well removed from the cheilanthoids, forming the cryptogrammoid clade (CR in Fig. 1). The cheilanthoid clade, as defined here, is not well supported as monophyletic—only in the three-gene combined MLBS analysis does this group receive good support (Fig. 1). The problem stems from the inclusion of *Doryopteris ludens*, which is here resolved as sister to all other cheilanthoids. This finding is in agreement with Yesilyurt (2004), who also reported an early diverging position for this species. Morphologically, *D. ludens* and its presumed allies (*D. papuana* and *D. allenae*) are quite similar to the other sampled *Doryopteris* species, which form a more derived monophyletic group within the cheilanthoid clade (Figs. 1 and 4). However, the early diverging species have longer-creeping rhizomes and fleshier leaves, are restricted to limestone substrates, and are apparently less adapted to xeric conditions (Schneider, 2001; Yesilyurt, 2004). The distribution of the *D. ludens* group (from northern India and southern China through southeast Asia to New Guinea) is also quite different than the remainder of the genus (mostly endemic to Brazil). Clearly, further study is required to better understand the phylogenetic position of these species.

The remaining cheilanthoid ferns form a large, well-supported clade, and the resolved relationships within this clade are generally in accord with those of earlier analyses (Gastony and Rollo, 1995, 1998; Zhang et al., 2005). However, it should be noted that our study improves upon the earlier analyses by including a substantial number of previously unsampled taxa (Fig. 4 and Appendix A).

Furthermore, the addition of *atpA* and *atpB* sequences for a smaller subset of taxa improves support for various subclades (Fig. 1).

Most notable among the newly sampled taxa is the genus *Adiantopsis* (we sampled the type species, *Adiantopsis radiata*). This genus was placed in subfamily Cheilanthoideae by Tryon et al. (1990) and in our analyses it is well-supported as a member of the derived *Doryopteris/Trachypteris* clade (Fig. 4). Also within this clade is the species variously known as *Cheilanthes viridis* or *Pellaea viridis* (six other generic combinations exist). The type species of both *Pellaea* (*P. atropurpurea*) and *Cheilanthes* (*C. micropteris*) are included in our current sampling, but neither is closely related to this taxon. *Pellaea atropurpurea* is resolved, as expected, with most other members of *Pellaea* (Fig. 4). *Cheilanthes micropteris*, on the other hand, occupies a rather isolated position in the cheilanthoid clade (Fig. 4).

Previous phylogenetic studies of cheilanthoid ferns (Gastony and Rollo, 1995, 1998) played a significant role in redefining generic limits within this clade, supporting the recognition of *Argyrochosma* (Windham, 1987), *Astrolepis* (Benham and Windham, 1992), and *Pentagramma* (Yatskievych et al., 1990) as distinct genera. However, it is obvious from our results that generic circumscriptions require further attention. For example, *Aleuritopteris* is not monophyletic in our analyses; instead it comprises several smaller groups associated with the genus *Sinopteris* and Asian species of the genus *Cheilanthes* (*C. insignis* and *C. nitidula*; Fig. 4). Unfortunately, the type species of *Aleuritopteris* (*A. farinosa*) is not included in our study, and it is unclear which (if any) of these groups should ultimately be recognized as *Aleuritopteris*. Such polyphyly seems to be rampant within cheilanthoid ferns; all of the largest genera (e.g., *Cheilanthes*, *Doryopteris*, and *Pellaea*) are not monophyletic as currently circumscribed (Fig. 4). Fixing these taxonomic problems may ultimately require the recognition of several additional genera within the cheilanthoid clade, but further sampling (including all generic types) and sequencing (analyses of *rbcL* alone are not sufficient to obtain good support for relationships, Fig. 4) will be required before making such decisions.

4.7. Ecological trends and evolutionary implications

In addition to emphasizing the need for a revised classification of the Pteridaceae, the phylogeny resulting from our analyses reveals some rather interesting ecological trends. As mentioned previously, the Pteridaceae occupies an unusually broad range of ecological niches, differing notably from most other fern families by encompassing terrestrial, epiphytic, xeric-adapted rupestral, and even aquatic species. In some habitats (e.g., among mangroves and in deserts) members of the Pteridaceae are virtually the only ferns present. But what is especially interesting is that some clades of Pteridaceae appear to be characterized by their ecological preferences. The ceratopteridoid clade (including *Acrostichum* and *Ceratopteris*; CE in Fig. 1) is restricted to aquatic habitats, including freshwater swamps and mangroves. The vittarioid subclade (vi within AD in Fig. 1) comprises only epiphytic (or occasionally epipetric) species, but epiphytes are absent in the remainder of the Pteridaceae. Similarly, although a preference for xeric habitats characterizes the cheilanthoid clade (CH in Fig. 1), it rarely occurs elsewhere in ferns; within the Pteridaceae, only the genera *Actiniopteris* and *Cosentinia* (in the pteridoid clade) are equally xeric-adapted. Based on this pattern, it appears that ecological innovation and specialization were together responsible for the initial diversification within the Pteridaceae. These processes may well be the basis for the diversity and success of this clade today.

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Appendix A

Taxonomic sampling, including voucher information and accession numbers, for this study of Pteridaceae phylogeny

Species	Voucher information[a]	Accession Nos.[a]	
		Fern DNA database	GenBank
Acrostichum aureum L.	Masuyama et al. (2002)	—	AB059586
Acrostichum danaeifolium Langsd. & Fisch.	Schuettpelz 616 (B), =, =	3663, =, =	EF452129, EF452008, EF452065
Actiniopteris dimorpha Pic. Serm.	Schneider s.n. (GOET), =, =	3515, =, =	EF452130, EF452009, EF452066
Actiniopteris radiata (Sw.) Link	Gastony and Johnson (2001)	—	AF336100
Adiantopsis radiata (L.) Fée	Christenhusz 4033 (TUR), =, =	3313, =, =	EF452131, EF452010, EF452067
Adiantum capillus-veneris L.	Wolf et al. (2003), =, =	—, —, —	AY178864, AY178864, AY178864
Adiantum malesianum J. Ghatak	Huiet 111 (UC), =, =	2506, =, =	EF452132, EF452011, EF452068
Adiantum pedatum L.	Hasebe et al. (1994), Huiet 117 (UC), =	636, 2499, =	U05602, EF452012, EF452069
Adiantum peruvianum Klotzsch	Huiet 103 (UC), =, =	2507, =, =	EF452133, EF452013, EF452070
Adiantum raddianum C. Presl	Wolf et al. (1994), Wolf (1997), Wolf 717 (UTC)	637, 638, =	U05906, U93840, EF452071
Adiantum tenerum Sw.	Huiet 107 (UC), =, =	2504, =, =	EF452134, EF452014, EF452072
Adiantum tetraphyllum Humb. & Bonpl. ex Willd.	Huiet 105 (UC), =, =	2505, =, =	EF452135, EF452015, EF452073
Adiantum venustum D. Don	Huiet 116 (UC)	2500	EF452136
Aleuritopteris albomarginata (C.B. Clarke) Ching	Zhang et al. (2005)	—	AY266411
Aleuritopteris argentea (S.G. Gmelin) Fée	Yatskievych 01-23 (MO), =, =	3734, =, =	EF452137, EF452016, EF452074
Aleuritopteris duclouxii (Christ) Ching	Gastony and Rollo (1995)	648	U27447
Aleuritopteris grisea (Blanf.) Panigrahi	Zhang et al. (2005)	—	AY299653
Aleuritopteris kuhnii (Milde) Ching	Zhang et al. (2005)	—	AY266412
Aleuritopteris niphobola (C. Chr.) Ching	Zhang et al. (2005)	—	AY266409
Ananthacorus angustifolius Underw. & Maxon	Crane et al. (1995)	696	U20932
Anetium citrifolium (L.) Splitg.	Crane et al. (1995), Christenhusz 4076 (TUR), =	697, 3339, =	U21284, EF452017, EF452075
Anogramma chaerophylla (Desv.) Link	Nakazato and Gastony (2003)	—	AY168712
Anogramma leptophylla (L.) Link	Nakazato and Gastony (2003)	—	AY168715
Anogramma lorentzii (Hieron.) Diels	Gastony and Johnson (2001)	—	AF336102
Anogramma novogaliciana Mickel	Nakazato and Gastony (2003)	—	AY168714
Antrophyum latifolium Blume	Ranker 1774 (COLO), =, =	3078, =, =	EF452138, EF452018, EF452076
Antrophyum plantagineum (Cav.) Kaulf.	Crane et al. (1995)	711	U21285
Antrophyum reticulatum (G. Forst.) Kaulf.	Hasebe et al. (1994)	698	U05604
Argyrochosma delicatula (Maxon & Weath.) Windham	Gastony and Rollo (1995)	642	U19500
Argyrochosma fendleri (Kunze) Windham	Gastony and Rollo (1995)	643	U27727
Argyrochosma limitanea (Maxon) Windham	Schuettpelz 472 (DUKE), =, =	3179, =, =	EF452139, EF452019, EF452077
Aspidotis californica (Hook.) Nutt. ex Copel.	Gastony and Johnson (2001)	—	AF336101
Asplenium unilaterale Lam.	Ranker 2072 (COLO), =, =	3470, =, =	EF452140, EF452020, EF452078
Astrolepis sinuata (Lag. ex Sw.) D.M. Benham & Windham	Schuettpelz 310 (DUKE), =, =	2955, =, =	EF452141, EF452021, EF452079
Blechnum occidentale L.	Wolf et al. (1994), Wolf (1997), Wolf 289 (UTC)	67, =, =	U05910, U93838, EF452080
Bommeria ehrenbergiana (Kotzsch) Underw.	Gastony and Rollo (1995)	644	U19497
Bommeria elegans (Davenp.) Ranker & Haufler	Gastony and Rollo (1995)	658	U27729
Bommeria hispida (Mett. ex Kuhn) Underw.	Schuettpelz 467 (DUKE), =, =	3174, =, =	EF452142, EF452022, EF452081
Ceratopteris pteridoides (Hook.) Hieron.	Masuyama et al. (2002)	—	AB059584

(*continued on next page*)

Appendix A (*continued*)

Species	Voucher information[a]	Accession Nos.[a]	
		Fern DNA database	GenBank
Ceratopteris richardii Brongn.	Masuyama et al. (2002), Pryer et al. (2004), Killip 44595 (GH)	—, 1027, =	AB059585, AY612691, EF452082
Ceratopteris thalictroides (L.) Brongn.	Masuyama et al. (2002)	—	AB059573
Cheilanthes alabamensis (Buckley) Kunze	Schuettpelz 319 (DUKE), =, =	2964, =, =	EF452143, EF452023, EF452083
Cheilanthes allosuroides Mett.	Gastony and Rollo (1995)	645	U27239
Cheilanthes aurea Baker	Gastony and Rollo (1995)	646	U28786
Cheilanthes bonariensis (Willd.) Proctor	Gastony and Rollo (1995)	647	U19499
Cheilanthes eatonii Baker	Schuettpelz 323 (DUKE), =, =	2968, =, =	EF452144, EF452024, EF452084
Cheilanthes horridula Maxon	Gastony and Rollo (1995)	649	U27448
Cheilanthes insignis Ching	Zhang et al. (2005)	—	AY266413
Cheilanthes lanosa (Michx.) D.C. Eaton	Gastony and Rollo (1995)	651	U27205
Cheilanthes micropteris Sw.	Deginani 1363 (MO)	3709	EF452145
Cheilanthes nitidula Hook.	Schneider s.n. (GOET), =, =	3513, =, =	EF452146, EF452025, EF452085
Cheilanthes viridis Sw.	Janssen 2701 (P), =, =	3555, =, =	EF452147, EF452026, EF452086
Cheiloplecton rigidum (Sw.) Fée	Gastony and Rollo (1995)	652	U29133
Coniogramme fraxinea (D. Don) Fée ex Diels	Korall et al. (2006), Pryer et al. (2004), Korall et al. (2006)	653, =, =	AM177359, AY612693, AM176470
Coniogramme japonica (Thunb.) Diels	Hasebe et al. (1994)	—	U05611
Cosentinia vellea (Aiton) Tod.	Nakazato and Gastony (2003)	—	AY168720
Cryptogramma brunoniana Wall. ex Hook. & Grev.	Zhang et al. (2005)	—	AY266407
Cryptogramma crispa (L.) R. Br. ex Hook.	Christenhusz 3871 (TUR), =, =	2949, =, =	EF452148, EF452027, EF452087
Cystopteris reevesiana Lellinger	Schuettpelz 419 (DUKE), =, =	3126, =, =	EF452149, EF452028, EF452088
Davallia solida (G. Forst.) Sw.	Tsutsumi and Kato (2005), Schuettpelz 300 (DUKE), =	—, 2560, =	AB212712, EF452029, EF452089
Dennstaedtia punctilobula (Michx.) T. Moore	Wolf et al. (1994), Wolf, 1997, Paris s.n. (UTC)	99, =, =	U05918, U93836, EF452090
Didymochlaena truncatula (Sw.) J. Sm.	Smith and Cranfill (2002), Schuettpelz 267 (DUKE), =	—, 2435, =	AF425105, EF452030, EF452091
Doryopteris concolor (Langsd. & Fisch.) Kuhn	Zhang et al. (2005)	—	AY266414
Doryopteris decora Brack.	Gastony and Rollo (1995)	656	U27446
Doryopteris ludens (Wall. ex. Hook.) J. Sm.	Schneider s.n. (GOET), =, =	3510, =, =	EF452150, EF452031, EF452092
Doryopteris pedata (L.) Fée	Gastony and Rollo (1995)	657	U27206
Doryopteris sagittifolia (Raddi) J. Sm.	Schuettpelz 562 (GOET), =, =	3617, =, =	EF452151, EF452032, EF452093
Dryopteris aemula (Aiton) Kuntze	Geiger and Ranker (2005), Christenhusz 3866 (TUR), =	—, 2944, =	AY268881, EF452033, EF452094
Eriosorus cheilanthoides (Sw.) A.F. Tryon	Moran 7579 (NY), =, =	3767, =, =	EF452152, EF452034, EF452095
Eriosorus flexuosus (Humb. & Bonpl.) Copel.	Nakazato and Gastony (2003)	—	AY168709
Haplopteris anguste-elongata (Hayata) E.H. Crane	Crane et al. (1995)	699	U21291
Haplopteris elongata (Sw.) E.H. Crane	Huiet 112 (UC), =, =	2546, =, =	EF452153, EF452035, EF452096
Haplopteris ensiformis (Sw.) E.H. Crane	Crane et al. (1995)	700	U21290
Haplopteris flexuosa (Fée) E.H. Crane	Hasebe et al. (1994)	701	U05656
Haplopteris zosterifolia (Willd.) E.H. Crane	Crane et al. (1995)	702	U21296
Hecistopteris pumila (Spreng.) J. Sm.	Crane et al. (1995), Christenhusz 3976 (TUR), =	703, 3278, =	U21286, EF452036, EF452097
Hemionitis levyi E. Fourn.	Gastony and Rollo (1995)	659	U27725
Hemionitis palmata L.	Ranker and Geiger (unpublished), Schuettpelz 297 (DUKE), =	—, 2557, =	AY357708, EF452037, EF452098
Hemionitis rufa (L.) Sw.	Ranker and Geiger (unpublished)	—	AY357707
Hemionitis tomentosa (Lam.) Raddi	Ranker and Geiger (unpublished)	—	AY357709
Jamesonia blepharum A.F. Tryon	Schuettpelz 269 (DUKE)	2437	EF452154
Jamesonia canescens Kunze	Nakazato and Gastony (2003)	—	AY168710

Appendix A (*continued*)

Species	Voucher information[a]	Accession Nos.[a]	
		Fern DNA database	GenBank
Jamesonia osteniana (Dutra) Gastony	Nakazato and Gastony (2003)	—	AY168711
Jamesonia verticalis Kunze	Moran 7593 (NY), =, =	3768, =, =	EF452155, EF452038, EF452099
Llavea cordifolia Lag.	Gastony and Rollo (1995), Schuettpelz 377 (DUKE), =	660, 3021, =	U27726, EF452039, EF452100
Microlepia platyphylla (D. Don) J. Sm.	Wolf (1995), Wolf (1997), Wolf 596 (UTC)	114, =, =	U18642, U93832, EF452101
Mildella intramarginalis (Kaulf. ex Link) Trevis.	Gastony and Rollo (1995)	650	U27449
Monachosorum henryi Christ	Wolf et al. (1994), Pryer et al. (2004), Korall et al. (2006)	478, =, =	U05932, AY612706, AM176469
Monogramma sp.	Ranker 1778 (COLO)	3375	EF452156
Monogramma graminea (Poir.) Schkuhr	Janssen 2692 (P), =, =	3548, =, =	EF452157, EF452040, EF452102
Nephrolepis cordifolia (L.) C. Presl	Wolf et al. (1994), Wolf 309 (UTC), =	479, =, =	U05933, EF452041, EF452103
Neurocallis praestantissima Bory ex Fée	Christenhusz 3997 (TUR), =, =	3294, =, =	EF452158, EF452042, EF452104
Notholaena aschenborniana Klotzsch	Schuettpelz 476 (DUKE), =, =	3183, =, =	EF452159, EF452043, EF452105
Notholaena rosei Maxon	Gastony and Rollo (1995)	661	U27728
Notholaena sulphurea (Cav.) J. Sm.	Gastony and Rollo (1995)	662	U28254
Ochropteris pallens (Sw.) J. Sm.	Janssen 2677 (P), =, =	3558, =, =	EF452160, EF452044, EF452106
Onychium contiguum Wall. ex C. Hope	Zhang et al. (2005)	—	AY266416
Onychium japonicum (Thunb.) Kunze	Hasebe et al. (1994), Schneider s.n. (GOET), =	663, 3463, =	U05641, EF452045, EF452107
Onychium lucidum (D. Don) Spreng.	Gastony and Johnson (2001)	—	AF360359
Onychium plumosum Ching	Zhang et al. (2005)	—	AY266408
Onychium tenuifrons Ching	Zhang et al. (2005)	—	AY266415
Paragymnopteris marantae (L.) K. H. Shing	Yatskievych 02-35 (KUN), =, =	3736, =, =	EF452161, EF452046, EF452108
Parahemionitis arifolia (Burm. f.) Panigrahi	Ranker and Geiger (unpublished)	—	AY357706
Pellaea andromedifolia (Kaulf.) Fée	Gastony and Rollo (1995)	664	U19501
Pellaea atropurpurea (L.) Link	Schuettpelz 312 (DUKE)	2957	EF452162
Pellaea boivinii Hook.	Gastony and Rollo (1995)	665	U29132
Pellaea cordifolia (Sessé & Moc.) A.R. Sm.	Gastony and Rollo (1995)	666	U28253
Pellaea intermedia Mett. ex Kuhn	Schuettpelz 481 (DUKE), =, =	3188, =, =	EF452163, EF452047, EF452109
Pellaea pringlei Davenp.	Gastony and Rollo (1995)	667	U28787
Pellaea rotundifolia (G. Forst.) Hook.	Gastony and Rollo (1995)	668	U28788
Pellaea truncata Goodd.	Schuettpelz 430 (DUKE), =, =	3137, =, =	EF452164, EF452048, EF452110
Pentagramma triangularis (Kaulf.) Yatsk., Windham & E. Wollenw.	Schuettpelz 445 (DUKE), =, =	3152, =, =	EF452165, EF452049, EF452111
Pityrogramma austroamericana Domin	Schuettpelz 301 (DUKE), =, =	2561, =, =	EF452166, EF452050, EF452112
Pityrogramma calomelanos (L.) Link	Gastony and Johnson (2001)	—	AF336103
Pityrogramma jamesonii (Baker) Domin	Moran 7592 (NY)	3769	EF452167
Pityrogramma trifoliata (L.) R.M. Tryon	Gastony and Johnson (2001)	—	AF336104
Platyzoma microphyllum R. Br.	Nakazato and Gastony (2003), Kato 303 (TI), =	—, 669, =	AY168721, EF452051, EF452113
Polytaenium cajenense (Desv.) Benedict	Crane et al. (1995), Schuettpelz 211 (DUKE), =	704, 2379, =	U20934, EF452052, EF452114
Polytaenium lanceolatum (L.) Benedict	Crane et al. (1995)	705	U21287
Polytaenium lineatum (Sw.) J. Sm.	Crane et al. (1995)	706	U20935
Pteridium esculentum (G. Forst.) Nakai	Wolf et al. (1994), Wolf (1997), Smith s.n. (UC)	125, —, 125	U05940, U93834, EF452115
Pteris arborea L.	Christenhusz 4050 (TUR), =, =	3321, =, =	EF452168, EF452053, EF452116
Pteris argyraea T. Moore	Schuettpelz 542 (GOET), =, =	3597, =, =	EF452169, EF452054, EF452117

(*continued on next page*)

Appendix A (*continued*)

Species	Voucher information[a]	Accession Nos.[a]	
		Fern DNA database	GenBank
Pteris cretica L.	Schuettpelz 597 (DUKE), =, =	3644, =, =	EF452170, EF452055, EF452118
Pteris fauriei Hieron.	Hasebe et al. (1994)	670	U05647
Pteris multifida Poir.	Schuettpelz 591 (GOET), =, =	3640, =, =	EF452171, EF452056, EF452119
Pteris propinqua J. Agardh	Schuettpelz 268 (DUKE), =, =	2436, =, =	EF452172, EF452057, EF452120
Pteris quadriaurita Retz.	Schuettpelz 546 (GOET), =, =	3601, =, =	EF452173, EF452058, EF452121
Pteris tremula R. Br.	Schuettpelz 620 (B), =, =	3667, =, =	EF452174, EF452059, EF452122
Pteris vittata L.	Wolf et al. (1994), Christenhusz 4195 (TUR), =	671, 3400, =	U05941, EF452060, EF452123
Pterozonium brevifrons (A.C. Sm.) Lellinger	Schuettpelz 285 (DUKE), =, =	2453, =, =	EF452175, EF452061, EF452124
Radiovittaria gardneriana (Fée) E.H. Crane	Crane et al. (1995), Schuettpelz 249 (DUKE), =	707, 2417, =	U21294, EF452062, EF452125
Radiovittaria minima (Baker) E.H. Crane	Crane et al. (1995)	708	U21288
Radiovittaria remota (Fée) E.H. Crane	Crane et al. (1995)	709	U21289
Radiovittaria stipitata (Kunze) E.H. Crane	Crane et al. (1995)	710	U21293
Rheopteris cheesmaniae Alston	Croft 1749 (A, K), =, =	3373, =, =	EF452176, EF452063, EF452126
Scoliosorus boryanum (Willd.) E.H. Crane	Crane et al. (1995)	712	U20930
Scoliosorus ensiforme (Hook.) T. Moore	Crane et al. (1995)	713	U20931
Sinopteris albofusca (Baker) Ching	Gastony and Rollo (1995)	641	U19498
Taenitis blechnoides (Willd.) Sw.	Hasebe et al. (1994)	672	U05654
Thelypteris palustris Schott	Wolf et al. (1994), Pryer et al. (2004), Wolf 284 (UTC)	694, =, =	U05947, AY612713, EF452127
Trachypteris pinnata (Hook. f.) C. Chr.	Gastony and Rollo (1995)	673	U27450
Vittaria appalachiana Farrar & Mickel	Crane (1997)	—	U88961
Vittaria dimorpha Müll.	Crane et al. (1995)	714	U21292
Vittaria graminifolia Kaulf.	Crane et al. (1995), Schuettpelz 227 (DUKE), =	715, 2395, =	U21295, EF452064, EF452128
Vittaria isoetifolia Bory	Crane et al. (1995)	717	U20936
Vittaria lineata (L.) Sm.	Crane et al. (1995)	718	U20937

[a] Voucher information and accession numbers are provided in the order: *rbcL*, *atpB*, *atpA*. "=" indicates same as previous; "—" indicates not available. Fern DNA database accession numbers correspond to records at <http://www.pryerlab.net/DNA_database.shtml/>.

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