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A Global Phylogenomic Study of the Thelypteridaceae

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Abstract—The generic classification of the Thelypteridaceae has been the subject of much controversy. Proposed taxonomic systems have varied from recognizing the approximately 1200 species in the family within the single genus *Thelypteris*, to systems favoring upwards of 30 genera. Insights on intrafamilial relationships, especially for neotropical taxa, have been gained from recent phylogenetic studies; however, in the most recent classification, 10 of 30 recognized genera are either non-monophyletic or untested. We sequenced 407 nuclear loci for 621 samples, representing all recognized genera and approximately half the known species diversity. These were analyzed using both maximum likelihood analysis of a concatenated matrix and multi-species coalescent methods. Our phylogenomic results, informed by recently published morphological evidence, provide the foundation for a generic classification which recircumscribed 14 genera and recognized seven new genera. The 37 monophyletic genera sampled demonstrate greater geographic coherence than previous taxonomic concepts suggested. Additionally, our results demonstrate that certain morphological characters, such as frond division, are evolutionarily labile and are thus inadequate for defining genera.

Keywords—*Amauropelta*, *Christella*, ferns, phylogeny, *Pneumatopteris*, *Pronephrium*, systematics, targeted enrichment, taxonomy.

With approximately 1200 species currently recognized, the Thelypteridaceae is one of the largest families of ferns, and its species are highly diverse morphologically (Fig. 1) and ecologically (Fawcett and Smith 2021). It is a member of the Aspleniinae, one of the two major clades of the eupolypod ferns, and is sister to a subclade that includes the Athyriaceae, Blechnaceae, Onocleaceae, and Woodsiaceae (PPG I 2016). The Thelypteridaceae is widespread throughout the tropics; a few species extend into boreal latitudes. The taxonomy of this diverse family remains contentious, and several differing generic classifications have been proposed.

Christensen (1913, 1920) was the first to suggest that thelypterids represent a natural group. In his monograph of New World members of the genus *Dryopteris*, he comprehensively treated American species now considered to belong to the Thelypteridaceae as subgenera of a broadly-defined *Dryopteris* Adans. With recognition of their many differences from *Dryopteris* s. s., most species now treated in Thelypteridaceae were subsequently transferred to *Thelypteris* in Asia (e.g. by Ching 1936) and in the Americas (e.g. by Morton 1963; Reed 1968). In these publications and others, *Thelypteris* had a very broad circumscription, including all, or nearly all, of the species belonging to modern-day Thelypteridaceae, ca. 1200 species. Many of the infrageneric taxa delimited by Christensen (1913, 1920) in *Dryopteris* were later recognized as subgenera in *Thelypteris*, with essentially the same circumscription. Ching (1963), who understood the distinctness of many Chinese and eastern Asia groups, went a step further and elevated these subgroups, as well as newly defined segregates, to generic status. Further taxonomic refinements were made by Pichi Sermolli (1970) and Holttum (1971), and later by Ching (1978) and Holttum (1982). With these more restricted circumscriptions, *Thelypteris* became a small genus with only about two species. Pichi Sermolli (1977) was the first to attempt a worldwide reclassification of the Thelypteridaceae within a phylogenetic context; he recognized 32 genera in the family. Before the availability of molecular data, intermediate solutions were also proposed (e.g. Smith 1990). The taxonomy of the group remains controversial, with some authors still favoring a single-genus system for the family, citing the difficulty of using micro-morphological features to distinguish genera (e.g. Fraser-Jenkins et al. 2017). However, there is growing support for recognition of more genera that are supported by both molecular and morphological data (PPG I 2016; Schuettpelz et al. 2018). For a more detailed history of the classification of the Thelypteridaceae, see Fawcett and Smith (2021).

With advances in microscopy, chromosome numbers provided a powerful new source of data for understanding the evolutionary relationships among ferns, using approaches pioneered by Irene Manton (1950). Some of the first attempts to develop hypotheses pertaining to phylogenetic relationships among genera incorporated cytological data in addition to morphology (Loyal 1963; Smith 1971; Pichi Sermolli 1977).

The first phylogenetic tree to infer relationships among genera of the Thelypteridaceae using molecular data was published by Smith and Cranfill (2002), based on three chloroplast DNA regions. This study confirmed the monophyly

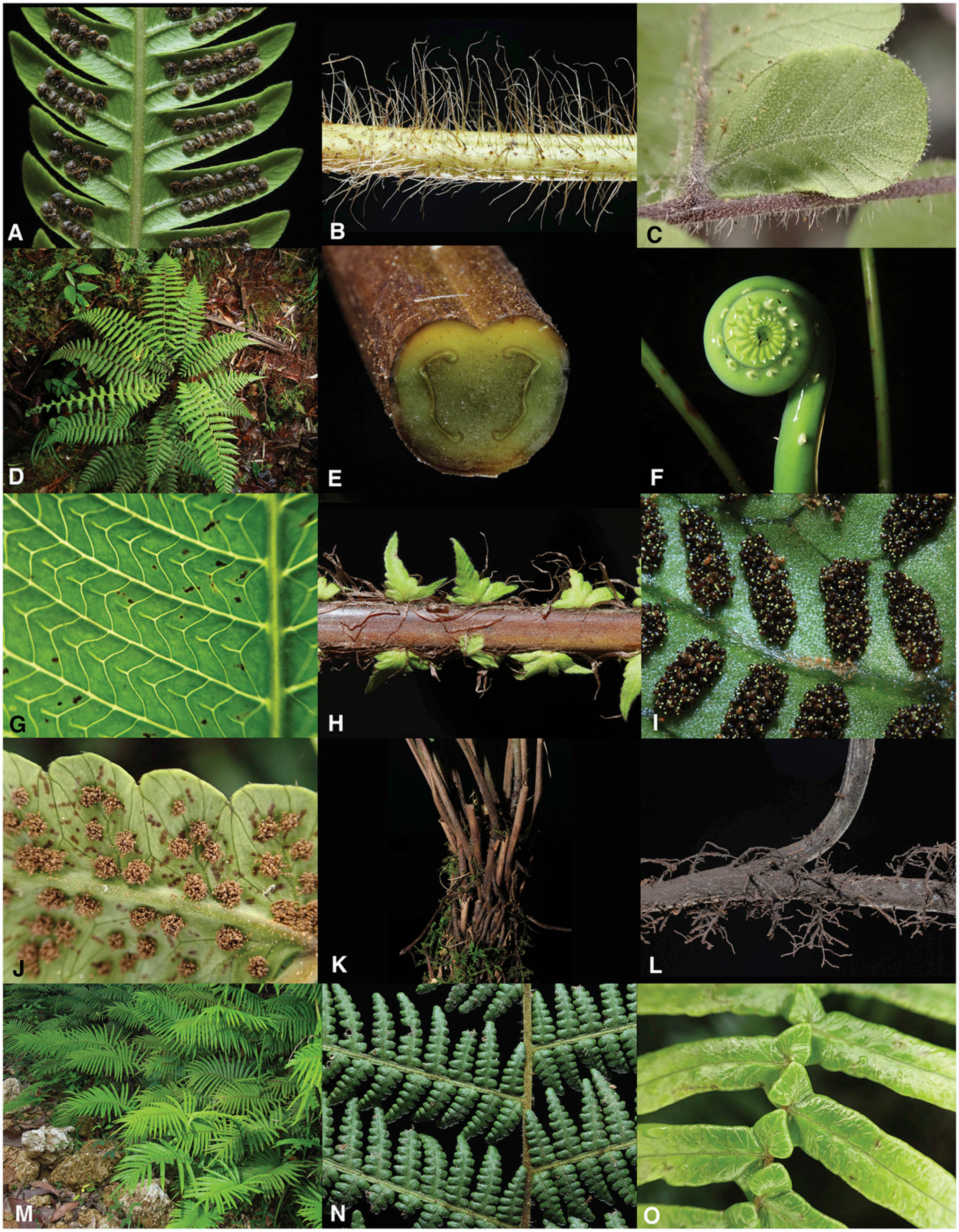

FIG. 1. Morphological diversity of the Thelypteridaceae. A. *Plesioneuron attenuatum*, indusiate sori. B. *Chingia malodora*, stipe with terete scales. C. *Goniopteris pellita*, rachis and pinna base, with both long hyaline acicular and short stellate hairs (these visible on lamina margin). D. *Coryphopteris kolombangarae*, habit. E. *Reholttumia magnifica*, stipe vasculature. F. *Pneumatopteris glandulifera*, mucilaginous crozier with peg-like aerophores. G. *Meniscium reticulatum*, venation. H. *Sphaerostephanos polycarpus*, auriculate proximal pinnae. I. *Sphaerostephanos beccarianus*, sori with spherical yellow glands. J. *Goniopteris serrulata*, exindusiate round sori. K. *Sphaerostephanos doodioides*, erect rhizome. L. *Strophocaulon invisum*, long-creeping rhizome. M. *S. unitum*, habit. N. *Macrothelypteris polypodioides*, adaxial lamina. O. *Goniopteris sagittata*, pinna bases. Photos C, G, J, O by S. Fawcett, all other photos by C.-W. Chen.

of the family and demonstrated the sister relationship of two major subclades within the family now recognized as subfamilies Phegopteridoideae and Thelypteridoideae. It also showed that the chromosome base number $x = 36$ is synapomorphic for the large lineage they named the cyclosoroid clade. The 27 taxa chosen for their study represented all major lineages within the family, and the relationships they inferred have been largely supported by all subsequent studies.

Later work (Schuettpelz and Pryer 2007; Ebihara 2011; He and Zhang 2012; Almeida et al. 2016; Patel et al. 2019), also relying primarily on cpDNA, increased taxon sampling and provided greater resolution and support for relationships inferred in earlier studies. However, even with limited sampling in the most diverse groups, these studies revealed that several genera were not monophyletic. In their study of Old World genera, He and Zhang (2012) demonstrated that *Christella*, *Parathelypteris*, and *Pronephrium* were non-monophyletic. Almeida et al. (2016) provided greater resolution for the monophyletic neotropical genera *Amauropelta*, *Goniopteris*, *Meniscium*, and *Steiropteris*, and published accompanying taxonomic changes (Salino et al. 2015). They also provided evidence that the paleotropical genera *Pneumatopteris* and *Sphaerostephanos* were non-monophyletic, based on very limited sampling. Most recently, Patel et al. (2019) corroborated these findings, notably the coherence of subgeneric taxa such as *Christella* sect. *Pelazoneuron* Holttum and *Pronephrium* sect. *Grypothrix* Holttum.

The Pteridophyte Phylogeny Group (PPG) was organized to develop a consensus-based classification system for all ferns and lycophytes, based on a collaborative effort of nearly 100 pteridologists from around the world, incorporating all available phylogenetic data. The resulting publication (PPG I 2016) proposed a family and genus-level taxonomy for all ferns and lycophytes, including species-number estimates, and phylogenetic status (e.g. monophyletic, non-monophyletic, or untested) for each genus. The resulting classification of the Thelypteridaceae largely followed the circumscriptions presented by Smith and Cranfill (2002), He and Zhang (2012), and Almeida et al. (2016). Although the Thelypteridaceae is by far most diverse in the Paleotropics, it was also the least studied there, with 10 of the 30 recognized genera known to be non-monophyletic or untested. In the absence of molecular data, the morphology-based taxonomy proposed by Holttum (1971, 1974, 1977, 1982) was largely adopted for these taxa.

The objectives of the present study are to: 1) infer the infrafamilial and infrageneric relationships within the Thelypteridaceae using a large nuclear-DNA dataset; 2) assess the taxonomic hypotheses proposed by PPG I (2016); and 3) provide the phylogenetic foundation for a revised generic classification of the Thelypteridaceae worldwide.

MATERIALS AND METHODS

Sampling Design—Our goal was to sample broadly across the family, but with an emphasis on the Paleotropics, which hosts the greatest diversity both in species richness and number of genera and has been poorly represented in previous phylogenetic studies. In most cases we included a single sample per species, but widespread or taxonomically complex species (e.g. *Christella hispidula*) were represented by multiple accessions. We sought to include the type species for each genus, but were unable to include those of *Leptogramma, Pronephrium,* or *Trigonospora*. Our sample includes 621 accessions of about 500 species (including several that are probably undescribed), representing nearly half of the approximately 1200 species in the family. Our sample includes all genera recognized by PPG I (2016), including the rare, monotypic African genus *Menisorus*, which has not previously been included in any molecular phylogenetic study. Tissue was derived from silica-dried samples and herbarium specimens, some of which were more than 100 years old. All samples collected by contributing authors were obtained under the respective collection and export permits of the collection countries, and by local landowner permission. Most tissue vouchers are at UC, TAIF, or VT, with others at BO, CMUH, CR, DUKE, F, FLAS, GH, GOET, HOXA, HUH, INB, JBSD, JEPS, KEP, KLU, LBG, LPB, MAPR, MICH, MO, NY, P, PAP, PE, PNH, PTBG, S, SBBG, TNS, and Z. (Appendix 1).

DNA Extraction and Sequencing—DNA extractions were performed at the University of Florida, Gainesville, using a cetyltrimethylammonium bromide (CTAB) extraction protocol (Doyle and Doyle 1987), with 2.5% polyvinylpyrrolidone and 0.4% beta-mercaptoethanol and two rounds of chloroform washes followed by an isopropanol precipitation and an ethanol wash. We also added 2μL of 10mg/mL RNase A (Qiagen, Valencia, CA, USA) to each sample between chloroform washes to remove RNA contamination. All samples yielded more than the minimum threshold of 5ng DNA required for sequencing.

We used a targeted enrichment sequencing approach with the *GoFlag 408* probe set to generate a large-scale nuclear data set (Breinholt et al. 2021). This probe set targets 408 conserved exons that are found within 229 of the single-copy nuclear genes identified by the 1KP transcriptome sequencing initiative (Leebens-Mack et al. 2019). The probes were designed from transcriptome and genomic sequences to target exons across flagellate land plants (mosses, liverworts, hornworts, lycophytes, ferns, and all gymnosperms) that were single or low-copy, at least 120 bp in length, and that had at least 65% pairwise sequence identity across land plants (see Breinholt et al. 2021). The library construction, targeted enrichment, and sequencing were all done by RAPiD Genomics (Gainesville, Florida) as part of the NSF-funded Genealogy of Flagellate Plants (GoFlag) project. After a bead-based DNA cleanup step, DNA was normalized to 250 ng and sheared to an average size of 300 base pairs (bp). Illumina-comparable libraries were constructed by repairing the ends of the sheared fragments followed by the addition of an adenine residue to the 3'-end of the blunt-end fragments (Bentley et al. 2008). Barcoded adapters suited for the Illumina sequencing platform were ligated to the libraries, and ligated fragments were PCR-amplified 9–11 cycles. Target enrichment was performed using the *GoFlag 408* probes following protocols based on Gnirke et al. (2009). After enrichment, samples were re-amplified for additional 6–12 cycles. All enriched samples were sequenced using an Illumina HiSeq 3000 with paired-end 100 bp reads. The sequence reads were deposited in the NCBI sequence read archive (SRA; BioProject 646399).

The raw reads were cleaned and assembled into sequence alignments containing both the targeted exon regions and the more variable flanking intron regions using the six-step iterative baited assembly pipeline described in Breinholt et al. (2021). In short, first adapters and bases with Phred scores less than 20 were trimmed from the paired-end raw reads with Trim Galore! v. 0.4.4 (https://www.bioinformatics.babraham.ac.uk/projects/trim_galore/), and we retained only pairs of reads in which both the forward and reverse read were at least 30 bp long. Next, raw reads with significant homology to each exonic target region based on reference transcriptome sequences were identified using USEARCH v. 7.0 (Edgar 2010), and then an iterative (3×) de novo assembly was performed with the set of homologous reads for each target locus with BRIDGER v. 2014–12–01 (Chang et al. 2015). The BRIDGER kmer size parameter was 25, and the minimum depth of coverage for the kmers to be included in the assembly was 10. We assessed orthology of the assembled sequences based on the best tblastx (Camacho et al. 2009) hit of the exonic target region of each assembled sequence to the coordinates of nine plant genomes representing hornworts, liverworts, mosses, lycophytes, ferns, and gymnosperms. We called an assembled sequence an ortholog of the probe region if it had no additional tblastx hits with $> 95\%$ of the best bit score, outside of a 1000 base pair flanking window around the genomic coordinates of the exonic target locus in any one of the reference genomes. Next, to filter out likely contaminants, for each assembled sequence we performed a tblastx search against the respective reference sequences for that locus. If a sequence's best hit was not a fern, that sequence was removed as a potential contaminant. Finally, we aligned the resulting sequences using MAFFT v. 7.425 (Katoh and Standley 2013). Alignments were done for the full sequences, which included the exonic target loci and flanking intron sequences. After the alignments, sequences from the same taxon with mismatches due to heterozygous sites were merged using nucleotide ambiguity codes to represent heterozygous sites. All the pipeline scripts with instructions are available on Dryad (Fawcett et al. 2021).

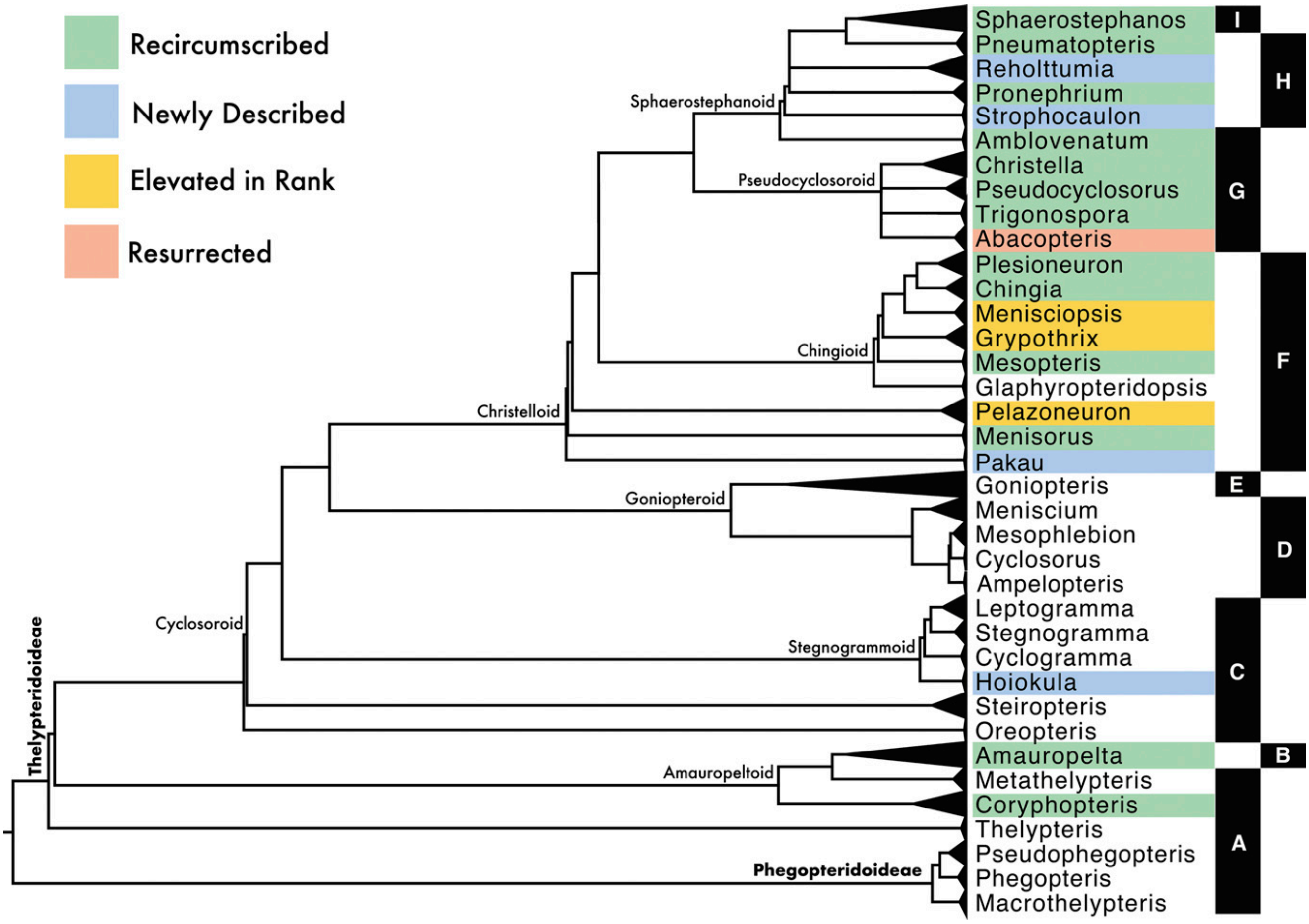

FIG. 2. A synoptical ML 1000 bootstrap consensus tree inferred from the 407-locus concatenated alignment illustrating relationships among genera of the Thelypteridaceae, and identifying major clades. Colors correspond to genera that underwent recent taxonomic changes. Letters indicate position in Figs. 3A–3I.

In some cases, after running the pipeline, a sample will have more than one sequence in locus alignment where the BRIDGER assembler identified potentially more than simple allelic variation. To minimize the possible effects of paralogy, in these cases, for each locus, we only retained sequences from samples with a single copy. We also removed any loci with sequences from fewer than 25 samples, and within each locus alignment, we removed any columns with fewer than 25 nucleotides. We then concatenated all the locus alignments into a supermatrix for phylogenetic analysis. One locus was inadvertently duplicated in the probe design process (Loci 91 and 92 are identical). The scripts used to perform these post-processing steps, as well as the resulting supermatrix, are available on Dryad (Fawcett et al. 2021).

Phylogenetic Analyses—The supermatrix was analyzed using maximum likelihood (ML) implemented in IQ-Tree v. 2.0.3 for Linux (Minh et al. 2020), with partitions representing each locus. We chose the edge-linked proportional substitution model, and GTR + F with separate rates for each partition was inferred by ModelFinder (Chernomor et al. 2016; Kalyaanamoorthy et al. 2017). Ultrafast bootstrap approximation with 1000 iterations (Minh et al. 2013; Hoang et al. 2017) was used to assess branch support. Ultrafast bootstrapping, which uses RELL (resampling estimated log-likelihoods) is a probabilistic approach, so we consider a minimum threshold of 95% to be "high support," in contrast to the lower threshold typically accepted for traditional bootstraps (Minh et al. 2013).

Maximum likelihood analyses were also performed on each of the 407 single-locus alignments in IQ-Tree. Gene concordance factors (gCF) and site concordance factors (sCF) were calculated using the ML tree inferred from the concatenated alignment (Fawcett et al. 2021). These metrics complement classical measures of branch support such as bootstraps by providing detailed information about the topological variation in the underlying data, while accounting for variable taxon coverage among gene trees. Concordance factors are especially useful for large phylogenomic datasets, because unlike bootstrap support, which tends to increase with the addition of loci, gCF and sCF are stable and informative with increasing sample size (Minh et al. 2020).

A species tree was inferred from the 407 individual ML gene trees using multi-species coalescence implemented in ASTRAL 5.7.3 (Fawcett et al. 2021; Zhang et al. 2017), and annotated with local posterior probabilities. Analyses were performed on the Vermont Advanced Computing Core at the University of Vermont and at the HiPerGator facility at the University of Florida. Raw sequence data were uploaded to the NCBI Sequence Read Archive, available at ncbi.nlm.nih.gov/bioproject/646399. The supermatrix alignment, partition file, multispecies coalescent analysis phylogeny, concordance analyses, and a spreadsheet of molecular vouchers are available on Dryad (Fawcett et al. 2021). Figures were created using FigTree v. 1.4.4. and Adobe Photoshop CC 2014.

RESULTS

Sequence Alignment—The supermatrix alignment of the Thelypteridaceae includes 621 total samples and 407 nuclear loci. Thirty-two samples initially included in the study were excluded. Among these, 14 were excluded because they amplified fewer than 50 loci. An additional 18 samples were excluded because they were resolved among outgroup taxa in preliminary phylogenetic analyses, and/or were on extremely long branches, likely indicating low sequence quality or contamination. In the remaining 621 samples, the average number of loci per included taxon is 378 (out of a possible 407), with a minimum of 113. An average of 5% of sequences per sample were discarded as possible paralogs. We found no significant difference ($t = -0.757$, $p = 0.449$) in the number

TABLE 1. A comparison of the classification system proposed by Fawcett and Smith (2021) to that of PPG I (2016), which largely follows He and Zhang (2012) and Holttum (1974, 1977, 1982) for the Old World, and Almeida et al. (2016) for the New World. Names in bold indicate new or recircumscribed genera. An asterisk (*) indicates a resurrected synonym, (**) indicates sections elevated in rank to genera, and (***) indicates newly described genera.

Fawcett and Smith 2021	PPG I (2016)
Abacopteris*	***Pronephrium***
Amauropelta	***Amauropelta, Parathelypteris***
Amblovenatum	***Amblovenatum***
Ampelopteris	*Ampelopteris*
Chingia	***Chingia, Amblovenatum, Plesioneuron***
Christella	***Christella, Pelazoneuron, Menisciopsis***
Coryphopteris	***Coryphopteris***
Cyclogramma	*Cyclogramma*
Cyclosorus	*Cyclosorus*
Glaphyropteridopsis	*Glaphyropteridopsis*
Goniopteris	*Goniopteris*
Grypothrix**	***Pronephrium***
Hoiokula***	***Pneumatopteris***
Leptogramma*	***Stegnogramma***
Macrothelypteris	*Macrothelypteris*
Menisciopsis**	***Pronephrium, Christella***
Meniscium	*Meniscium*
Menisorus	***Menisorus, Pneumatopteris***
Mesophlebion	*Mesophlebion*
Mesopteris	***Mesopteris, Amblovenatum***
Metathelypteris	*Metathelypteris*
Oreopteris	*Oreopteris*
Pakau***	***Pneumatopteris***
Pelazoneuron**	***Christella***
Phegopteris	*Phegopteris*
Plesioneuron	***Plesioneuron, Pneumatopteris, Chingia***
Pneumatopteris	***Pneumatopteris***
Pronephrium	***Pronephrium, Nannothelypteris***
Pseudocyclosorus	*Pseudocyclosorus*
Pseudophegopteris	*Pseudophegopteris*
Reholttumia***	***Pneumatopteris***
Sphaerostephanos	***Sphaerostephanos, Pneumatopteris, Pronephrium, Strophocaulon***
Stegnogramma	***Stegnogramma***
Steiropteris	*Steiropteris*
Strophocaulon***	***Sphaerostephanos***
Thelypteris	*Thelypteris*
Trigonospora	*Trigonospora*

of loci recovered from tissue that was silica-dried in the field (mean loci = 379, N = 375) or tissue taken from herbarium specimens (mean loci = 377, N = 246), and the age of the specimen had little effect on the number of loci recovered ($R^2 = 0.03$, $p = 0.007$). The oldest specimen sequenced for this study was collected in 1889. The final supermatrix alignment (exons plus flanking regions) included 621 samples with 533,059 nucleotide sites, and is 49.6% full; 61% of these sites are parsimony-informative, 16% are singletons, and 23% are invariant. The supermatrix alignment and data organized by voucher specimen and by locus are available on Dryad (Fawcett et al. 2021).

Phylogenetic Analyses—The topologies of the phylogenetic trees inferred both through maximum likelihood analysis of the concatenated matrix (Figs. 2, 3) and multi-species coalescent analysis (Fawcett et al. 2021) are largely congruent with each other and with previously published trees based primarily on Sanger sequencing of cpDNA (Smith and Cranfill 2002; He and Zhang 2012; Almeida et al. 2016; Patel et al. 2019). Our focus on problematic taxa, a three-fold increase in taxon sampling, and a large nuclear DNA dataset enabled us to find support for previously unresolved nodes and provides evidence for the resolution of many previously intractable taxonomic problems.

The average bootstrap support for all nodes in the ML analysis was 97%. All crown nodes corresponding to our generic classification have 100% bootstrap support except *Christella* (92%). Some upper backbone nodes are variable or have low support (e.g. the chingioid clade (Figs. 2, 3F) has 100% BS support, but low concordance factors, gCF = 0.5, sCF = 35), and a few rogue taxa are present, discussed in detail below. The two subfamilies Phegopteridoideae and Thelypteridoideae each resolve as monophyletic if the root is placed between them, as done here based on robust results of previous phylogenetic analyses (Smith and Cranfill 2002; He and Zhang 2012; Almeida et al. 2016).

To evaluate the tree, and to better understand widespread species throughout their ranges, we included multiple accessions of 77 species in the analyses. All species represented by multiple accessions resolved within the expected genus-level clade. Among these, more than half of species represented by more than one accession (N = 40) form a clade, as expected. Of the remainder, an additional 21 had a near sister relationship in the phylogeny, while 13 were resolved as less closely related. Three additional species represented by more than two accessions resolved in a combination of the above states. Some of these species include varieties that are not sister to the typical variety of that species (e.g. *Christella patens*, *Christella ovata*, and *Steiropteris glandulosa*). In other cases, currently accepted species concepts are broadly applied, and are potentially polyphyletic (e.g. *Chingia longissima* and *Coryphopteris japonica*). Other widespread and variable taxa, however, were resolved as monophyletic; for example, all three varieties of *Christella hispidula*, comprising seven accessions from its native range in North America, South America, Africa, and Malesia, constitute a clade.

Assessment of PPG I Genera—A primary goal of this study is to test the taxonomic hypotheses of the Thelypteridaceae proposed by PPG I (2016). Of the 30 genera in that classification, 17 are supported without modification. These include *Ampelopteris, Coryphopteris, Cyclogramma, Cyclosorus, Glaphyropteridopsis, Goniopteris, Macrothelypteris, Meniscium, Mesophlebion, Metathelypteris, Oreopteris, Phegopteris, Pseudocyclosorus, Pseudophegopteris, Steiropteris, Thelypteris*, and *Trigonospora*. The remaining 13 genera sensu PPG I (2016) are presented below, with an explanation of their phylogenetic status. To facilitate the communication of phylogenetic results, major clades have been given informal names (Fig. 2), several of which have been applied in previous molecular analyses of the family (e.g. Smith and Cranfill 2002; Almeida et al. 2016; Patel et al. 2019; Fawcett and Smith 2021) and a summary of changes is provided in Table 1. All taxonomic authorities for species included in the analyses are listed in the appendix.

Amauropelta—Although *Amauropelta* is monophyletic, the genus *Parathelypteris* is not, with some species nested within *Coryphopteris* and others in three well supported clades along a basal grade terminating in all sampled species of *Amauropelta* s. s. Although each of these three clades is well supported, their relationships to one another are in conflict among individual gene trees (Fig. 3B; Fawcett et al. 2021).

Amblovenatum—The members of this genus (homotypic synonym: *Amphineuron*) resolve in two distantly related clades; one includes the type species *Amblovenatum*

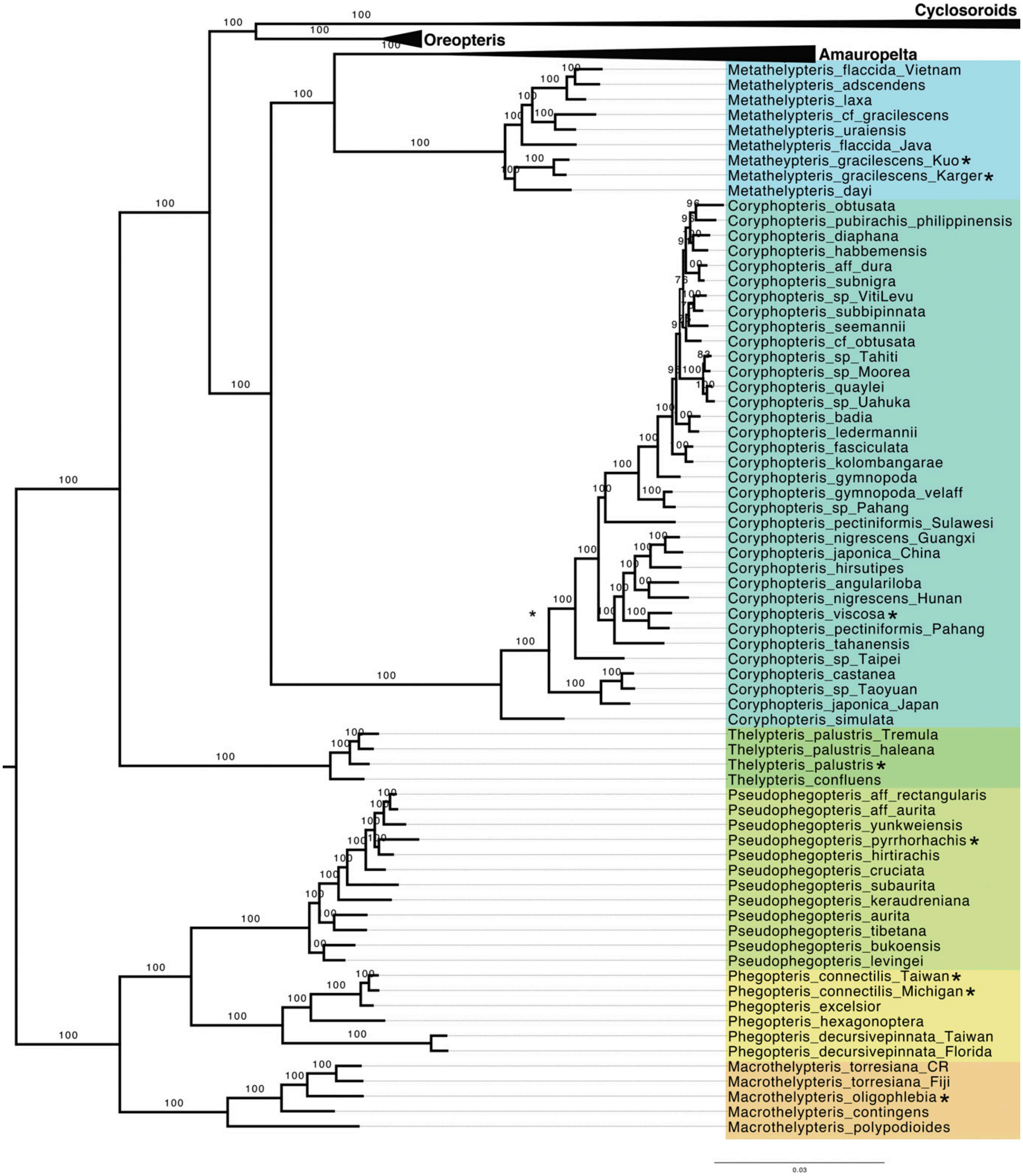

FIG. 3A. The Phegopteridoideae (*Macrothelypteris*, *Phegopteris*, and *Pseudophegopteris*) and early diverging genera of the Thelypteridoideae in the maximum likelihood phylogeny of the 407-locus concatenated alignment. The nodes are annotated with ultrafast bootstrap support values, and genera are emphasized by distinct colors. Type species of genera are denoted with an asterisk (*).

opulentum, but the others resolve with the previously monotypic genus *Mesopteris tonkinensis*. The phylogenetic position of *Amblovenatum* s. s. variously resolves among sphaerostephanoids in the ML bootstrap consensus (Fig. 2), but as sister to sphaerostephanoids plus pseudocyclosoroids in the ML tree (Fig. 3G) and coalescent tree (Fawcett et al. 2021).

CHINGIA—This genus represents a well-supported, nearly exclusive clade, except that a single species (unusual in having fully bipinnate laminae), *Plesioneuron marattioides*, is nested within it.

CHRISTELLA—The members of *Christella* resolve in four distantly related clades (Fig. 4), with the predominantly Asian group corresponding to *Christella* sect. *Christella*, and mostly

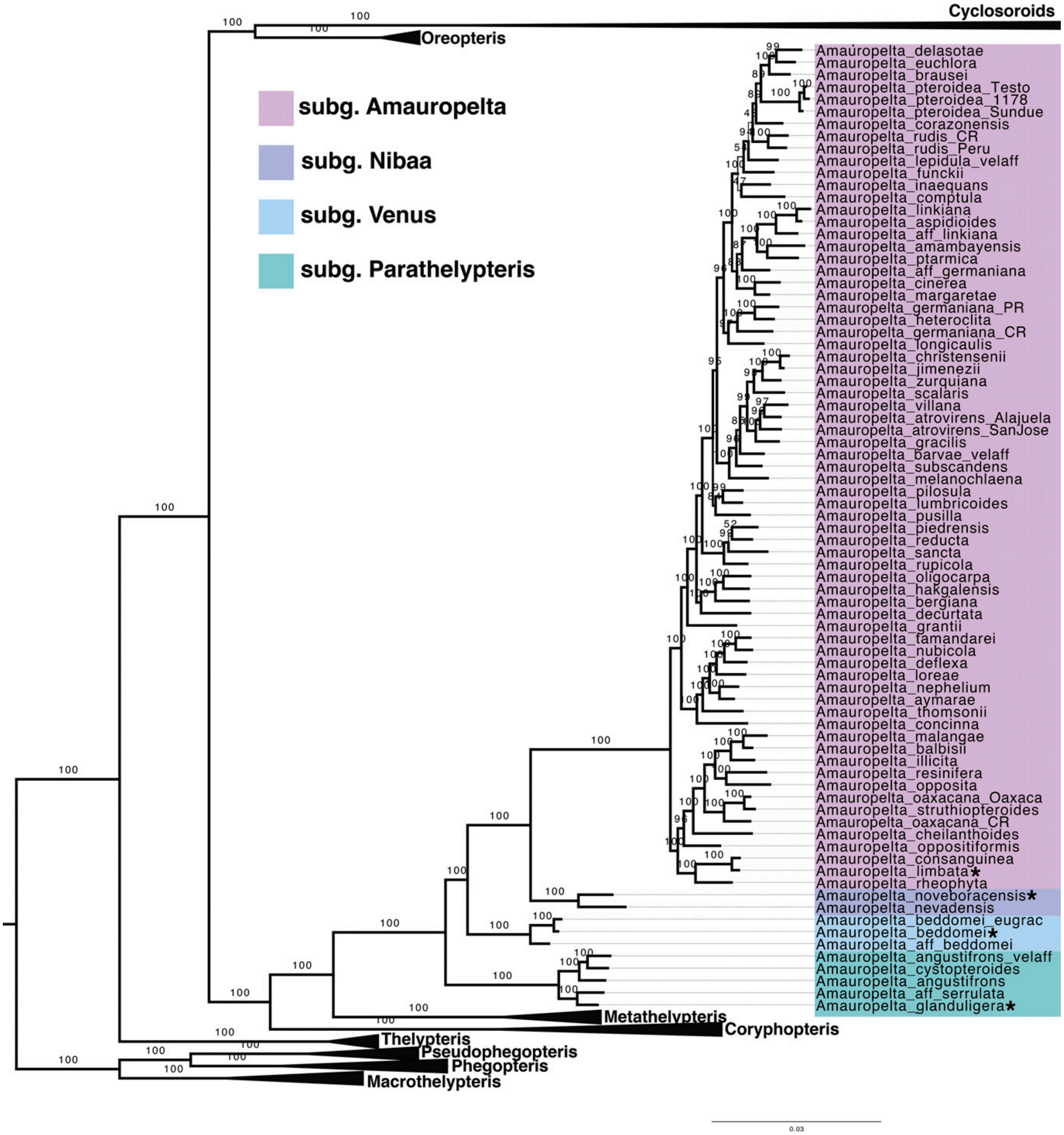

FIG. 3B. The genus *Amauropelta* in the maximum likelihood phylogeny of the 407-locus concatenated alignment. The nodes are annotated with ultrafast bootstrap support values, and colors correspond to subgenera of *Amauropelta* proposed by Fawcett and Smith (2021). Type species of genera and subgenera are denoted with an asterisk (*).

neotropical species corresponding to *Christella* sect. *Pelazoneuron*. A small group of African species including *C. chaseana* and *C. gueintziana* resolves as sister to *Christella* sect. *Christella* in most trees, but there is some conflicting support for these species as members of the pseudocyclosoroid clade. The three endemic Hawaiian *Christella* species resolve with members of *Pronephrium* s. l.

Menisorus—This previously monotypic African genus had never been included in a molecular phylogenetic study. It is sister to another African species that also has proliferous buds, *Pneumatopteris unita* (Kunze) Holttum (Fig. 3F).

Mesopteris—Considered a monotypic genus endemic to China and neighboring Vietnam, this taxon is sister to two species of *Amblovenatum* from Malesia, but this clade is distantly related to the type of that genus, *A. opulentum* (Figs. 3F, 3G).

Nannothelypteris—The type of this genus, *N. aoristisora*, is nested within a clade of *Pronephrium* that includes several species that are morphologically similar to the type of that genus, *P. lineatum* (Blume) C. Presl (Fig. 3H).

Parathelypteris—The members of this genus resolve in five distinct clades (Figs. 3A, 3B); two of these resolve

FIG. 3C. The genus *Oreopteris*, and non-christelloid members of the cyclosoroid clade, including the stegnogrammoid subclade (*Hoiokula*, *Cyclogramma*, *Stegnogramma*, and *Leptogramma*) in the maximum likelihood phylogeny of the 407-locus concatenated alignment. The nodes are annotated with ultrafast bootstrap support values, and genera are emphasized by distinct colors. Type species of genera are denoted with an asterisk (*).

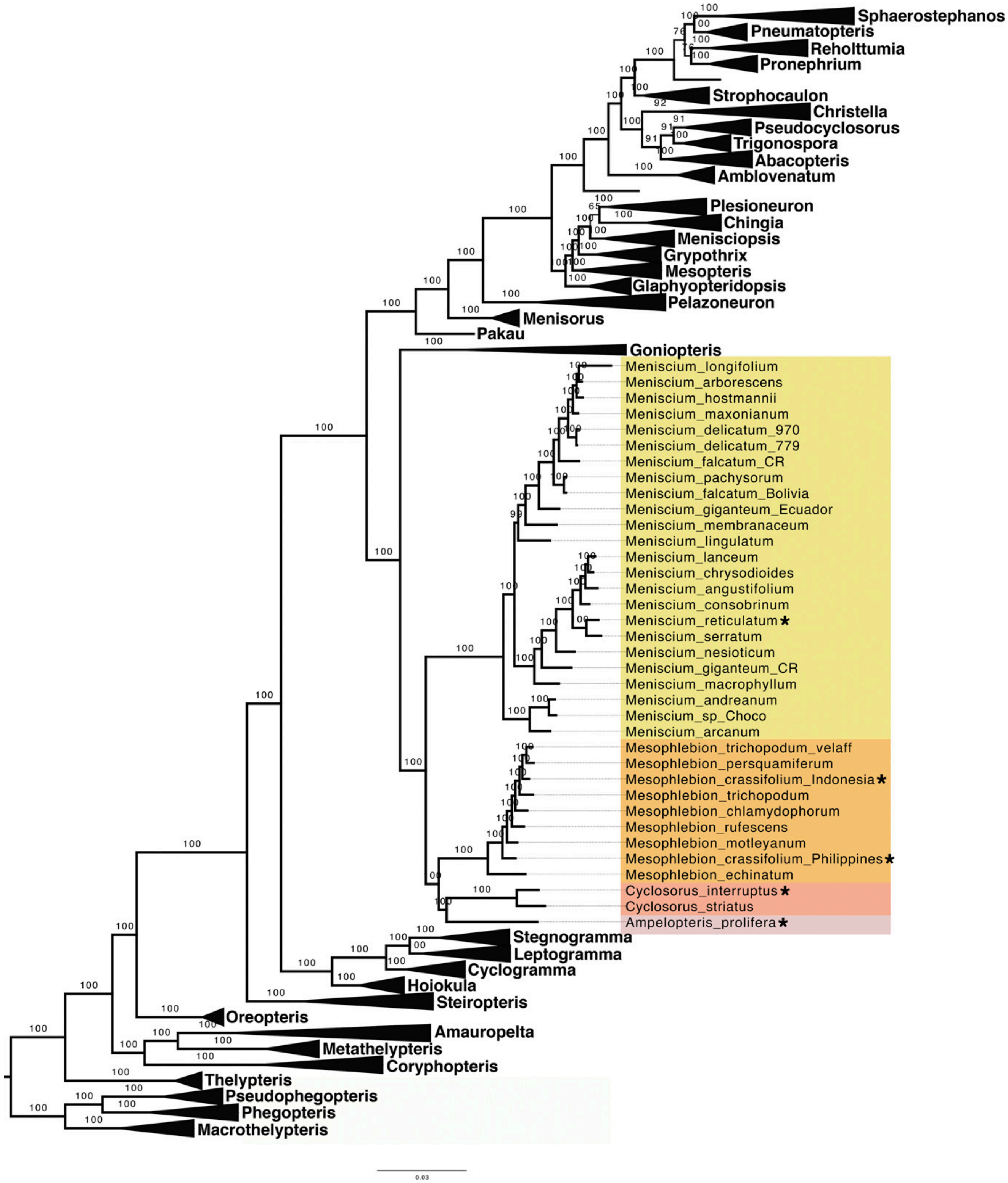

FIG. 3D. Members of the goniopteroid clade in the maximum likelihood phylogeny of the 407-locus concatenated alignment. The nodes are annotated with ultrafast bootstrap support values, and genera are emphasized by distinct colors. Type species of genera are denoted with an asterisk (*).

among species of *Coryphopteris* and the other three clades include the North American sister species *P. noveboracensis* (L.) Ching and *P. nevadensis* (Baker) Holttum, which are sister to *Amauropelta*, and two Asian clades, one including the type species *P. glanduligera* (Kunze) Ching, and the other including *P. beddomei* (Baker) Ching. Although each of these three clades is well supported as monophyletic, the relationships among them (*Amauropelta* plus North American *Parathelypteris* and the two Asian clades) are in conflict among individual gene trees (Fawcett et al. 2021).

Plesioneuron—Sequence data were available for only a single species of *Plesioneuron* when PPG I (2016) was published. This genus as recognized by PPG I (2016) corresponds to a nearly exclusive clade with the exception of *Pneumatopteris*

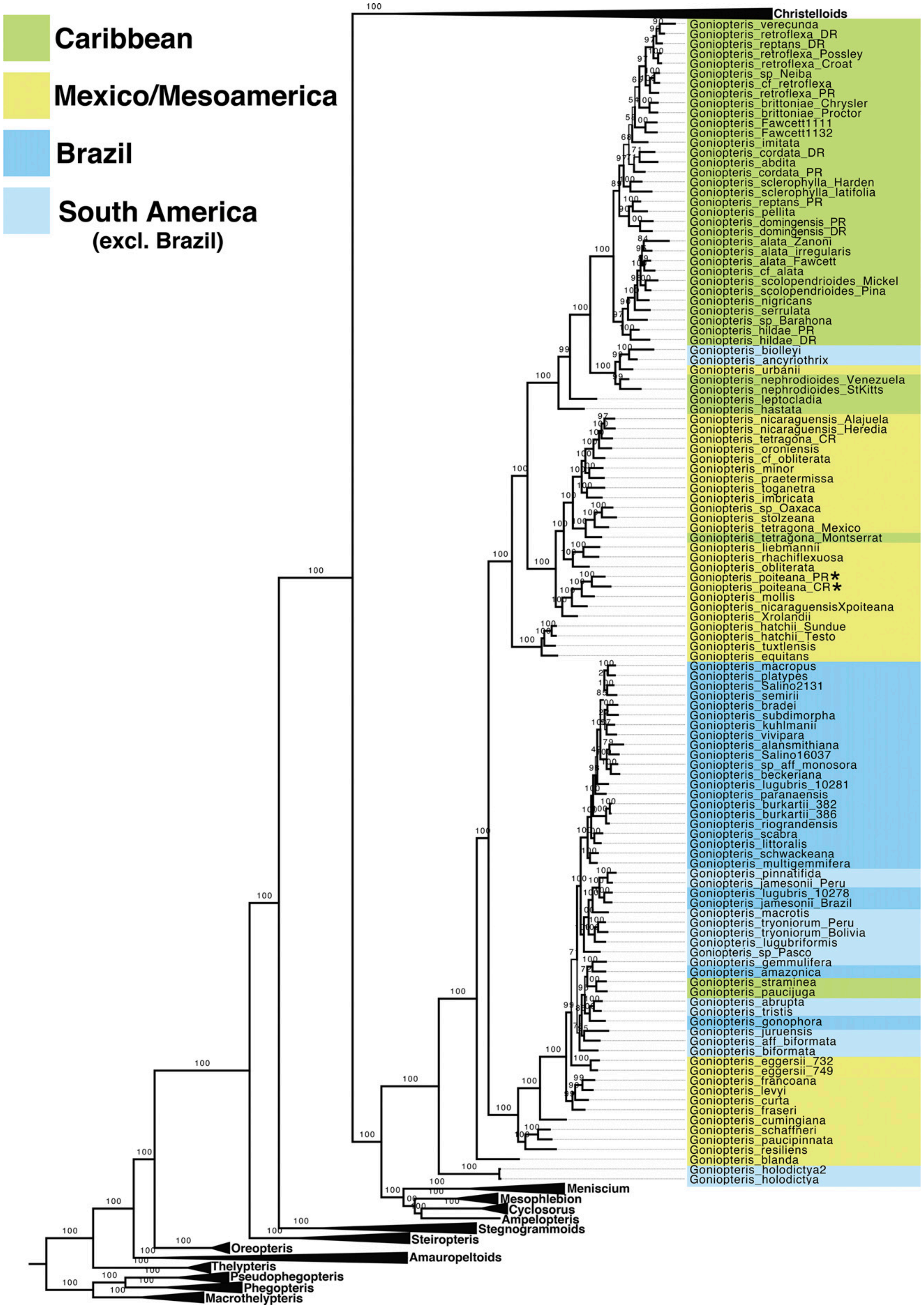

FIG. 3E. The genus *Goniopteris* in the maximum likelihood phylogeny of the 407-locus concatenated alignment. The nodes are annotated with ultrafast bootstrap support values, and the colors correspond to geographic regions where the molecular vouchers were collected. Type species of genera are denoted with an asterisk (*).

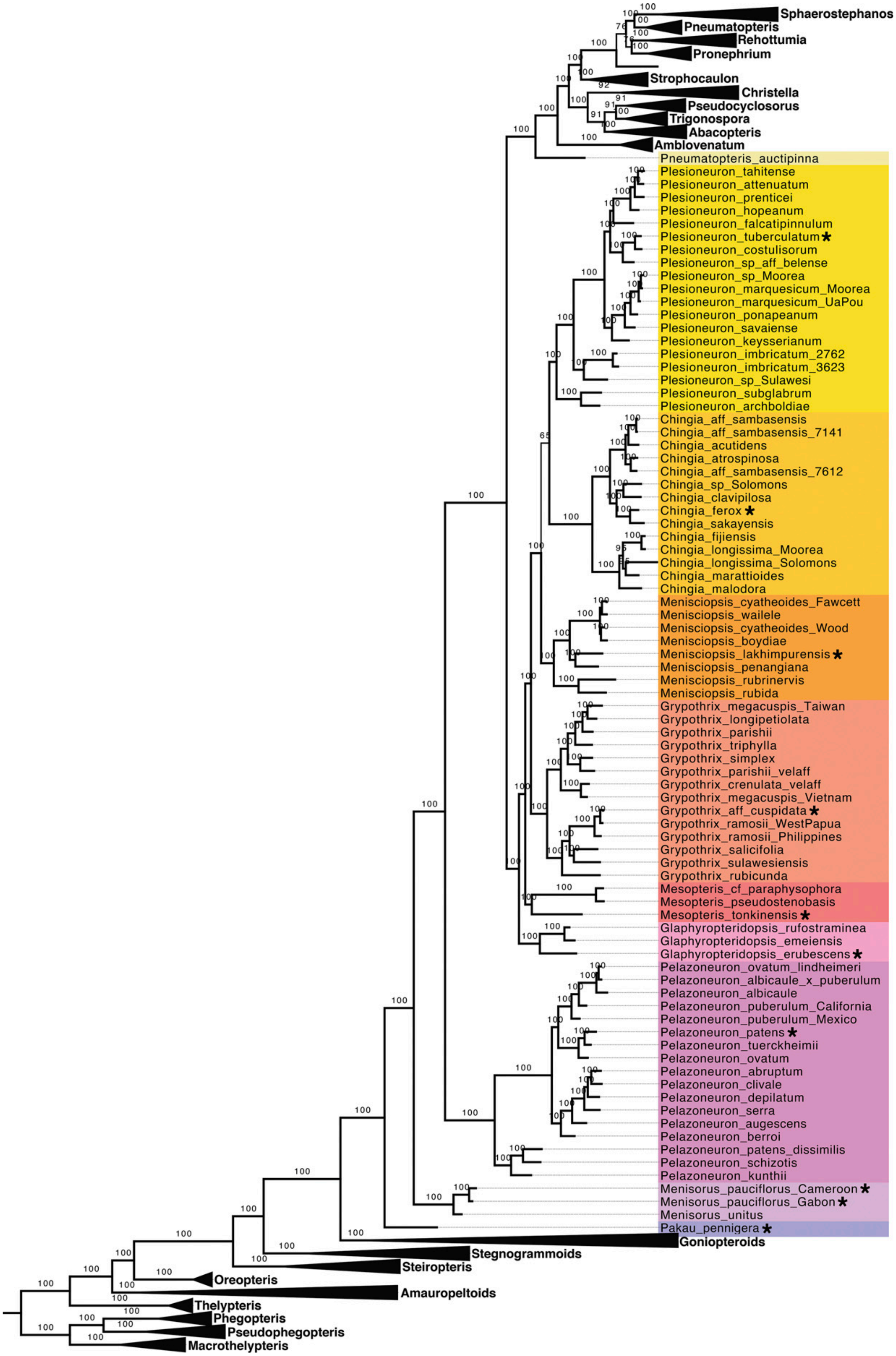

FIG. 3F. The monotypic genus *Pakau*, and the members of the chingioid clade in the maximum likelihood phylogeny of the 407-locus concatenated alignment. The nodes are annotated with ultrafast bootstrap support values, and genera are emphasized by distinct colors. Type species of genera are denoted with an asterisk (*).

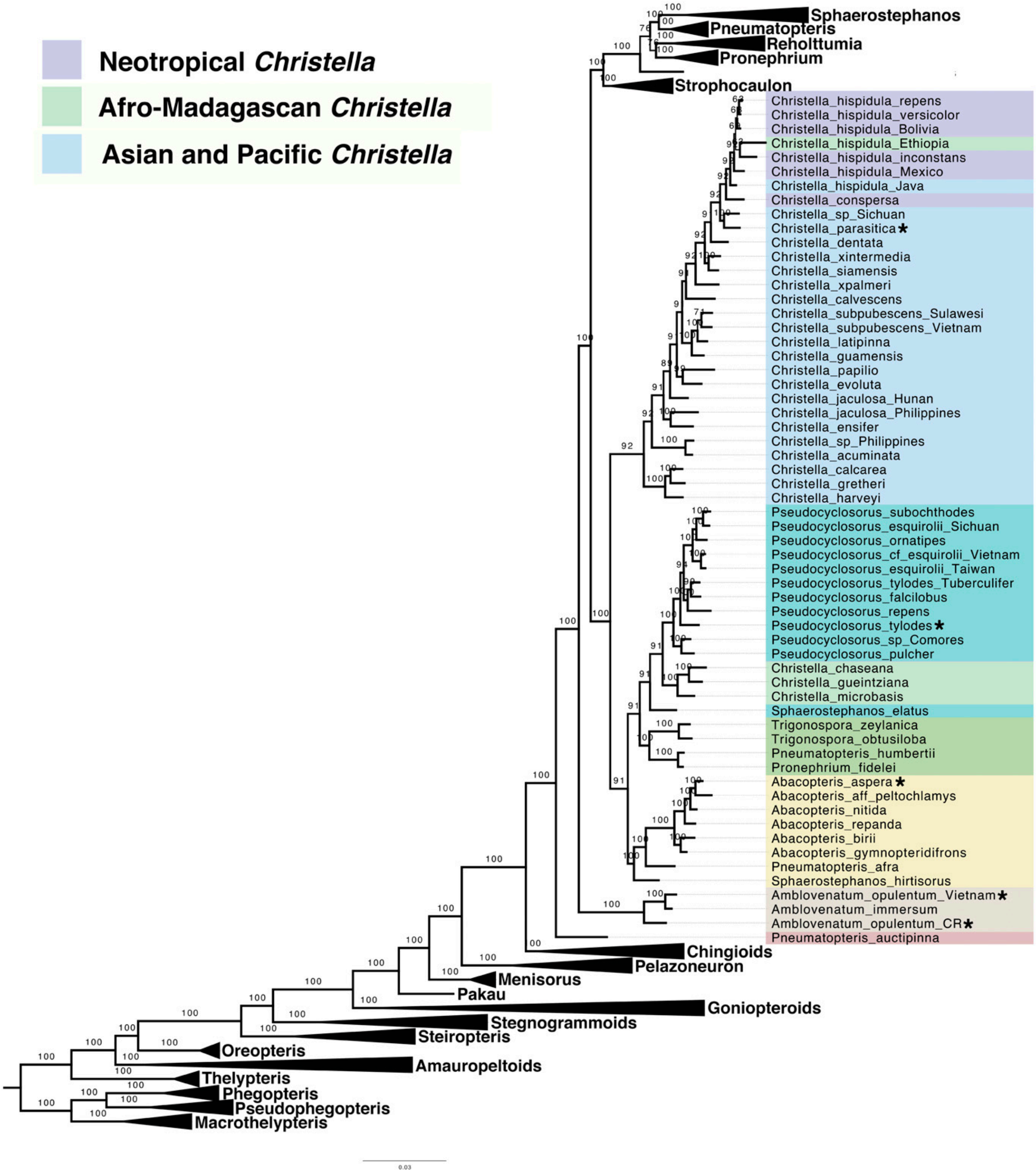

FIG. 3G. The genus *Amblovenatum*, and members of the pseudocyclosoroid clade in the maximum likelihood phylogeny of the 407-locus concatenated alignment. The nodes are annotated ultrafast bootstrap support values, and colors indicate the biogeographic affinities of *Christella* s. s., and emphasize major clades. The position of several lineages (e.g. *Amblovenatum*, the clade of three African *Christella* species) differs in the ML bootstrap consensus tree and/or the multispecies coalescent tree (Fawcett et al. 2021). Type species of genera are denoted with an asterisk (*).

keysseriana Holttum, which is nested within it, and *Plesioneuron marattioides* (Alston) Holttum, which resolves in *Chingia* (Fig. 3F).

PNEUMATOPTERIS—This is by far the most polyphyletic genus recognized by Holttum (1971) and PPG I (2016) (Fig. 4). Its species are scattered in more than a dozen lineages throughout the tree, resolving within clades corresponding to *Menisorus*, *Plesioneuron*, and *Sphaerostephanos*. Three lineages are distinct and do not fall within currently recognized genera: two Hawaiian species are sister to *Stegnogramma* plus *Cyclogramma*; the New Zealand and Australian endemic *Pneumatopteris pennigera* (G. Forst.) Holttum resolves on a

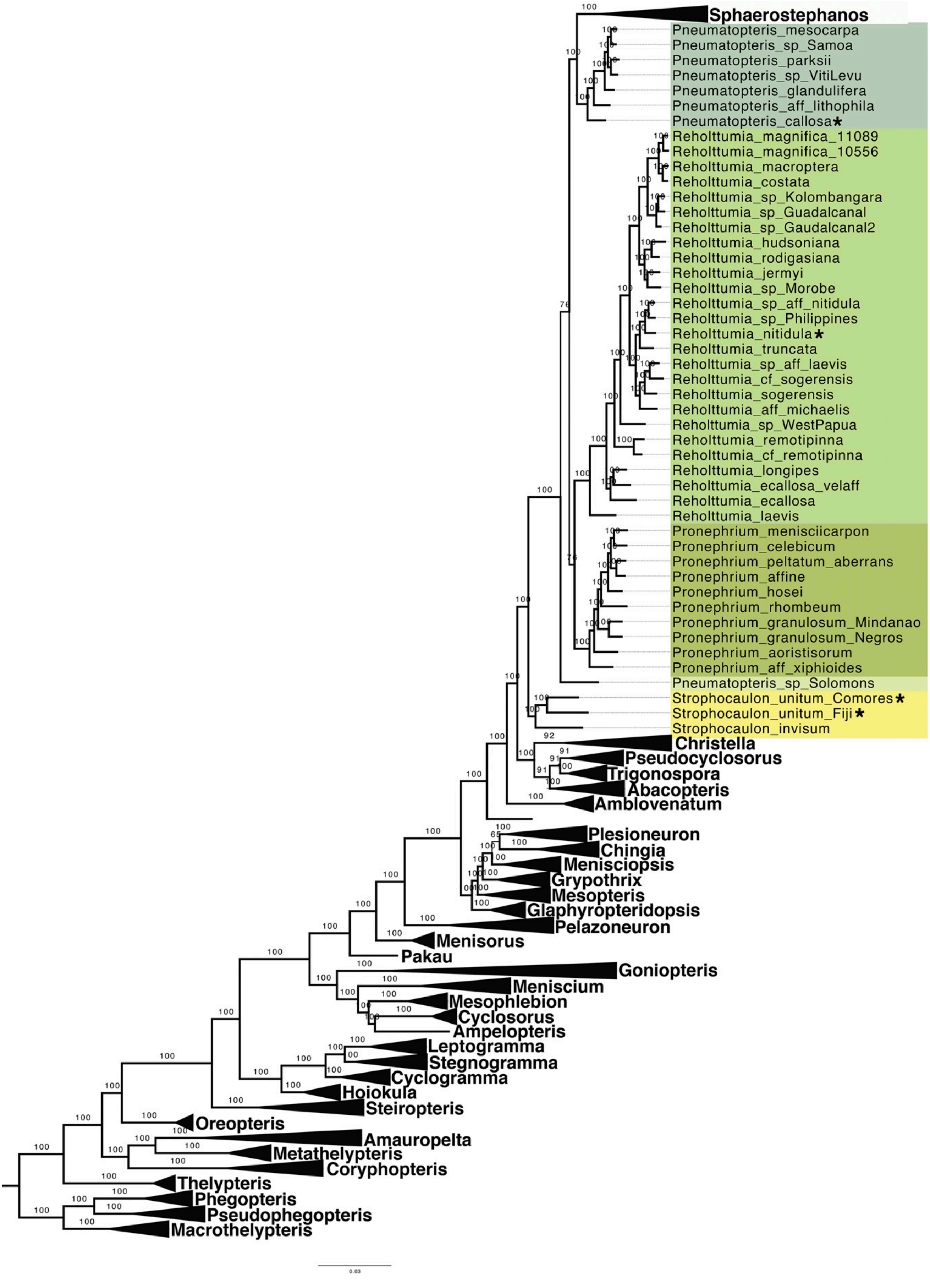

FIG. 3H. Members of the sphaerostephanoid clade in the maximum likelihood phylogeny of the 407-locus concatenated alignment. The nodes are annotated with ultrafast bootstrap support values, and genera are emphasized by distinct colors. Type species of genera are denoted with an asterisk (*).

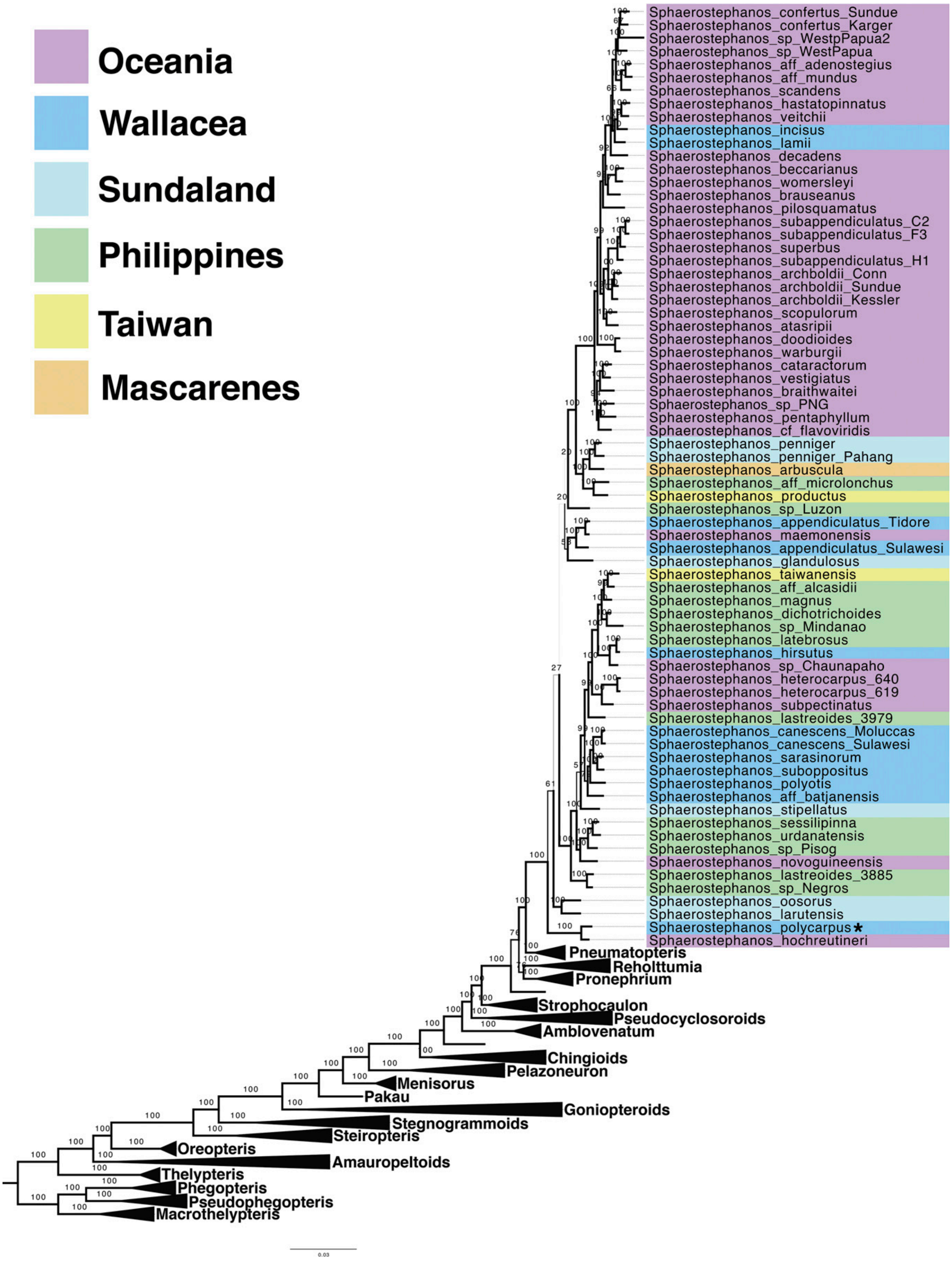

FIG. 3I. The genus *Sphaerostephanos* in the maximum likelihood phylogeny of the 407-locus concatenated alignment. The nodes are annotated ultrafast bootstrap support values, and colors correspond to biogeographical regions illustrated by Mayr (1944), corresponding to collection localities of the molecular vouchers. Type species of genera are denoted with an asterisk (*).

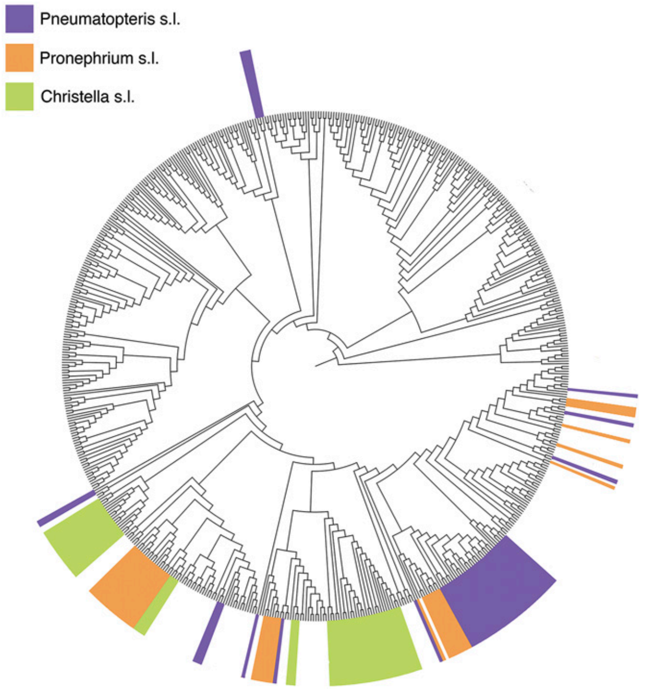

FIG. 4. A phylogeny of the Thelypteridaceae illustrating the polyphyly of *Christella*, *Pneumatopteris*, and *Pronephrium* sensu PPG I (2016), and their recently proposed disposition (Fawcett and Smith 2021).

long branch at the base of the christelloid clade; and the majority of species constitute a single clade sister to *Sphaerostephanos* plus a relatively small clade of primarily Pacific Island *Pneumatopteris* species including the type species, *P. callosa*. Other taxa resolve as sister to *Trigonospora*, or to one of the four clades of *Pronephrium*, while two other taxa, *Pneumatopteris auctipinna* and an undescribed species from the Solomon Islands, resolve on long branches diverging from the backbone within the christelloid clade, but with low support.

PRONEPHRIUM—The members of this polyphyletic genus all share once-pinnate fronds with entire to shallowly incised margins, but its species resolve in four distinct, well-supported clades, while a few species are scattered throughout the *Sphaerostephanos* clade (Figs. 3H, 4). One of these four clades corresponds perfectly to *Pronephrium* sect. *Grypothrix*, and the other three correspond in part to the infrageneric taxa of *Pronephrium* proposed by Holttum (1982). Although the type species, *P. lineatum* (Blume) Presl, was not sampled, the type specimen exhibits the combination of dimorphic fronds and the presence of yellow spherical glands on the sporangia, which are characteristic of *Pronephrium* sensu Fawcett and Smith (2021) and are uncommon among other genera.

SPHAEROSTEPHANOS—Most members of this large and morphologically complex genus represent a nearly exclusive clade (Fig. 3I). Several species recognized in *Pronephrium* and *Pneumatopteris* fall within it, and two distinctive, widespread species with long-creeping rhizomes, *S. unitus* (L.) Holttum and *S. invisus* (G. Forst.) Holttum, form a clade sister to the core christelloids (the sphaerostephanoids, pseudocyclosoroids, plus *Amblovenatum*) (Fig. 3H). A few species, mainly of India and Africa, resolve variously in the christelloid or pseudocyclosoroid clades (Fig. 3G).

STEGNOGRAMMA—This genus (including *Leptogramma* and *Dictyocline* T. Moore) is monophyletic as recognized by PPG I (2016). However, our phylogenetic results lend equal support for the recognition of two sister genera, *Stegnogramma* (including *Dictyocline*) and *Leptogramma* (Fig. 3C).

Discordance Among Gene Trees—Congruence among gene trees, and among phylogenies inferred using concatenated and coalescent methods, was generally high, but with conflicting support for some taxa and clades (Fawcett et al. 2021). The average gene concordance factor (gCF) for crown nodes corresponding to genera is 43%. The highest gCF values corresponded to species-poor genera on long branches, exemplified by *Thelypteris* s. s. (gCF = 98%), while the lowest value was seen in *Christella* (gCF = 0.25%), a clade which contains rogue taxa (discussed below). The average site concordance factor (sCF) for generic clades is 69%, ranging from 97% in *Cyclosorus* s. s. to 32% in *Ampelopteris*.

Among taxa with conflicting support is a small group of African species, including *Christella gueintziana* and *C. chaseana*, which resolve as sister to the rest of *Christella* sect. *Christella* in the coalescent analysis; however, these species sometimes resolve within the pseudocyclosoroid clade in individual gene trees and in the ML tree (Fig. 3G). The conflicting position of this rogue clade contributes to the uniquely low bootstrap support of the crown node of *Christella*. There is also some conflict among gene trees for *Christella* (*Pelazoneuron*) *kunthii*, *C.* (*P.*) *schizotis*, and *C.* (*P.*) *patens* var. *dissimilis*; all three are supported as members of the *Pelazoneuron* clade, but are also inferred to be members of the *Christella* sect. *Christella* clade in some individual gene trees.

The phylogenetic position of the clade comprising three species of *Amblovenatum* s. s. resolve variously in the sphaerostephanoid clade in the ML bootstrap consensus tree, (Fig. 2) and coalescent tree (Fawcett et al. 2021), or as sister to the sphaerostephanoids plus pseudocyclosoroids (ML tree, Fig. 3G).

Two of the Hawaiian species of *Pneumatopteris* resolve as sister to *Stegnogramma* plus *Cyclogramma* with 100% support in both concatenated and coalescent analyses; however, individual gene trees resolve these species as nested among members of *Pronephrium* or highly nested within *Leptogramma*.

Finally, a few morphologically aberrant taxa of Africa, Madagascar, and India resolve as sister to large clades with low support, and often are in conflicting positions among individual gene trees. These include *Sphaerostephanos elatus*, *Sphaerostephanos hirtisorus*, and *Pneumatopteris afra*; all three are rogue taxa within the pseudocyclosoroid clade (Fig. 3G).

DISCUSSION

Support for Taxonomic Revision—Our results support the continued recognition of 17 of the 30 genera of the Thelypteridaceae as circumscribed by PPG I (2016), and taxonomic revision of the remaining 13 genera (Table 1), as proposed by Fawcett and Smith (2021). Two of these genera, *Parathelypteris* (H.Ito) Ching, and *Nannothelypteris* Holttum, we treat in synonymy. Of the remaining 11 genera, some require only minor revisions to be monophyletic, while others, notably *Pneumatopteris* and *Pronephrium*, require more substantial changes. We recognize four recently described genera, *Hoiokula, Pakau, Reholttumia*, and *Strophocaulon*. We recommend the elevation in rank from section to genus for *Christella* sect. *Pelazoneuron*, *Pronephrium* sect. *Grypothrix*, and *Pronephrium* sect. *Menisciopsis* Holttum, and the resurrection of the genus *Abacopteris*. We recognize the expanded circumscription of *Amauropelta* to include *Parathelypteris* pro parte, and recognize three new subgenera within *Amauropelta*. All necessary taxonomic combinations, a key to genera, and descriptions of the 37 genera here recognized are available in Fawcett and Smith (2021). These genera, which include ca. 1200 species worldwide, are recognized on the basis of both monophyly, and improved morphological diagnosability. A brief discussion of newly recognized genera and subgenera follows:

Abacopteris—This genus was treated as a synonym of *Pronephrium* by Holttum (1971, 1982), but based on the morphology of the type species, *Pronephrium lineatum*, we recognize *Pronephrium* s. s. as a member of the distantly related sphaerostephanoid clade. *Abacopteris*, in the sense we apply the name, is more closely allied to *Christella* and *Pseudocyclosorus* (Fig. 3G).

Amauropelta—Following Kuo et al. (2019) we expand the concept of *Amauropelta* to include three paraphyletic clades of *Parathelypteris*, now treated as *Amauropelta* subg. *Nibaa* (the two North American species), *Amauropelta* subg. *Parathelypteris* (including the type of *Parathelypteris*, *P. glanduligera*), and *Amauropelta* subg. *Venus* (including *P. beddomei*) (Fig. 3B).

Grypothrix—This genus corresponds perfectly to *Pronephrium* sect. *Grypothrix* (Holttum 1982), a group that is defined by hooked (hamate) hairs somewhere on the body of the plant. It is in the chingioid clade (Fig. 3F).

Hoiokula—This new genus corresponds to the two native Hawaiian species treated in *Pneumatopteris* by Holttum (1982) but are more closely related to *Leptogramma*, *Stegnogramma*, and *Cyclogramma* in our analyses (but see comments under Discordance Among Gene Trees) (Fig. 3C).

Leptogramma—Our data give equal support to the recognition of *Stegnogramma* s. l. or *Stegnogramma* s. s. plus *Leptogramma*. In light of the morphological differences between these two clades, we follow Kuo et al. (2020), in which the type species was sampled, in recognizing *Leptogramma* (including *Craspedosorus* Ching & W.M.Chu) as a distinct genus (Fig. 3C).

Menisciopsis—This genus includes continental Asian and Malesian members of the genus *Pronephrium* as well as the three Hawaiian endemic species of *Christella* (Fig. 3F).

Pakau—This monotypic genus corresponds to *Pneumatopteris pennigera*, which is endemic to New Zealand and eastern Australia. It occurs on a long branch, and is seemingly distantly related to any other taxon in the family (Fig. 3F).

Pelazoneuron—In his treatment of African Thelypteridaceae, Holttum (1974) described *Pelazoneuron* as a section of *Christella* comprising several African species he believed to be allied to neotropical taxa; he designated the American species *Christella patens* as the type of this section. Based on our results, neither those African taxa nor *Christella* sect. *Christella* are closely related to *C. patens*, but following Holttum's typification, this name corresponds to a well-defined group of American species (Smith 1971) (Fig. 3F).

Reholttumia—The greatest number of *Pneumatopteris* species resolve in this clade; however, the type of *Pneumatopteris*, *P. callosa*, is in a small clade more closely related to *Sphaerostephanos*, which is the older name. Rather than expand *Sphaerostephanos*, a polymorphic but recognizable genus already containing more than 200 species, we recognize this clade as a segregate of *Pneumatopteris* (Fig. 3H). Its name honors R. E. Holttum, whose keen insights and dedication laid the groundwork that made the present study possible.

Strophocaulon—This genus of two species includes only *Sphaerostephanos unitus* and *S. invisus*, (Fig. 3H) both of which are widespread and have long-creeping rhizomes (Fig. 1L), distinct from the short-creeping or ascending rhizomes typical of most species of *Sphaerostephanos* (Fig. 1K).

Discordance Among Gene Trees—Various factors may contribute to conflict among gene trees, including reticulation and introgression, gene duplication and loss, and incomplete lineage sorting (Degnan and Rosenberg 2009), horizontal gene transfer (Davis et al. 2005; Li et al. 2014, 2018), and error in gene tree inference. Different patterns of discordance may indicate either lack of support or conflicting support (Pease et al. 2018). For example, among recent rapid radiations, especially for species with large populations, incomplete lineage sorting may be expected, with stochastic patterns of conflict across gene trees. For taxa of hybrid origin, in contrast, gene trees may exhibit consistent patterns of conflicting support, e.g. a taxon resolving in two distinct (and rarely, highly divergent) clades. Because of the large size of our dataset, and the use of, at most, a single sequence to represent each taxon at each locus, we expect taxa of allopolyploid origin to resolve with one progenitor, or sister to a larger clade including a progenitor, with high support, as has been previously demonstrated in phylogenetic analyses that include hybrid taxa (McDade 1992). The primary goal of this study is to resolve generic circumscription, and the great degree of congruence among our gene trees gives us confidence in our conclusions. However, we are continuing to investigate the potential of hybrid origin for the small minority of rogue taxa and lineages.

Biogeographic Patterns—The taxonomic concepts proposed by Holttum and adopted by PPG I (2016) in some cases include geographically widespread and polymorphic genera, best exemplified by *Pneumatopteris* s. l., the range of which includes Hawaii, Africa, Madagascar, East Asia, and New Zealand. Holttum (1977: 226) was clearly aware of the distinctive morphology of its most aberrant species, regarded here as *Hoiokula* (Hawai'i), *Pakau* (Australia, New Zealand), *Plesioneuron* (Malesia and Oceania), and *Reholttumia* (scattered from Madagascar to Oceania). These genera were recognized only with the benefit of a molecular dataset to guide morphological observations. Our newly segregated genera tend to be more geographically restricted, as is the case for those mentioned above, two of which are endemic to regions beyond the range of *Pneumatopteris* s. s., which is restricted to Oceania and Malesia.

Regional geographic affinities, exemplified by *Goniopteris* (Fig. 3E) and *Amauropelta* subg. *Amauropelta*, show distinct phylogeographic patterns, with major clades largely restricted to the Caribbean, Mexico/Mesoamerica, the Andes, or Brazil. Other lineages (e.g. *Sphaerostephanos*; Fig. 3I) show much less clear-cut biogeographical patterns within and between clades, suggesting extensive dispersal and possibly also extinction events. This raises the intriguing question why some genera appear to undergo limited dispersal and extensive regional diversification, whereas others have a much more dynamic biogeographical history.

Classifying the Thelypteridaceae of Africa has proven to be especially challenging, partly because the present diversity has likely been shaped by high rates of extinction (Aldasoro et al. 2004), leaving a flora of disparate relicts that are difficult to contextualize within extant diversity. For example, the four Afro-Madagascan species of *Pneumatopteris* s. l. included in our analysis are each resolved in a distinct lineage, most closely allied to *Abacopteris*, *Menisorus*, *Reholttumia*, and *Trigonospora*; yet each is quite morphologically distinct from the typical species in each of these nearest clades.

Morphological Observations—The often subtle morphological characters needed to distinguish genera and identify species have contributed to the reputation of this family as taxonomically difficult (Fraser-Jenkins et al. 2017). Many of the genera can only be identified using a combination of characters, some seen only with the aid of a microscope, and the most salient features are often shared among distantly related taxa (Fawcett and Smith 2021). For example, all species within the genus *Pronephrium* s. l. share once-pinnate laminae with entire or shallowly incised pinna margins. However, our analyses demonstrate that members of *Pronephrium* s. l. resolve in distinct clades (Fig. 4), three of which are now recognized as the segregate genera *Abacopteris*, *Grypothrix*, and *Menisciopsis*, and others in multiple clades across *Sphaerostephanos*. In nearly all instances, these clades are more closely related to pinnate-pinnatifid taxa (the most common blade-division in the Thelypteridaceae) than they are to each other. These genera may be more reliably distinguished from each other by more subtle characters, including the presence of setae or glands on the sporangia and indusia, presence of proliferous buds, position of sori, and distribution and morphology of the indument (Fawcett and Smith 2021).

Conclusions—We present a densely sampled nuclear DNA phylogenomic dataset, representing half of the species diversity in the Thelypteridaceae; this broad sampling facilitates the revision of the generic classification of the family. However, species-level diversity, especially in the Paleotropics, remains poorly understood. For instance, at the time of the most recent treatment of *Sphaerostephanos* (Holttum 1982), of the 185 species recognized, 66 (36%) were known only from the type, or the type plus one or two other collections. Yet, even modern treatments of neotropical genera show the same pattern, with, e.g. 12 (22%) of the 54 Bolivian species of *Amauropelta* known from only one to three collections (Smith and Kessler 2017). This likely reflects a combination of factors, including narrow endemism, rarity, paucity of herbarium collections, and failure of general collectors to recognize subtle variations in the field. We do not doubt that many additional species remain undescribed, especially in Malesia. It is our hope that this work, and the complementary publication of a taxonomic monograph (Fawcett and Smith 2021) that provides a key to genera, detailed generic descriptions, and diagnoses, will provide a framework to facilitate the discovery, recognition, and conservation of thelypterid biodiversity.

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AUTHOR CONTRIBUTIONS

SF, ARS, GB, and EBS designed and implemented the study. GB, EBS, WLT, and GFC generated the data, SF and GB analyzed the data, and SF, MS, MK, LYK, CWC, and WLT contributed critical tissue samples and associated herbarium vouchers. SF drafted the manuscript, with contributions from all co-authors.

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APPENDIX 1. Voucher data for specimens used in molecular phylogenetic analyses. Specimens are arranged alphabetically by genus, with collector name and number, species, locality, country, year of collection, and herbaria where deposited, for tissue samples taken in the field. Many vouchers are digitized and images are hosted by the Pteridophyte Collections Consortium <pteridoportal.org>.

Abacopteris **Fée**—*Karger 1408*, *Abacopteris aspera* (C.Presl) Ching, Bacan, Mauluku Utara, Indonesia, 2010 (UC 2048328, Z); *Chen Wade1431*, *Abacopteris birii* (R.D.Dixit & Balkr.) S.E.Fawc. & A.R.Sm., Lam Dong, Vietnam, 2010 (TAIF 409716); *Kuo 857*, *Abacopteris gymnopteridifrons* (Hayata) Ching, Pingtung, Taiwan, 2010 (TAIF); *Cicuzza 693*, *Abacopteris nitida* (Holttum) S.E.Fawc. & A.R.Sm., Maleo, Sulawesi, 2008 (UC, Z); *Karger 1756*, *Abacopteris* aff. *peltochlamys* (C.Chr.) Holttum, West Papua, Indonesia, 2008 (UC 2048607, Z); *Karger 1260*, *Abacopteris repanda* (Fée) S.E.Fawc. & A.R.Sm., Seram, Indonesia, 2010 (UC 2048311; UC 2048312, Z).

***Amauropelta* Kunze**—*Mazziero 805*, *Amauropelta amambayensis* (Christ) Salino & A.R.Sm., Parana, Brazil, 2011 (VT 197107); *Chang 20090720-013*, *Amauropelta angustifrons* (Miq.) Y.H.Chang, Taipei, Taiwan, 2009 (TAIF); *Chen Wade3649*, *Amauropelta angustifrons* (Miq.) Y.H.Chang, Okinawa, Japan, 2013 (TAIF 440124); *Testo 738*, *Amauropelta aspidioides* (Willd.) Pic.Serm., Puntarenas, Costa Rica, 2015 (VT); *Nitta 2237*, *Amauropelta atrovirens* (C.Chr.) Salino & T.E.Almeida, Alajuela, Costa Rica, 2013 (UC, GH); *Smith 1746*, *Amauropelta atrovirens* (C.Chr.) Salino & T.E.Almeida, San José, Costa Rica, 1986 (UC 1524076); *Jiménez 1869*, *Amauropelta aymarae* (A.R.Sm. & M.Kessler) Salino & T.E.Almeida, La Paz, Bolivia, 2003 (GOET, LPB, MO, UC 11717973); *Rothfels 2673*, *Amauropelta balbisii* (Spreng.) A.R.Sm., Sarapiquí, Costa Rica, 2008 (UC 1970891); *Kluge 5520*, *Amauropelta barvae* (A.R.Sm.) Salino & T.E.Almeida, vel aff., Sarapiquí, Costa Rica, 2003 (UC 1784822); *Kluge 7446*, *Amauropelta beddomei* (Baker) Y.H.Chang, Sulawesi, Rorekatimbu, Indonesia, 2007 (UC, BO); *Karger 363*, *Amauropelta beddomei* (Baker) Y.H.Chang var. *eugracilis* (Copel.) Holttum, Mindanao, Philippines, 2009 (UC 2048277, Z); *Kuo 1376*, *Amauropelta* aff. *beddomei* (Baker) Y.H.Chang, Yunnan, China, 2010 (UC); *Kluge 7706*, *Amauropelta bergiana* (Schltdl.) Holttum, Mt. Karthala, Grand Comores, 2008 (GOET, UC); *Rothfels 4883*, *Amauropelta brausei* (Hieron.) A.R.Sm., Junín, Peru, 2016 (HOXA, UC); *Rothfels 5080*, *Amauropelta cheilanthoides* (Kunze) Á.Löve & D.Löve, Pasco, Peru, 2016 (HOXA, UC); *Lellinger 1883*, *Amauropelta christensenii* (Christ ex C.Chr.) Salino & T.E.Almeida, Puntarenas, Costa Rica, 1975 (UC 1610288); *Jiménez 1545*, *Amauropelta cinerea* (Sodiro) A.R.Sm., Cochabamba, Bolivia, 2002 (GOET, LPB, UC 1780392); *Jiménez 2680*, *Amauropelta comptula* (A.R.Sm.) Salino & T.E.Almeida, La Paz, Bolivia, 2004 (UC 1790495); *Barriga 4656*, *Amauropelta concinna* (Willd.) Pic.Serm., Querétaro, Mexico, 1988 (UC 1604224); *Hill 21259*, *Amauropelta consanguinea* (Fée) Salino & T.E.Almeida, St. Paul Parish, Dominica, 1990 (UC 1563529); *Jiménez 741*, *Amauropelta corazonensis* (Baker) Salino & T.E.Almeida, La Paz, Bolivia, 2001 (LPB, UC 1764778); *Kuo 1081*, *Amauropelta cystopteroides* (D.C.Eaton) S.E.Fawc. & A.R.Sm., Kagoshima, Japan, 2010 (TAIF); *Serrano 7007*, *Amauropelta decurtata* (Kunze) Salino & T.E.Almeida, Chuquisaca, Bolivia, 2005 (UC 1921855); *Rothfels 5055*, *Amauropelta deflexa* (C.Presl) Á.Löve & D.Löve, Pasco, Peru, 2016 (HOXA, UC, F); *Mickel 3223*, *Amauropelta delasotae* (A.R.Sm. & Lellinger) Salino & T.E.Almeida, Cartago, Costa Rica, 1967 (UC 1528494); *Jiménez 1280*, *Amauropelta euchlora* (Sodiro) A.R.Sm., Cochabomba, Bolivia, 2002 (GOET, LPB, UC 1781382); *Gómez 19587*, *Amauropelta funckii* (Mett.) A.R.Sm., Cartago, Costa Rica, (UC 1510398); *Fawcett 737*, *Amauropelta germaniana* (Fée) Salino & T.E.Almeida, Puntarenas, Costa Rica, 2017 (VT); *Fawcett 474*, *Amauropelta germaniana* (Fée) Salino & T.E.Almeida, Adjuntas, Puerto Rico, 2016 (VT); *Smith 2597*, *Amauropelta* aff. *germaniana* (Fée) Salino & T.E.Almeida, Costa Rica, 1999 (UC 1735262); *Chang 20090919-027*, *Amauropelta glanduligera* (Kunze) Y.H.Chang, Taipei, Taiwan, 2009 (TAIF); *Vivant s.n.*, *Amauropelta gracilis* (Heward) A.R.Sm., (UC 1609989); *Game 92/21*, *Amauropelta grantii* (Copel.) Holttum, Tahiti, Society Islands, 1992 (UC); *Faden 1976/272*, *Amauropelta hakgalensis* Holttum, Hakgala, Sri Lanka, 1976 (UC 1484718); *Axelrod 11263*, *Amauropelta heteroclita* (Desv.) Pic.Serm., Adjuntas, Puerto Rico, 2000 (UC 1794604); *Croat 78966*, *Amauropelta illicita* (Christ) Salino & T.E.Almeida, San José, Costa Rica, 1996 (UC 1740681); *Smith 2182*, *Amauropelta inaequans* (C.Chr.) Salino & T.E.Almeida, Cartago, Costa Rica, 1986 (UC 1526033); *Testo 1028*, *Amauropelta jimenezii* (Maxon & C.Chr.) R.C.Moran & A.R.Sm., Puntarenas, Costa Rica, 2016 (UC 2048961); *Smith 2245*, *Amauropelta lepidula* (Hieron.) A.R.Sm., vel aff., Alajuela, Costa Rica, 1986 (UC 1526132); *Vivant s.n.*, *Amauropelta limbata* (Sw.) Pic.Serm., St. Claude, Guadeloupe, 1994 (UC 1609991); *Fawcett 725*, *Amauropelta linkiana* (C.Presl) Pic.Serm., Alajuela, Costa Rica, 2017 (UC 2048988, VT); *Rothfels 5081*, *Amauropelta* aff. *linkiana* (C.Presl) Pic.Serm., Pasco, Peru, 2016 (HOXA, UC, F); *Kessler 14739*, *Amauropelta longicaulis* (Baker) Salino & T.E.Almeida, Antioquia, Colombia, 2015 (UC 2079595); *Lorea 1913*, *Amauropelta loreae* (A.R.Sm.) Salino & T.E.Almeida, Guerrero, Mexico, 1982 (UC 1727998); *Jiménez 1901*, *Amauropelta lumbricoides* (A.R.Sm. & M.Kessler) Salino & T.E.Almeida, La Paz, Bolivia, 2003 (LPB, MO, UC 1719767); *Axelrod 12247*, *Amauropelta malangae* (C.Chr.) Salino & T.E.Almeida, Luquillo, Puerto Rico, 2002 (UC 1794602); *Paulay 278*, *Amauropelta margaretae* (E.Brown) Holttum, Ororangi, Rapa, 1980 (UC 2016197); *Krömer 3813*, *Amauropelta melanochlaena* (C.Chr.) Salino & T.E.Almeida, Veracruz, Mexico, 2009 (UC 2043510); *Jiménez 1631*, *Amauropelta nephelium* (A.R.Sm. & M.Kessler) Salino & T.E.Almeida, Cochabomba, Bolivia, 2002 (GOET, LPB, UC); *Fawcett 835*, *Amauropelta nevadensis* (Baker) S.E.Fawc. & A.R.Sm., California, U.S.A., 2017 (VT); *Fawcett 567*, *Amauropelta noveboracensis* (L.) S.E.Fawc. & A.R.Sm., Michigan, U.S.A., 2016 (UC 2049131, VT); *Jiménez 2403*, *Amauropelta nubicola* (de la Sota) Salino & T.E.Almeida, Tarija, Bolivia, 2004 (UC 1790497); *Nitta 759*, *Amauropelta oaxacana* (A.R.Sm.) Salino & T.E.Almeida, Alajuela, Costa Rica, 2011 (UC, CR); *Mickel 6730*, *Amauropelta oaxacana* (A.R.Sm.) Salino & T.E.Almeida, Oaxaca, Mexico, 1972 (UC 1468999); *Rothfels 4818*, *Amauropelta oligocarpa* (Humb. & Bonpl. ex Willd.) Pic.Serm., Junín, Peru, 2016 (HOXA, UC, F); *Rothfels 4985*, *Amauropelta opposita* (Vahl) Pic.Serm., Pasco, Peru, 2016 (HOXA, UC, F.); *Kluge 7746*, *Amauropelta oppositiformis* (C.Chr.) Holttum, Mt. Karthala, Grand Comores, 2008 (UC 1924762); *Fawcett 465*, *Amauropelta piedrensis* (C.Chr.) Salino & T.E.Almeida, Adjuntas, Puerto Rico, 2016 (VT); *Jiménez 1328*, *Amauropelta pilosula* (Klotzsch & H.Karst. ex Mett.) Á.Löve & D.Löve, Cochabamba, Bolivia, 2002 (GOET, LPB, UC 1780760); *Barbosa 203*, *Amauropelta ptarmica* (Kunze ex Mett.) Pic.Serm., Parana, Brazil, 1998 (UC 1732296); *Testo 1178*, *Amauropelta pteroidea* (Klotzsch) A.R.Sm., Antioquia, Colombia, 2016 (VT); *Sundue 16*, *Amauropelta pteroidea* (Klotzsch) A.R.Sm., Colombia, Colombia, 2016 (VT); *Rothfels 5108*, *Amauropelta pusilla* (Mett.) A.R.Sm., Pasco, Peru, 2016 (HOXA, UC); *Mickel 9094*, *Amauropelta reducta* (C.Chr.) Salino & T.E.Almeida, San Cristobal-Peravia, Dominican Republic, 1983 (UC 1529155); *Chambers J12*, *Amauropelta resinifera* (Desv.) Pic.Serm., St. Thomas, Jamaica, 1976 (VT); *Escobar 8880*, *Amauropelta rheophyta* (Proctor) Salino & T.E.Almeida, Rio Grande, Puerto Rico, 1991 (UC1970917); *Rothfels 4826*, *Amauropelta rudis* (Kunze) Pic.Serm., Junín, Peru, 2016 (HOXA, UC, F); *Testo 708*, *Amauropelta rudis* (Kunze) Pic.Serm., San José, Costa Rica, 2015 (VT); *Mickel 8181*, *Amauropelta rupicola* (C.Chr.) Salino & T.E.Almeida, Pedernales, Dominican Republic, 1982 (UC 1529109); *Fawcett 390*, *Amauropelta sancta* (L.) Pic.Serm., Arecibo, Puerto Rico, 2016 (VT); *Sundue 4012*, *Amauropelta scalaris* (Christ) Á.Löve & D.Löve, Oaxaca, Mexico, 2015 (VT); *Kuo 1588*, *Amauropelta* aff. *serrulata* (Ching) S.E.Fawc. & A.R.Sm., Zhejiang, China, 2010 (UC); *Farrera 1400*, *Amauropelta struthiopteroides* (C.Chr.) Salino & T.E.Almeida, Chiapas, Mexico, 1996 (UC 1874227); *Kluge 5448*, *Amauropelta subscandens* (A.R.Sm.) Salino & T.E.Almeida, Sarapiquí, Costa Rica, 2003 (UC 1784820); *Jiménez 1516*, *Amauropelta tamandarei* (Rosenst.) Salino & T.E.Almeida, Cochabomba, Bolivia, 2002 (GOET, LPB, UC 1780393); *Mickel 8918*, *Amauropelta thomsonii* (Jenman) Pic.Serm., Pedernales, Dominican Republic, 1983 (UC 1529118); *Maas 8006*, *Amauropelta villana* (L.D.Gómez) Salino & T.E.Almeida, San José, Costa Rica, 1991 (UC 1612368); *Smith 1665*, *Amauropelta zurquiana* (A.R.Sm. & Lellinger) Salino & T.E.Almeida, San José, Costa Rica, 1986 (UC 1524433).

***Amblovenatum* J.P.Roux**—*Elmer 1080*, *Amblovenatum immersum* (Blume) Mazumdar, Mindanao, Philippines, 1909 (VT 197264); *Fawcett 732*, *Amblovenatum opulentum* (Kaulf.) J.P.Roux, Puntarenas, Costa Rica, 2017 (UC 2049035, VT); *Chen Wade4152*, *Amblovenatum opulentum* (Kaulf.) J.P.Roux, Khánh Hòa, Vietnam, 2014 (TAIF).

***Ampelopteris* Kunze**—*Chang 20110103-002*, *Ampelopteris prolifera* (Retz.) Copel., Yilan, Taiwan, 2011 (TAIF).

***Chingia* Holttum**—*Chen Wade3989*, *Chingia acutidens* Holttum, vel aff., Negros, Philippines, 2014 (TAIF 455808, 455809); *Cicuzza 58*, *Chingia atrospinosa* (C.Chr.) Holttum, Sulawesi, Bariri, Indonesia, 2008 (UC, Z); *Chen Wade4658*, *Chingia clavipilosa* Ching, Sabah, Borneo, 2016 (UC); *Chen Wade1920*, *Chingia ferox* (Blume) Holttum, Gede-Pangrango, Java, Indonesia, 2011 (TAIF 388273, 388274, 388275, 388276); *Fawcett 611*, *Chingia fijiensis* Game, S.E.Fawc. & A.R.Sm., Viti Levu, Fiji, 2016 (VT, UC 2049805); *Chen Wade2725*, *Chingia longissima* (Brack.) Holttum, Kolombangara, Solomon Islands, 2013 (TAIF 444977, 444978, 444979); *Nitta 1756a*, *Chingia longissima* (Brack.) Holttum, Moorea, Society Islands, 2012 (GH, UC); *SITW 11121*, *Chingia malodora* (Copel.) Holttum, Guadalcanal, Solomon Islands, 2016 (TAIF); *Karger 2742*, *Chingia marattioides* (Alston) S.E.Fawc. & A.R.Sm., West Papua, Indonesia, 2011 (UC 2048181, 2048180; Z); *Schuettpelz 815*, *Chingia sakayensis* (Zeiller) Holttum, Malaysia, (DUKE, KEP); *Kluge 7141*, *Chingia* aff. *sambasensis* Holttum, Sulawesi, Bariri, Sulawesi, 2007 (BO, UC 1930545,); *Kluge 7612*, *Chingia* aff. *sambasensis* Holttum, Nokilalaki, Sulawesi, 2007 (UC 1930545); *SITW 11087*, *Chingia* sp., Santa Cruz, Solomon Islands, 2016 (UC 2048647).

***Christella* H.Lév.**—*Lorence 9627*, *Christella* × *palmeri* (W.H.Wagner) ined., Hawaii, Kauai, U.S.A., 2007 (UC 1972589); *Nitta 336*, *Christella acuminata* (Houtt.) H.Lév., Iriomote-jima, Japan, 2008 (TNS, UC); *SITW 11156*, *Christella calcarea* D.Glenny, ined., Guadalcanal, Solomon Islands, 2016 (UC 2048637); *Kuo 1856*, *Christella calvescens* (Ching) Holttum, Tam Dao, Vietnam, 2010 (TAIF); *Kayombo 2589*, *Christella chaseana*

(Schelpe) Holttum, Iringa, Tanzania, 1999 (UC 1877795); *Calzadilla 363*, *Christella conspersa* (Schrad.) Á.Löve & D.Löve, Bolivia, 2008 (UC); *Fawcett 662*, *Christella dentata* (Forssk.) Brownsey & Jermy, Taveuni, Fiji, 2016 (UC, VT); *Kluge 7775*, *Pronephrium fidelei* Rakotondr., Singani, Grand Comores, 2008 (Comores, GOET, UC 1924704); *Chang 20090523-002*, *Christella ensifer* (Tagawa) Holttum ex C.M.Kuo, Pingtung, Taiwan, 2009 (TAIF); *Kuo 766*, *Christella evoluta* (C.B.Clarke & Baker) Holttum, Hunan, China, 2009 (TAIF); *Raulerson 11209*, *Christella gretheri* (W.H.Wagner) Holttum, Guam, U.S.A., 1985 (UC 2016162); *Tucker s.n.*, *Christella guamensis* Holttum, Guam, U.S.A., 1992 (UC 1734692); *Schelpe 3143*, *Christella gueintziana* (Mett.) Holttum, Natal, South Africa, 1952 (UC1085411); *Fawcett 661*, *Christella harveyi* (Mett.) Holttum, Taveuni, Fiji, 2016 (UC 2049804, VT); *Pichi Sermolli 7223*, *Christella hispidula* (Decne.) Hottum, Kaffa, Ethiopia, 1967 (UC 1429533); *Lott 2989*, *Christella hispidula* (Decne.) Hottum, Colima, Mexico, 1990 (UC 1583194); *Jiménez 2430*, *Christella hispidula* (Decne.) Hottum, Tarija, Bolivia, 2004 (UC 1790608); *Mousset 163*, *Christella hispidula* (Decne.) Hottum, Java, Indonesia, 1910 (UC 392029); *Mickel 8573*, *Christella hispidula* (Decne.) Holttum var. *inconstans* (C.Chr.) C.Sánchez, Santiago Rodriguez, Dominican Republic, 1982 (UC 1529135); *Mexia 4613a*, *Christella hispidula* (Decne.) Holttum var. *repens* (A.R.Sm.) comb. ined., Minas Gerais, Brazil, 1930 (UC 419595); *Thomas 35842*, *Christella hispidula* (Decne.) Holttum var. *versicolor* (R.St.John) A.R.Sm., Louisiana, U.S.A., 1973 (UC 1428387); *Chang 20130726-012*, *Christella* cf. × *intermedia* (W.C.Shieh & J.L.Tsai) D.D.Palmer, Kaohsiung, Taiwan, 2013 (TAIF); *Kuo 762*, *Christella jaculosa* (Christ) Holttum, Hunan, China, 2009 (TAIF); *Chen Wade3964*, *Christella jaculosa* (Christ) Holttum, Negros, Philippines, 2014 (TAIF 454818, 454819, 454820, 454821); *Kuo 636*, *Christella latipinna* (Benth.) H.Lév., Kalinga, Philippines, 2009 (UC); *Fay 1182*, *Christella microbasis* (Baker) Holttum, Sierra Leone, 1985 (NY); *Kuo 3367*, *Christella papilio* (Hope) Holttum, Nantou, Taiwan, 2012 (TAIF); *Fawcett 266*, *Christella parasitica* (L.) H.Lév., Hawaii, Kauai, U.S.A., 2015 (UC, VT); *Chen Wade2402*, *Christella siamensis* (Tagawa & K.Iwats.) Holttum, Guangxi, China, 2013 (TAIF 441591); *Chen Wade1369*, *Christella subpubescens* (Blume) Holttum, Bù Gia Mp, Vietnam, 2010 (TAIF 411043); *Cicuzza 876*, *Christella subpubescens* (Blume) Holttum, Noki, Sulawesi, 2008 (UC, Z); *Zheng-yu 15533*, *Christella* sp., Sichuan, China, 1996 (UC 1727981); *Kuo 650*, *Christella* sp., Kalinga, Philippines, 2009 (TAIF).

***Coryphopteris* Holttum**—*Kuo 2363*, *Coryphopteris angulariloba* (Ching) L.J.He & X.C.Zhang, Taipei, Taiwan, 2011 (TAIF); *Kessler 13932*, *Coryphopteris badia* (Alderw.) Holttum, West Papua, Indonesia, 2008 (UC 2048617); *Chang 20090701-029*, *Coryphopteris castanea* (Tagawa) Y.H.Chang, Taichung, Taiwan, 2009 (TAIF); *Kluge 9175*, *Coryphopteris diaphana* (Brause) Holttum, West Papua, Indonesia, 2008 (UC 2048596); *Kessler 13860*, *Coryphopteris* aff. *dura* (Copel.) Holttum, West Papua, Indonesia, 2008 (UC 2048606); *Karger 2643*, *Coryphopteris fasciculata* (E.Fourn.) Holttum, West Papua, Indonesia, 2011 (UC 2048200, Z); *Rothfels 4705*, *Coryphopteris gymnopoda* (Baker) Holttum, Kinabalu, Borneo, 2016 (UC 2048748); *Chen Wade4803*, *Coryphopteris gymnopoda* (Baker) Holttum var. *gymnopoda*, vel aff., Pahang, Peninsular Malaysia, 2017 (KLU, TAIF, UC); *Karger 2547*, *Coryphopteris habbemensis* (Copel.) Holttum, West Papua, Indonesia, 2011 (UC 2048205, Z); *Chen Wade2629*, *Coryphopteris hirsutipes* (C.B.Clarke) Holttum, Lam Dong, Vietnam, 2013 (TAIF); *Kuo 999*, *Coryphopteris japonica* (Baker) L.J.He & X.C.Zhang, Ibaraki, Japan, 2010 (UC); *Chen Wade2370*, *Coryphopteris japonica* (Baker) L.J.He & X.C.Zhang, Guangxi, China, 2013 (TAIF); *Chen Wade3367*, *Coryphopteris kolombangarae* Holttum, Kolombangara, Solomon Islands, 2013 (TAIF 464813, 464814); *Chen Wade4274*, *Coryphopteris ledermannii* (Hieron.) Holttum, Sabah, Malaysia, 2015 (TAIF 468094); *Kuo 792*, *Coryphopteris nigrescens* (Ching ex K.H.Shing) S.E.Fawc. & A.R.Sm., Hunan, China, 2009 (UC); *Chen Wade2332*, *Coryphopteris nigrescens* (Ching ex K.H.Shing) S.E.Fawc. & A.R.Sm., Guangxi, China, 2013 (TAIF); *Kessler 13803*, *Coryphopteris obtusata* (Alderw.) Holttum, West Papua, Wamena, Indonesia, 2008 (UC 2048605); *Kessler 14074*, *Coryphopteris* cf. *obtusata* (Alderw.) Holttum, West Papua, Indonesia, 2008 (UC); *Chen Wade4819*, *Coryphopteris pectiniformis* (C.Chr.) Holttum, Pahang, Peninsular Malaysia, 2017 (TAIF, KLU, UC); *Kessler 13620*, *Coryphopteris pectiniformis* (C.Chr.) Holttum, Sulawesi, Indonesia, 2008 (GOET, UC); *Kuo 3422*, *Coryphopteris pubirachis* (Baker) Holttum var. *philippinensis* Holttum, Bukidnon, Philippines, 2012 (UC); *Wood 10448*, *Coryphopteris quaylei* (E.Brown) Holttum, Ua Pou, Marquesas Islands, (PTBG); *Game 95/147, Coryphopteris seemannii* Holttum, Viti Levu, Fiji, 1995 (UC 1750064); *Fawcett 593*, *Coryphopteris simulata* (Davenp.) S.E.Fawc., Ontario, Canada, 2016 (UC 2049134, VT); *Chen Wade3348*, *Coryphopteris subbipinnata* Holttum, Kolombangara, Solomon Islands, 2013 (TAIF 463422, 463423); *Karger 2651*, *Coryphopteris subnigra* (Brause) Holttum, West Papua, Indonesia, 2011 (UC 2048206, Z); *Chen Wade4806*, *Coryphopteris tahanensis* Holttum, Pahang, Peninsular Malaysia, 2017 (KLU, TAIF, UC); *Kessler 13618*, *Coryphopteris viscosa* (Baker) Holttum, Sulawesi, Indonesia, 2008 (GOET, UC); *Nitta 2794*, *Coryphopteris* sp., Moorea, Society Islands, 2013 (GH, UC); *Chang 20120817-016*, *Coryphopteris* sp., New Taipei, Taiwan, 2012 (TAIF); *Game s.n. 3*, *Coryphopteris* sp., Viti Levu, Fiji, 1995 (UC); *Chen Wade4829*, *Coryphopteris* sp., Pahang, Peninsular Malaysia, 2017 (KLU, TAIF, UC); *Wood 10475*, *Coryphopteris* sp., Ua Huka, Marquesas Islands, (PTBG); *Lu 10162*, *Coryphopteris* sp., Taoyuan, Taiwan, 2005 (VT 197604); *Nitta 3275*, *Coryphopteris* sp., Tahiti, Society Islands, 2013 (GH, UC).

***Cyclogramma* Tagawa**—*Kuo 2399*, *Cyclogramma auriculata* (J.Sm.) Ching, Chiayi, Taiwan, 2011 (TAIF); *Chang 20090413-002*, *Cyclogramma leveillei* (Christ) Ching, Hualien, Taiwan, 2009 (TAIF); *Kuo 3268*, *Cyclogramma neoauriculata* (Ching) Tagawa, Yunnan, China, 2012 (TAIF); *Kuo 2974*, *Cyclogramma omeiensis* (Baker) Tagawa, Yunnan, China, 2012 (TAIF).

***Cyclosorus* Link**—*Ezrom 34*, *Cyclosorus interruptus* (Willd.) H.Ito, Lindi, Tanzania, 2005 (UC); *Rwaburindore 3306*, *Cyclosorus striatus* (Schum.) Ching, Kashari, Uganda, 1991 (UC).

***Glaphyropteridopsis* Ching**—*Kuo 2192*, *Glaphyropteridopsis emeiensis* Y.X.Lin, Sichuan, China, 2011 (TAIF); *Kuo 4156*, *Glaphyropteridopsis erubescens* (Hook.) Ching, Nantou, Taiwan, 2015 (TAIF); *Zhang 20100618027*, *Glaphyropteridopsis rufostraminea* (Christ) Ching, Chongqing, China, 2010 (VT).

***Goniopteris* C.Presl**—*Fawcett 457D*, *Goniopteris abdita* (Proctor) Salino & T.E.Almeida, Arecibo, Puerto Rico, 2016 (VT); *Seidel 2890*, *Goniopteris abrupta* (Desv.) A.R.Sm., La Paz, Bolivia, 1990 (UC); *Salino 16032*, *Goniopteris alan-smithiana* (L.D.Gómez) Salino & T.E.Almeida, Bahia, Brazil, 2014 (UC); *Zanoni 26365*, *Goniopteris alata* (L.) Ching, Pedernales, Dominican Republic, 1983 (UC 1609882); *Fawcett 1094*, *Goniopteris alata* (L.) Ching, Pedernales, Dominican Republic, 2018 (VT); *Clase 4757*, *Goniopteris alata* (L.) Ching var. *irregularis* (C.Chr.) comb. ined., Barahona, Dominican Republic, 2007 (JBSD); *Judd 4434*, *Goniopteris* cf. *alata* (L.) Ching, Massif de la Selle, Haiti, 1984 (HUH); *Fernandes 300*, *Goniopteris amazonica* (Salino & R.S.Fern.) Salino & T.E.Almeida, Para, Brazil, 2008 (UC 2029563); *Fuentes 4368*, *Goniopteris ancyriothrix* (Rosenst.) Salino & T.E.Almeida, La Paz, Bolivia, 2002 (UC); *Barcelona 1161*, *Goniopteris pellita* (Willd.) A.R.Sm., St. Elizabeth, Jamaica, 1997 (NY); *Matos 1558*, *Goniopteris beckeriana* (F.B.Matos, A.R.Sm. & Labiak) Salino & T.E.Almeida, Bahia, Brazil, 2008 (UC 1927131); *Kessler 13354*, *Goniopteris biformata* (Rosenst.) Salino & T.E.Almeida, Cochabomba, Bolivia, 2004 (GOET, LPB, UC 1785589); *Croat 20491*, *Goniopteris* aff. *biformata* (Rosenst.) Salino & T.E.Almeida, Loreto, Peru, 1972 (UC 1502856); *Weigelt 90409*, *Goniopteris biolleyi* (Christ) Pic.Serm., La Paz, Bolivia, 2009 (GOET, LPB, UC 1970824); *Krömer 2276*, *Goniopteris blanda* (Fée) Salino & T.E.Almeida, Veracruz, Mexico, 2005 (UC); *Salino 14680*, *Goniopteris bradei* Salino, Espirito Santo, Brazil, 2009 (UC 2048950); *Procter 39806*, *Goniopteris brittoniae* (Sloss.) Ching, Maricao, Puerto Rico, 1983 (UC); *Chrysler 6540*, *Goniopteris brittoniae* (Sloss.) Ching, Maricao, Puerto Rico, 1947 (HUH); *Labiak 3787*, *Goniopteris burkartii* Abbiatti, Parana, Brazil, 2006 (UC); *Labiak 3787*, *Goniopteris burkartii* Abbiatti, Parana, Brazil, 2006 (UC 1872916); *Fawcett 1078*, *Goniopteris cordata* (Fée) Salino & T.E.Almeida, Pedernales, Dominican Republic, 2018 (VT); *Fawcett 454*, *Goniopteris cordata* (Fée) Salino & T.E.Almeida, Arecibo, Puerto Rico, 2016 (VT); *Fawcett 1111*, *Goniopteris* cf. *cordata* (Fée) Salino & T.E.Almeida, Pedernales, Dominican Republic, 2018 (VT); *Fawcett 1132*, *Goniopteris* cf. *cordata* (Fée) Salino & T.E.Almeida, Independencia, Dominican Republic, 2018 (VT); *Valdespino 269*, *Goniopteris cumingiana* (Kunze) de Jonch. & U.Sen, Panamá, Panama, 1986 (UC 1529318); *Rothfels 08-172*, *Goniopteris curta* (Christ) A.R.Sm., Sarapiquí, Costa Rica, 2008 (CR, DUKE, INB, UC); *Testo 749, Goniopteris eggersii* (Hieron.) Alston, Puntarenas, Costa Rica, 2015 (VT); *Testo 732*, *Goniopteris eggersii* (Hieron.) Alston, Puntarenas, Costa Rica, 2015 (VT); *Testo 1252*, *Goniopteris equitans* (Christ) Salino & T.E.Almeida, Puntarenas, Costa Rica, 2017 (VT); *Liesner 14815*, *Goniopteris francoana* (E.Fourn.) Á.Löve & D.Löve, Alajuela, Costa Rica, 1983 (UC); *Croat 68968*, *Goniopteris fraseri* (Mett. ex Kuhn) A.R.Sm., Darién, Panama, 1988 (UC 1553799); *Gonzales 2117*, *Goniopteris gemmulifera* (Hieron.) Vareschi, Cayenne, French Guiana, 2010 (UC 2047245); *Pietrobom 54366*, *Goniopteris gonophora* (Weath.) Salino & T.E.Almeida, Pernambuco, Brazil, 2001

(UC); *Fawcett 401*, *Goniopteris hastata* Fée, Hatillo, Puerto Rico, 2016 (VT); *Sundue 4007*, *Goniopteris hatchii* (A.R.Sm.) Á.Löve & D.Löve, Oaxaca, Mexico, 2015 (VT); *Testo 877*, *Goniopteris hatchii* (A.R.Sm.) Á.Löve & D.Löve, Oaxaca, Mexico, 2015 (VT); *Mejia 1619*, *Goniopteris hildae* (Proctor) Salino & T.E.Almeida, Samaná, Dominican Republic, 1985 (JBSD); *Fawcett 369*, *Goniopteris hildae* (Proctor) Salino & T.E.Almeida, Arecibo, Puerto Rico, 2016 (VT); *Jansen-Jacobs 7034*, *Goniopteris holodictya* (K.U.Kramer) Salino & T.E.Almeida, Marowijne, Suriname, 2004 (UC 1869861); *Gonzales 17141*, *Goniopteris imbricata* (Liebm.) Á.Löve & D.Löve, Tabasco, Mexico, 1985 (UC); *Zanoni 42430*, *Goniopteris imitata* (C.Chr.) Salino & T.E.Almeida, Santiago, Dominican Republic, 1989 (UC); *Salino 1306*, *Goniopteris jamesonii* (Hook.) Salino & T.E.Almeida, São Paulo, Brazil, 1992 (UC); *Rothfels 4987*, *Goniopteris jamesonii* (Hook.) Salino & T.E.Almeida, Pasco, Peru, 2016 (HOXA, UC); *Weigelt 90605*, *Goniopteris juruensis* (C.Chr.) Brade, Beni, Bolivia, 2009 (GOET, LPB, UC 1970821); *Salino 3569*, *Goniopteris kuhlmanii* (Brade) Brade, Minas Gerais, Brazil, 1997 (UC); *Proctor 21906*, *Goniopteris leptocladia* Fée, Jamaica, Jamaica, 1961 (HUH); *Moran 3136*, *Goniopteris levyi* (E.Fourn.) C.V.Morton, San José, Costa Rica, 1983 (UC 1265894); *Carvajal Hernandez 943*, *Goniopteris liebmannii* (Maxon & C.V.Morton) A.R.Sm. & Salino, Oaxaca, Mexico, 2014 (UC); *Prado 977*, *Goniopteris littoralis* (Salino) Salino & T.E.Almeida, São Paulo, Brazil, 1999 (UC 1730162); *Webster 23408*, *Goniopteris lugubriformis* (Rosenst.) Salino & T.E.Almeida, Loreto, Peru, 1978 (UC 158912); *Salino 10281*, *Goniopteris lugubris* (Mett.) Brade, São Paulo, Brazil, 2005 (UC); *Salino 10278*, *Goniopteris lugubris* (Mett.) Brade, São Paulo, Brazil, 2005 (UC); *Salino 7950*, *Goniopteris macropus* (Blume) Ching, Minas Gerais, Brazil, 2002 (UC); *Woytkowski 35241*, *Goniopteris macrotis* (Hook.) Pic.Serm., San Martín, Peru, 1947 (UC 1013950); *Pena Chocarro 2620*, *Goniopteris minor* (C.Chr.) Salino & T.E.Almeida, Ahuachapan, El Salvador, 2007 (UC); *Testo 923*, *Goniopteris mollis* Fée, Heredia, Costa Rica, 2015 (VT); *Matos 1559*, *Goniopteris* aff. *monosora* (C.Presl) Salino, Bahia, Brazil, 2008 (UC 1927130); *Fawcett 1093*, *Goniopteris domingensis* (Spreng.) Pic. Serm. (=*G. moranii* C.Sánchez), Dominican Republic, 2018 (VT); *Fawcett 372*, *Goniopteris domingensis* (Spreng.) Pic. Serm., Arecibo, Puerto Rico, 2016 (VT); *Salino 1800*, *Goniopteris multigemmifera* (Salino) Salino & T.E.Almeida, São Paulo, Brazil, 1993 (UC 1605693); *Proctor 19256*, *Goniopteris nephrodioides* (Klotzsch) Vareschi, St. Kitts, St. Kitts, 1959 (HUH); *Rivero 925*, *Goniopteris nephrodioides* (Klotzsch) Vareschi, Lara, Venezuela, 1985 (UC); *Testo 530*, *Goniopteris nicaraguensis* (E.Fourn.) Salino & T.E.Almeida, Heredia, Costa Rica, 2014 (VT); *Fawcett 722*, *Goniopteris nicaraguensis* (E.Fourn.) Salino & T.E.Almeida, Alajuela, Costa Rica, 2017 (UC 2049028, VT); *Sundue 3931*, *Goniopteris nicaraguensis* (E.Fourn.) Salino & T.E.Almeida × *G. poiteana* (Bory) Ching, Heredia, Costa Rica, 2013 (VT); *Hilaire 2405*, *Goniopteris nigricans* (Ekman & C.Chr.) Salino & T.E.Almeida, Massif de la Hotte, Haiti, 2006 (JBSD); *Sander 17618*, *Goniopteris obliterata* (Sw.) C.Presl, Puntarenas, Costa Rica, 1995 (UC); *Testo 1047*, *Goniopteris* cf. *obliterata* (Sw.) C.Presl, Rivas, Nicaragua, 2016 (VT); *Grayum 3633*, *Goniopteris oroniensis* (L.D. Gómez) Salino & T.E.Almeida, Limón, Costa Rica, 1984 (UC 1506549); *Salino 10140*, *Goniopteris paranaensis* (Salino) Salino & T.E.Almeida, São Paulo, Brazil, 2005 (UC); *Mostacero 735*, *Goniopteris paucijuga* (Klotzsch) A.R.Sm., Aragua, Venezuela, 2007 (UC 1964920); *Krömer 4079*, *Goniopteris paucipinnata* (Donn. Sm.) Salino & T.E.Almeida, Veracruz, Mexico, 2013 (UC); *van der Werff 13165*, *Goniopteris pinnatifida* (A.R.Sm.) Salino & T.E.Almeida, Zamora-Chinchipe, Ecuador, 1994 (UC 1611138); *Salino 2685*, *Goniopteris platypes* Fée, Minas Gerais, Brazil, 1996 (UC); *Fawcett 395*, *Goniopteris poiteana* (Bory) Ching, Hatillo, Puerto Rico, 2016 (VT); *Testo 1053*, *Goniopteris poiteana* (Bory) Ching, Rivas, Nicaragua, 2016 (UC 2049013, VT); *Croat 24548*, *Goniopteris praetermissa* (Maxon) Salino & T.E.Almeida, Stann Creek, Belize, 1973 (UC); *Fawcett 382*, *Goniopteris reptans* (J.F.Gmel.) C.Presl, Arecibo, Puerto Rico, 2016 (VT); *Fawcett 1073*, *Goniopteris reptans* (J.F.Gmel.) C.Presl, Barahona, Dominican Republic, 2018 (VT); *Krömer 4082*, *Goniopteris resiliens* (Maxon) Salino & T.E.Almeida, Veracruz, Mexico, 2013 (UC); *Fawcett 1118*, *Goniopteris retroflexa* (L.) Salino & T.E.Almeida, Pedernales, Dominican Republic, 2018 (VT); *Croat 97637*, *Goniopteris retroflexa* (L.) Salino & T.E.Almeida, La Vega, Dominican Republic, 2006 (MO, UC); *Fawcett 471*, *Goniopteris retroflexa* (L.) Salino & T.E.Almeida, Adjuntas, Puerto Rico, 2016 (VT); *Possley WPT347*, *Goniopteris retroflexa* (L.) Salino & T.E.Almeida, Yauco, Puerto Rico, 2016 (MAPR); *Acevedo-Rodriguez 13237*, *Goniopteris* aff. *retroflexa* (L.) Salino & T.E.Almeida, Baoruco, Dominican Republic, 2003 (VT); *Perez Farrera 2412*, *Goniopteris rhachiflexuosa* (Riba) Salino & T.E.Almeida, Chiapas, Mexico, 2000 (UC); *Salino 6910*, *Goniopteris riograndensis* (Lindm.) Pic.Serm., Minas Gerais, Brazil, 2001 (UC); *van der Werff 858*, *Goniopteris* × *rolandii* (C.Chr.) A.R.Sm., Falcón, Venezuela, 1979 (UC 1465700); *Salino 8572*, *Goniopteris scabra* (C.Presl) Brade, São Paulo, Brazil, 2003 (UC); *Caranza Gonzales 2575*, *Goniopteris schaffneri* (Fée) Salino & T.E.Almeida, Querétaro, Mexico, 1994 (UC); *Salino 1783*, *Goniopteris schwackeana* Brade, São Paulo, Brazil, 1993 (UC); *Possley 144*, *Goniopteris sclerophylla* (Poepp. ex Spreng.) Wherry, Florida, U.S.A., 2014 (UC); *Fawcett 1040*, *Goniopteris* cf. *sclerophylla* (Kunze) Wherry var. *latifolia* C.Sánchez, comb. ined., Barahona, Dominican Republic, 2018 (VT); *Mickel 8979*, *Goniopteris scolopendrioides* (Sw.) C.Presl, Barahona, Dominican Republic, 1983 (UC); *Pina s.n.*, *Goniopteris scolopendrioides* (Sw.) C.Presl, Barahona, Dominican Republic, 2018 (JBSD); *Salino 709*, *Goniopteris semirii* (Salino & Melo) Salino & T.E.Almeida, Minas Gerais, Brazil, 1989 (UC 1605684); *Christenhusz 3300*, *Goniopteris serrulata* (Sw.) J.Sm., St. Catherine, Jamaica, 2005 (UC); *Silva 221*, *Goniopteris stolzeana* (A.R.Sm.) Salino & T.E.Almeida, Chiapas, Mexico, 2015 (Z); *van der Werff 3186*, *Goniopteris straminea* (Baker) Ching, Falcón, Venezuela, 1978 (UC 1465386); *Salino 9695*, *Goniopteris subdimorpha* Salino, Minas Gerais, Brazil, 2004 (UC 2048663); *Krömer 4053*, *Goniopteris tetragona* (Sw.) C.Presl, Veracruz, Mexico, 2013 (UC); *Proctor 18875*, *Goniopteris tetragona* (Sw.) C.Presl, Montserrat, Montserrat, 1959 (HUH); *Testo 791*, *Goniopteris tetragona* (Sw.) C.Presl, Heredia, Costa Rica, 2015 (VT); *Martinez S. 11754*, *Goniopteris toganetra* (A.R.Sm.) Á.Löve & D.Löve, Chiapas, Mexico, 1985 (UC); *Weigelt 90410*, *Goniopteris tristis* (Kunze) Brade, La Paz, Bolivia, 2009 (GOET, LPB); *Rothfels 4999*, *Goniopteris tryoniorum* (A.R.Sm.) Salino & T.E.Almeida, Pasco, Peru, 2016 (HOXA, UC); *Jimenez 2521*, *Goniopteris tryoniorum* (A.R.Sm.) Salino & T.E.Almeida, La Paz, Bolivia, 2004 (UC 1790499); *Krömer 3627*, *Goniopteris tuxtlensis* (T.Krömer, Acebey & A.R.Sm.) Salino & T.E.Almeida, Verracruz, Mexico, 2008 (UC); *Onesis Vasquez 267*, *Goniopteris urbanii* (Sodiro) comb. ined., Canal Zone, Panama, 1980 (UC); *Fawcett 427*, *Goniopteris verecunda* Proctor, Lares, Puerto Rico, 2016 (VT); *Almeida 1946*, *Goniopteris vivipara* (Raddi) Brack., Minas Gerais, Brazil, 2009 (UC); *Testo 1547*, *Goniopteris* sp., Oaxaca, Mexico, 2018 (VT); *Fawcett 1070*, *Goniopteris baorucensis* S.E.Fawc., Barahona, Dominican Republic, 2018 (VT); *Salino 2131*, *Goniopteris* sp., Minas Gerais, Brazil, 1995 (UC 1605682); *Fawcett 1131*, *Goniopteris* sp., Independencia, Dominican Republic, 2018 (VT); *Salino 16037*, *Goniopteris* sp., Bahia, Brazil, 2014 (UC 2047348); *Rothfels 4991*, *Goniopteris* sp., Pasco, Peru, 2016 (HOXA, UC).

***Grypothix* (Holttum) S.E.Fawc. & A.R.Sm.**—*Chen Wade4104*, *Grypothrix crenulata* (Holttum) S.E.Fawc. & A.R.Sm., Lam Dong, Vietnam, 2014 (TAIF 458791, 458792); *Chen Wade4074*, *Grypothrix cuspidata* (Blume) S.E.Fawc. & A.R.Sm., Isabel, Solomon Islands, 2014 (TAIF 451883); *Kuo 931*, *Grypothrix longipetiolata* (K.Iwats.) S.E.Fawc. & A.R.Sm., Pingtung, Taiwan, 2010 (TAIF); *Kuo 958*, *Grypothrix megacuspis* (Baker) S.E.Fawc. & A.R.Sm., Pingtung, Taiwan, 2010 (TAIF); *Chen Wade1449*, *Grypothrix megacuspis* (Baker) S.E.Fawc. & A.R.Sm., Lam Dong, Vietnam, 2010 (TAIF 397403); *Kuo 932*, *Grypothrix parishii* (Bedd.) S.E.Fawc. & A.R.Sm., Pingtung, Taiwan, 2010 (TAIF); *Kuo 1720*, *Grypothrix parishii* (Bedd.) S.E.Fawc. & A.R.Sm., vel aff., Hainan, China, 2010 (TAIF); *Kessler 13727*, *Grypothrix ramosii* (C.Chr.) S.E.Fawc. & A.R.Sm., West Papua, Indonesia, 2008 (UC 2048621); *Chen Wade3972*, *Grypothrix ramosii* (C.Chr.) S.E.Fawc. & A.R.Sm., Negros, Philippines, 2014 (TAIF 454810, 454811); *Chen Wade4847*, *Grypothrix rubicunda* (Alderw.) S.E.Fawc. & A.R.Sm., Pahang, Peninsular Malaysia, 2017 (KLU, TAIF, UC); *Chen Wade2193*, *Grypothrix salicifolia* (Wall. ex Hook.) S.E.Fawc. & A.R.Sm., cultivated, Malaysia, 2012 (TAIF 430576, 430577, 430578, 430579); *Kuo 907*, *Grypothrix simplex* (Hook.) S.E.Fawc. & A.R.Sm., Pingtung, Taiwan, 2010 (TAIF); *Karger 916*, *Grypothrix sulawesiensis* (K.Iwats.) S.E.Fawc. & A.R.Sm., Lore Lindu, Sulawesi, 2010 (UC 2048338; UC 2048377); *Sundue 2243*, *Grypothrix triphylla* (Sw.) S.E.Fawc. & A.R.Sm., Bukit Timah, Singapore, 2010 (VT 197731).

***Hoiokula* S.E.Fawc. & A.R.Sm.**—*Hobdy 2664*, *Hoiokula pendens* (D.D.Palmer) S.E.Fawc. & A.R.Sm., Maui, Hawaiian Islands, 1986 (UC 1547482); *Wood 11291*, *Hoiokula* cf. *pendens* (D.D.Palmer) S.E.Fawc. & A.R.Sm., Maui, Hawaiian Islands, 2005 (UC 2013587); *Grether 3404*, *Hoiokula sandwicensis* (Brack.) S.E.Fawc. & A.R.Sm., Hawaii, Oahu, U.S.A., 1945 (UC 96990).

***Leptogramma* J.Sm.**—*Kuo 2126*, *Leptogramma cyrtomioides* (C.Chr.) Y.H.Chang & L.Y.Kuo, Sichuan, China, 2011 (TAIF); *Liu 9476*, *Leptogramma himalaica* Ching, Yunnan, China, 2008 (TAIF); *Chang 20140714043*, *Leptogramma intermedia* Ching ex Y.H.Chang & L.Y.Kuo, Guizhou, China, 2014 (TAIF); *Liu 9463B*, *Leptogramma latipinna* (Ching ex Y.X.Lin) Y.H.Chang & L.Y.Kuo, Yunnan, China, 2008 (TAIF); *Kuo 1426*, *Leptogramma* aff. *leptogrammoides* (K.Iwats.) Y.H.Chang &

L.Y.Kuo, Yunnan, China, 2010 (TAIF); *Chang 20100917-029*, *Leptogramma mollissima* (Fisch. ex Kunze) Ching, Taitung, Taiwan, 2010 (TAIF); *Kuo 1086*, *Leptogramma mollissima* (Fisch. ex Kunze) Ching, Kagoshima, Japan, 2010 (TAIF); *Kuo 1009*, *Leptogramma mollissima* (Fisch. ex Kunze) Ching, Tateyama type, Tsukuba, Japan, 2010 (TAIF); *Pringle s.n.*, *Leptogramma pilosa* (M.Martens & Galeotti) Underw. var. *major* (Crawford) comb. ined., Puebla, Mexico, 1908 (VT); *Pringle 2589*, *Leptogramma pilosa* (M.Martens & Galeotti) Underw. var. *pilosa*, Jalisco, Mexico, 1889 (VT); *Quintanilla 1095*, *Leptogramma pozoi* (Lag.) Heywood, A Coruna, Spain, 2016 (TAIF); *Chang 20140712024*, *Leptogramma scallanii* (Christ) Ching, Guizhou, China, 2014 (TAIF); *Schuettpelz 1135*, *Leptogramma tottoides* Hayata ex H.Ito, Taiwan, 2007 (DUKE, TAIF); *Kuo 3818*, *Leptogramma tottoides* Hayata ex H.Ito, Nantou, Taiwan, 2013 (TAIF); *Kuo 2238*, *Leptogramma* sp., Sichuan, China, 2011 (TAIF).

***Macrothelypteris* (H.Ito) Ching**—*Tagawa 7912*, *Macrothelypteris contingens* Ching, Honshu, Japan, 1957 (UC 1180602); *Bartholomew 1436*, *Macrothelypteris oligophlebia* (Baker) Ching var. *elegantissima* (Hayata) Ching, Hubei, China, 1980 (UC 1492073); *Nitta 307*, *Macrothelypteris polypodioides* (Hook.) Holttum, Moorea, Society Islands, 2008 (P, PAP, TNS, UC); *Fawcett 696*, *Macrothelypteris torresiana* (Gaudich.) Ching, Taveuni, Fiji, 2016 (UC 2049797, VT); *Testo 730*, *Macrothelypteris torresiana* (Gaudich.) Ching, Puntarenas, Costa Rica, 2015 (VT).

***Menisciopsis* (Holttum) S.E.Fawc. & A.R.Sm.**—*Wood 15623*, *Menisciopsis boydiae* (D.C.Eaton) S.E.Fawc. & A.R.Sm., Hawaii, Maui, U.S.A., 2013 (PTBG); *Wood 16205*, *Menisciopsis cyatheoides* (Kaulf.) S.E.Fawc. & A.R.Sm., Hawaii, Kauai, U.S.A., 2015 (PTBG); *Fawcett 277*, *Menisciopsis cyatheoides* (Kaulf.) S.E.Fawc. & A.R.Sm., Hawaii, Kauai, U.S.A., 2015 (UC, PTBG, VT); *Chen Wade2564*, *Menisciopsis lakhimpurensis* (Rosenst.) S.E.Fawc. & A.R.Sm., Lam Dong, Vietnam, 2013 (TAIF 439708, 439709, 439710); *Chen Wade2533*, *Menisciopsis penangiana* (Hook.) S.E.Fawc. & A.R.Sm., Guangxi, China, 2013 (TAIF 440168, 440169); *Karger 386*, *Menisciopsis rubida* (J.Sm. ex Hook.) S.E.Fawc. & A.R.Sm., Sibuyon, Philippines, 2009 (Z); *Fawcett 716*, *Menisciopsis rubrinervis* (Mett.) S.E.Fawc. & A.R.Sm., Taveuni, Fiji, 2016 (UC 2049790 VT); *Wood 16708*, *Menisciopsis wailele* (Flynn) S.E.Fawc. & A.R.Sm., Hawaii, Kauai, U.S.A., 2016 (PTBG, UC).

***Meniscium* Schreber**—*Smith 2835*, *Meniscium andreanum* Sodiro, Pichincha, Ecuador, 2001 (UC 1763551); *Churchill 3028*, *Meniscium angustifolium* Willd., Toro Negro, Puerto Rico, 1978 (VT 197522); *Jiménez 1967*, *Meniscium arborescens* Humb. & Bonpl. ex Willd., Pando, Bolivia, 2003 (UC 1785614, 1785615); *Tuomisto 11935*, *Meniscium arcanum* (Maxon & C.V.Morton) Pic.Serm., Napo, Ecuador, 1998 (UC 1788069); *Weigelt 90436*, *Meniscium chrysodioides* Fée, La Paz, Bolivia, 2009 (GOET, LPB, UC 1970780; UC 1970781); *Rothfels 5013*, *Meniscium consobrinum* (Maxon & C.V.Morton) Pic.Serm., Pasco, Peru, 2016 (HOXA, UC); *Fernandes 779*, *Meniscium delicatum* R.S. Fern. & Salino, Piaui, Brazil, 2012 (UC 2015504); *Fernandes 970*, *Meniscium delicatum* R.S. Fern. & Salino, Piaui, Brazil, 2012 (UC 2048953); *Testo 782*, *Meniscium falcatum* Liebm., Heredia, Costa Rica, 2017 (VT); *Jiménez 1047*, *Meniscium falcatum* Liebm., La Paz, Bolivia, 2001 (LPB); *Testo 1233*, *Meniscium giganteum* Mett., Heredia, Costa Rica, 2017 (VT); *Foster 85-101*, *Meniscium giganteum* Mett., Pichincha, Ecuador, 1985 (UC 1505353); *Ortega 3137*, *Meniscium hostmannii* (Klotzsch) R.S.Fern. & Salino, Mérida, Venezuela, 1988 (UC 1541929); *Sundue 890*, *Meniscium lanceum* (A.R.Sm.) R.S.Fern. & Salino, Santa Cruz, Bolivia, 2003 (VT 197535); *Rothfels 08-180*, *Meniscium lingulatum* (C.Chr.) Pic.Serm., Heredia, Costa Rica, 2008 (CR, DUKE, INB, MO, UC 2030226); *Conant 895*, *Meniscium longifolium* Desv., Amazonas, Brazil, 1975 (VT 197530); *Matos 1561*, *Meniscium macrophyllum* Kunze, Bahia, Brazil, 2008 (UC 1927134); *Arruda 963*, *Meniscium maxonianum* (A.R.Sm.) R.S. Fern. & Salino, Para, Brazil, 2012 (UC 2015502); *Acebey 769*, *Meniscium membranaceum* (Mett.) Pic.Serm., Cochabamba, Bolivia, 1997 (UC 1736854); *Windisch 4774*, *Meniscium nesioticum* (Maxon & C.V.Morton) Jermy & T.G.Walker, Mato Grosso, Brazil, 1986 (UC 1540486); *Wood 16435*, *Meniscium pachysorum* (Hieron.) R.S. Fern. & Salino, La Paz, Bolivia, 2000 (UC 1789057); *Fawcett 480*, *Meniscium reticulatum* (L.) Sw., Rio Grande, Puerto Rico, 2016 (VT 197547); *Testo 528*, *Meniscium serratum* Cav., Heredia, Costa Rica, 2014 (VT); *Testo 1455*, *Meniscium* sp., Chocó, Colombia, 2017 (VT).

***Menisorus* Alston**—*Leeuwenberg 6707*, *Menisorus pauciflorus* (Hook.) Alston, Lomie', Cameroon, 1965 (UC 1385267); *Reitsma 1069*, *Menisorus pauciflorus* (Hook.) Alston, Doussala, Gabon, 1985 (NY); *Lovett 353*, *Menisorus unitus* (Kunze) S.E.Fawc. & A.R.Sm., Iringa, Tanzania, 1991 (UC 2027666).

***Mesophlebion* Holttum**—*Karger 1044*, *Mesophlebion chlamydophorum* (C.Chr.) Holttum, Buru, Maluku, 2010 (UC 2048281, Z); *Chen Wade3817*, *Mesophlebion crassifolium* (Blume) Holttum, Negros, Philippines, 2014 (TAIF 454524, 454535); *Cicuzza 456*, *Mesophlebion crassifolium* (Blume) Holttum, Sulawesi, Pono, Indonesia, 2007 (UC, Z); *Chen Wade4227*, *Mesophlebion echinatum* (Mett.) Holttum, Sabah, Malaysia, 2015 (TAIF 468069, 468070); *Chen Wade4242*, *Mesophlebion motleyanum* (Hook.) Holttum, Sabah, Malaysia, 2015 (TAIF 468057, 468058); *Cicuzza 532*, *Mesophlebion persquamiferum* (Alderw.) Holttum, Sulawesi, Pono, Indonesia, 2008 (UC 2048261); *Kessler 13721*, *Mesophlebion rufescens* Holttum, Oransbari, West Papua, 2008 (UC 2048600); *Chen Wade2197*, *Mesophlebion trichopodum* (C.Chr.) Holttum, Cultivated, Malaysia, 2012 (TAIF 430525, 430584, 430585, 430586); *Kluge 7057*, *Mesophlebion trichopodum* (C.Chr.) Holttum, vel aff., Sulawesi, Bariri, Indonesia, 2007 (BO, UC).

***Mesopteris* Ching**—*Chen Wade4186*, *Mesopteris* cf. *paraphysophora* (Alderw.) S.E.Fawc. & A.R.Sm., Sabah, Malaysia, 2015 (TAIF 467321, 467322); *Chen Wade3208*, *Mesopteris pseudostenobasis* (Copel.) S.E.Fawc. & A.R.Sm., Vangunu, Solomon Islands, 2013 (TAIF 451637). *Wang s.n.*, *Mesopteris tonkinensis* (C.Chr.) Ching, Guangxi, China, 2011 (IBG).

***Metathelypteris* (H.Ito) Ching**—*Chang 20090724-013*, *Metathelypteris adscendens* (Ching) Ching, Taipei, Taiwan, 2009 (TAIF); *Kessler 13545*, *Metathelypteris dayi* (Bedd.) Holttum, Peninsular Malaysia, Malaysia, 2008 (GOET, UC 1951588); *Chen Wade4138*, *Metathelypteris flaccida* (Blume) Ching, Lam Dong, Vietnam, 2014 (TAIF); *Chen Wade1926*, *Metathelypteris flaccida* (Blume) Ching, Gede-Pangrango, Java, Indonesia, 2011 (TAIF 388290); *Karger 863*, *Metathelypteris gracilescens* (Blume) Ching, Mindanao, Philippines, 2010 (Z); *Kuo 3420*, *Metathelypteris gracilescens* (Blume) Ching, Bukidnon, Philippines, 2012 (UC); *Chang 20091106-036*, *Metathelypteris* cf. *gracilescens* (Blume) Ching, Tam Dao, Vietnam, 2009 (TAIF); *Chen Wade2365*, *Metathelypteris laxa* (Franch. & Sav.) Ching, Guangxi, China, 2013 (TAIF); *Kuo 2347*, *Metathelypteris uraiensis* (Rosenst.) Ching, Taipei, Taiwan, 2011 (TAIF).

***Oreopteris* Holub**—*Wardlaw s.n.*, *Oreopteris limbosperma* (All.) Holub, Arran, Scotland, 2001 (UC 1763849); *Barrington 2408*, *Oreopteris quelpartensis* (Christ) Holub, Alaska, U.S.A., 2011 (VT 197585).

***Pakau* S.E.Fawc. & A.R.Sm.**—*Walker 4393*, *Pakau pennigera* (G.Forst.) S.E.Fawc. & A.R.Sm., Auckland, New Zealand, 1949 (UC 916383).

***Pelazoneuron* (Holttum) A.R.Sm. & S.E.Fawc.**—*Fawcett 368*, *Pelazoneuron abruptum* (C.Presl) A.R.Sm. & S.E.Fawc., Arecibo, Puerto Rico, 2016 (VT); *Yatskievych 85-208*, *Pelazoneuron albicaule* (Fée) A.R.Sm. & S.E.Fawc., Oaxaca, Mexico, 1985 (UC); *Mickel 5078b*, *Pelazoneuron albicaule* (Fée) A.R.Sm. & S.E.Fawc. × *puberulum* (Baker) C.V.Morton, Oaxaca, Mexico, 1970 (UC 1507582); *Montreal Botanic Garden 1593-1954*, *Pelazoneuron augescens* (Link) A.R.Sm. & S.E.Fawc., cultivated, Canada, 2017 (UC, VT); *Barbosa 1593*, *Pelazoneuron berroi* (C.Chr.) A.R.Sm. & S.E.Fawc., Mato Grosso do Sul, Brazil, 2006 (UC); *Wood 15027*, *Pelazoneuron clivale* (A.R.Sm.) A.R.Sm. & S.E.Fawc., La Paz, Bolivia, 1999 (UC 1788776); *Rothfels 5019*, *Pelazoneuron depilatum* (A.R.Sm.) A.R.Sm. & S.E.Fawc., Pasco, Peru, 2016 (HOXA, UC); *Carvajal Hernandez 700*, *Pelazoneuron kunthii* (Desv.) A.R.Sm. & S.E.Fawc., Veracruz, Mexico, 2013 (UC); *Gonzales 17140*, *Pelazoneuron ovatum* (R.P.St.John) A.R.Sm. & S.E.Fawc. var. *lindheimeri* (C.Chr.) A.R.Sm., Tabasco, Mexico, 1985 (UC); *Torres 17250*, *Pelazoneuron ovatum* (R.P.St.John) A.R.Sm. & S.E.Fawc. var. *lindheimeri* (C.Chr.) A.R.Sm., Oaxaca, Mexico, 2012 (VT); *Fawcett 744*, *Pelazoneuron patens* (Sw.) A.R.Sm. & S.E.Fawc., Puntarenas, Costa Rica, 2017 (UC 2049033, VT); *Mexia 4478*, *Pelazoneuron patens* (Sw.) A.R.Sm. & S.E.Fawc. var. *dissimilis* (Schrad.) comb. ined., Minas Gerais, Brazil, 1930 (UC 419565); *Charlton 1338*, *Pelazoneuron puberulum* (Baker) A.R.Sm. & S.E.Fawc. var. *sonorense* (A.R.Sm.) A.R.Sm. & S.E.Fawc., Baja Norte, Mexico, 1988 (UC); *Fawcett 752*, *Pelazoneuron puberulum* (Baker) A.R.Sm. & S.E.Fawc. var. *sonorense* (A.R.Sm.) A.R.Sm. & S.E.Fawc., California, U.S.A., 2017 (JEPS, SBBG, VT); *Calzadilla 379*, *Pelazoneuron schizotis* (Hook.) A.R.Sm. & S.E. Fawc., Santa Cruz, Bolivia, 2008 (UC); *Fawcett 1034*, *Pelazoneuron serra* (Sw.) A.R.Sm. & S.E.Fawc., Barahona, Dominican Republic, 2018 (VT); *Vargas 1062*, *Pelazoneuron tuerckheimii* (Donn.Sm.) A.R.Sm. & S.E.Fawc., Huehuetenango, Guatemala, 2005 (UC).

Phegopteris **(C.Presl) Fée**—*Fawcett 566*, *Phegopteris connectilis* (Michx.) Watt, Michigan, U.S.A., 2016 (UC 2049132, VT); *Moran 5420*, *Phegopteris connectilis* (Michx.) Watt., Yilan, Taiwan, 1991 (UC 1593301); *Testo s.n.*, *Phegopteris decursive-pinnata* (H.C.Hall) Fée, Florida, U.S.A., 2019 (FLAS); *Kuo 3371*, *Phegopteris decursive-pinnata* (H.C.Hall) Fée, Nantou, Taiwan, 2012 (TAIF); *Gilman 18022*, *Phegopteris excelsior* A.V.Gilman & N.R.Patel, Vermont, U.S.A., 2018 (VT); *Rothfels 3484*, *Phegopteris hexagonoptera* Fée, Indiana, U.S.A., 2009 (DUKE).

Plesioneuron **Holttum**—*Smith 9348*, *Plesioneuron archboldiae* (Copel.) Holttum, Viti Levu, Fiji, 1953 (UC 1438794); *Wood 16859*, *Plesioneuron attenuatum* (Brack.) Holttum, Upolu, Samoa, 2016 (PTBG); *Johns 10052*, *Plesioneuron* aff. *belense* (Copel.) Holttum, Mimika, Papua New Guinea, 1999 (UC 1877604); *Karger 2796*, *Plesioneuron costulisorum* (Copel.) Holttum, West Papua, Indonesia, 2011 (UC 2048199, Z); *James SAJ0921*, *Plesioneuron falcatipinnulum* (Copel.) Holttum, Siboma, Papua New Guinea, 2012 (UC 2043771); *Fawcett 654*, *Plesioneuron hopeanum* Holttum, Taveuni, Fiji, 2016 (UC 2049789, VT); *Chen Wade2762*, *Plesioneuron imbricatum* (Holttum) S.E.Fawc. & A.R.Sm., Kolombangara, Solomon Islands, 2013 (TAIF 444985, 444988, 444989, 444990, 445986, 445987); *Chen Wade3623*, *Plesioneuron imbricatum* (Holttum) S.E.Fawc. & A.R.Sm., Kolombangara, Solomon Islands, 2013 (TAIF); *Karger 2718*, *Plesioneuron keysserianum* (Rosenst.) S.E.Fawc. & A.R.Sm., West Papua, Indonesia, 2011 (UC 2048198, Z); *Nitta 281*, *Plesioneuron marquesicum* Holttum, Moorea, French Polynesia, 2008 (P, TNS, UC 1969692); *Wood 10431*, *Plesioneuron marquesicum* Holttum, Ua Pou, Marquesas Islands, (PTBG); *Wood 13564*, *Plesioneuron ponapeanum* (Hosok.) Holttum, Pohnpei, Caroline Islands (PTBG); *Fawcett 612*, *Plesioneuron prenticei* Holttum, Viti Levu, Fiji, 2016 (UC, VT); *Kessler 13948*, *Plesioneuron savaiense* (Baker) Holttum, Oransbari, West Papua, 2008 (UC 2048609); *SITW10504*, *Plesioneuron subglabrum* Holttum, Isabel, Solomon Islands, 2016 (UC 2048662); *Wood 11026*, *Plesioneuron tahitense* Holttum, Huahine, Society Islands, 2004 (PTBG); *Karger 1752*, *Plesioneuron tuberculatum* (Ces.) Holttum, West Papua, Indonesia, 2008 (UC 2048613, Z); *Karger 1015*, *Plesioneuron* sp., Sulawesi, Gunung Duasudara, Indonesia, 2010 (UC 2048303, Z); *Nitta 2772*, *Plesioneuron* sp., Moorea, Society Islands, 2013 (GH, UC).

Pneumatopteris **Nakai**—*Schmidt 2167*, *Pneumatopteris afra* (Christ) Holttum, Volta, Ghana, 1996 (UC 1617976); *Mousset 144*, *Pneumatopteris auctipinna* Holttum, Java, Indonesia, (UC 352868); *Chen Wade1867*, *Pneumatopteris callosa* (Blume) Nakai, Cibodas, Java, Indonesia, 2011 (TAIF 388639, 388640, 388641, 388642, 388643); *SITW11069*, *Pneumatopteris glandulifera* (Brack.) Holttum, Santa Cruz, Solomon Islands, 2016 (UC 2048653, 2048654); *Kluge 7832*, *Pneumatopteris humbertii* Holttum, Marojejy, Madagascar, 2009 (UC); *Lu 18318*, *Pneumatopteris* aff. *lithophila* Holttum, Bontoc, Philippines, 2009 (TAIF 334863); *Nitta 2748*, *Pneumatopteris mesocarpa* (Copel.) Holttum, Moorea, Society Islands, 2013 (GH, UC); *Fawcett 645*, *Pneumatopteris parksii* Holttum, Taveuni, Fiji, 2016 (UC 2049795, VT); *Fawcett 638*, *Pneumatopteris* sp., Viti Levu, Fiji, 2016 (UC 2049796, VT); *Wood 17058*, *Pneumatopteris* sp., Savaii, Samoa, 2016 (PTBG); *SITW11157*, *Pneumatopteris* sp., Guadalcanal, Solomon Islands, 2016 (UC).

Pronephrium **C.Presl**—*Chen Wade2061*, *Pronephrium affine* (Blume) C.Presl, West Java, Halimum, Indonesia, 2011 (TAIF 389026); *Price 670*, *Pronephrium aoristisorum* (Harr.) S.E.Fawc. & A.R.Sm., Luzon, Philippines, 1970 (UC); *Cicuzza 966*, *Pronephrium celebicum* (Baker) Holttum, Sulawesi, Pono, Indonesia, 2008 (Z); *Chen Wade3994*, *Pronephrium granulosum* (C.Presl) Holttum, Negros, Philippines, 2014 (TAIF); *Karger 722*, *Pronephrium granulosum* (C.Presl) Holttum, Mindanao, Philippines, 2010 (Z 104927); *Chen Wade4755*, *Pronephrium hosei* (Baker) Holttum, Sabah, Borneo, 2016 (UC); *Chen Wade2194*, *Pronephrium menisciicarpon* (Blume) Holttum, Cultivated, Malaysia, 2012 (TAIF 430588); *Chen Wade4719*, *Pronephrium peltatum* (Alderw.) Holttum var. *aberrans* Holttum, Sabah, Borneo, 2016 (UC); *Williams 208*, *Pronephrium rhombeum* (Christ) Holttum, Luzon, Philippines, 1903 (UC 419282); *Karger 912*, *Pronephrium* aff. *xiphioides* (C.Chr.) Holttum, Lore Lindu, Sulawesi, 2010 (UC 2048294).

Pseudocyclosorus **Ching**—*Kuo 3372*, *Pseudocyclosorus esquirolii* (Christ) Ching, Nantou, Taiwan, 2012 (TAIF); *Zheng-yu 15516*, *Pseudocyclosorus esquirolii* (Christ) Ching, Sichuan, China, 1996 (UC 1727977); *Chen Wade1451*, *Pseudocyclosorus* cf. *esquirolii* (Christ) Ching, Lam Dong, Vietnam, 2010 (TAIF 410818); *Heng 21921*, *Pseudocyclosorus falcilobus* (Hook.) Ching, Yunnan, China, 2004 (UC 1923513); *Holttum s.n.*, *Pseudocyclosorus ornatipes* Holttum & J.W.Grimes, Kalimpong, India, 1972 (UC 1948785); *Mwangulango 1103*, *Pseudocyclosorus pulcher* (Bory ex Willd.) Holttum, Mbeya, Tanzania, 2003 (UC 1877798); *Stewart 15940*, *Pseudocyclosorus repens* (C.Hope) Ching, Uttarakhand, India, 1937 (UC 770798); *Kuo 2913*, *Pseudocyclosorus subochthodes* (Ching) Ching, Yunnan, China, 2012 (TAIF); *Kuo 1391*, *Pseudocyclosorus tylodes* (Kunze) Ching, Yunnan, China, 2010 (TAIF); *Chen Wade2523*, *Pseudocyclosorus tylodes* (Kunze) Ching, Guangxi, China, 2013 (TAIF); *Kluge 7655*, *Pseudocyclosorus* sp., Singani, Grand Comores, 2008 (UC 1924776).

Pseudophegopteris **Ching**—*Kessler 14142*, *Pseudophegopteris aurita* (Hook.) Ching, West Papua, Wamena, Indonesia, 2008 (UC 2048595); *Rothfels 4735A*, *Pseudophegopteris* aff. *aurita* (Hook.) Ching, Kinabalu, Borneo, 2016 (UC); *Togasi 1216*, *Pseudophegopteris bukoensis* (Tagawa) Holttum, Honshu, Japan, 1955 (UC 1087169); *Janssen 2725*, *Pseudophegopteris cruciata* (Willd.) Holttum, Reunion, France, 2005 (P); *Kuo 3887*, *Pseudophegopteris hirtirachis* (C.Chr.) Holttum, Nantou, Taiwan, 2013 (TAIF); *Degener 31419*, *Pseudophegopteris keraudreniana* (Gaudich.) Holttum, Hawaii, U.S.A., 1967 (UC 1367107); Chang 2015*0715-004*, *Pseudophegopteris levingei* (C.B.Clarke) Ching, Nantou, Taiwan, 2015 (TAIF); *Bartholomew 758*, *Pseudophegopteris pyrrhorhachis* (Kunze) Ching, Hubei, China, 1980 (UC 1493503); *Rothfels 4735B*, *Pseudophegopteris* aff. *rectangularis* (Zoll.) Holttum, Kinabalu, Borneo, 2016 (UC); *Chang 20110703-009*, *Pseudophegopteris subaurita* (Tagawa) Ching, Yilan, Taiwan, 2011 (TAIF); *Miehe 94-227-17*, *Pseudophegopteris tibetana* Ching & S.K.Wu, Xizang, China, 1994 (UC 1747534); *Chen Wade4136*, *Pseudophegopteris yunkweiensis* (Ching) Ching, Lam Dong, Vietnam, 2014 (TAIF 458834, 458835, 458836).

Reholttumia **S.E.Fawc. & A.R.Sm.**—*Lorence 10592*, *Reholttumia costata* (Brack.) S.E.Fawc. & A.R.Sm., Savaii, Samoa, 2016 (PTBG); *Chen Wade4808*, *Reholttumia ecallosa* (Holttum) S.E.Fawc. & A.R.Sm., Pahang, Peninsular Malaysia, 2017 (TAIF, KLU, UC); *Chen Wade1842*, *Reholttumia ecallosa* (Holttum) S.E.Fawc. & A.R.Sm., vel aff., Cibodas, Java, Indonesia, 2011 (TAIF 388637, 388638); *Edmonds ME224*, *Reholttumia hudsoniana* (Brack.) S.E.Fawc. & A.R.Sm., Hawaii, Kauai, U.S.A., 2014 (UC); *Kessler 14129*, *Reholttumia jermyi* (Holttum) S.E.Fawc. & A.R.Sm., West Papua, Indonesia, 2008 (UC2048579); *Karger 183*, *Reholttumia laevis* (Mett.) S.E.Fawc. & A.R.Sm., Panay, Philippines, 2009 (Z); *Kuo 3500*, *Reholttumia* aff. *laevis* (Mett.) Holttum, Bukidnon, Philippines, 2012 (UC); *Chen Wade1900*, *Reholttumia longipes* (Blume) S.E.Fawc. & A.R.Sm., Gede-Pangrango, Java, Indonesia, 2011 (TAIF 388228, 388229, 388230); *Parks 16040*, *Reholttumia macroptera* (Copel.) S.E.Fawc. & A.R.Sm., Eua, Tonga, 1926 (UC 297574); *SITW11089*, *Reholttumia magnifica* (Copel.) S.E.Fawc. & A.R.Sm., Santa Cruz, Solomon Islands, 2016 (UC 2048643); *SITW10556*, *Reholttumia magnifica* (Copel.) S.E.Fawc. & A.R.Sm., Santa Cruz, Solomon Islands, 2016 (UC 2048650, 2048651); *Chen Wade4266*, *Reholttumia* aff. *michaelis* (Holttum) S.E.Fawc. & A.R.Sm., Sabah, Malaysia, 2015 (TAIF 468030, 468031, 468032, 468033, 468034); *Kuo 2051*, *Reholttumia nitidula* (C.Presl) S.E.Fawc. & A.R.Sm., Laguna, Philippines, 2011 (TAIF); *Kuo 540*, *Reholttumia* aff. *nitidula* (C.Presl) Holttum, Mountain, Philippines, 2009 (UC); *Kluge 7830*, *Reholttumia remotipinna* (Bonap.) S.E.Fawc. & A.R.Sm., Marojejy, Madagascar, 2009 (UC 2014697); *Kluge 7830*, *Reholttumia* cf. *remotipinna* (Bonap.) S.E.Fawc. & A.R. Sm., Marojejy, Madagascar, 2009 (UC, Z); *SITW11114*, *Reholttumia rodigasiana* (T.Moore) S.E.Fawc. & A.R.Sm., Guadalcanal, Solomon Islands, 2016 (UC 2048645); *Karger 1265*, *Reholttumia sogerensis* (Gepp) S.E.Fawc. & A.R.Sm., Seram, Indonesia, 2010 (UC 2048301, Z); *Elmer 9845*, *Reholttumia* cf. *sogerensis* (Gepp) S.E.Fawc. & A.R.Sm., Negros, Philippines, 1908 (VT 197761); *Kuo 963*, *Reholttumia truncata* (Poir.) S.E.Fawc. & A.R.Sm., Pingtung, Taiwan, 2010 (TAIF); *James 470*, *Reholttumia* sp., Morobe, Papua New Guinea, 2012 (UC 2043754); *SITW11115*, *Reholttumia* sp., Guadalcanal, Solomon Islands, 2016 (UC 2048649); *Chen Wade3630*, *Reholttumia* sp., Kolombangara, Solomon Islands, 2013 (TAIF 460000); *SITW11589*, *Reholttumia* sp., Guadalcanal, Solomon Islands, 2016 (TAIF); *Karger 1753*, *Reholttumia* sp., West Papua, Indonesia, 2008 (UC 2048592, Z); *Kuo 543*, *Reholttumia* sp., Mountain, Philippines, 2009 (UC).

Sphaerostephanos **J.Sm.**—*Sundue 3775*, *Sphaerostephanos* aff. *adenostegius* (Copel.) Holttum, Madang, Papua New Guinea, 2014 (UC 2049168); *Kuo 565, Sphaerostephanos* aff. *alcasidii* Holttum, Philippines, 2009 (TAIF); *Karger 1467*, *Sphaerostephanos appendiculatus* (Blume) Holttum, Tidore, Maluku Utara, 2010 (UC 2048331, Z); *Kessler 13708*, *Sphaerostephanos appendiculatus* (Blume) Holttum, Sulawesi, Indonesia, 2008 (GOET, UC 1930527); *Kessler 13907*, *Sphaerostephanos arbuscula* (Willd.) Holttum, Reunion, France, 2008 (UC 1925690); *Sundue 3715*, *Sphaerostephanos archboldii* (C.Chr.) Holttum, Madang, Papua New Guinea, 2014 (UC 2049100); *Kessler 14130*, *Sphaerostephanos archboldii* (C.Chr.) Holttum, West Papua, Wamena, Indonesia, 2008 (UC 2048587); *Conn 5509*, *Sphaerostephanos archboldii* (C.Chr.) Holttum, Papua New Guinea, 2010 (UC 2043794); *Sundue 3848*, *Sphaerostephanos atasripii* (Rosenst.) Holttum, vel aff., Madang, Papua New Guinea, 2014 (UC 2049098); *Karger 1022*, *Sphaerostephanos* aff. *batjanensis* (Rosenst.) Holttum, Sulawesi, Gunung Duasudara, Indonesia, 2010 (UC 2048305, Z); *Fawcett 701*, *Sphaerostephanos beccarianus* (Ces.) S.E.Fawc. & A.R.Sm., Taveuni, Fiji, 2016 (UC 2049798, VT); *SITW11593*, *Sphaerostephanos braithwaitei* Holttum, Guadalcanal, Solomon Islands, 2016 (UC 2048659, 2048660, 2048661); *Kessler 13850*, *Sphaerostephanos brauseanus* (Holttum) S.E.Fawc. & A.R.Sm., West Papua, Indonesia, 2008 (UC 2048589); *Karger 990*, *Sphaerostephanos canescens* (Blume) Holttum, Sulawesi, Gunung Duasudara, Indonesia, 2010 (UC 2048288); *Alston 16718*, *Sphaerostephanos canescens* (Blume) Holttum, Tidore, Maluku Utara, (MICH); *Grether 3971*, *Sphaerostephanos cataractorum* (W.H.Wagner & Grether) Holttum, Manus, Admiralty Islands, 1945 (UC 732987); *Karger 2801*, *Sphaerostephanos confertus* (Brause) Holttum, West Papua, Indonesia, 2011 (UC 2048202, Z); *Sundue 3850*, *Sphaerostephanos confertus* (Brause) Holttum, Madang, Papua New Guinea, 2014 (UC 2049099); *Chen Wade3098*, *Sphaerostephanos decadens* (Baker) Holttum, Viti Levu, Fiji, 2013 (TAIF 439697); *Kuo 3656*, *Sphaerostephanos dichotrichoides* (Alderw.) Holttum, Bukidnon, Philippines, 2012 (UC); *Chen Wade3113*, *Sphaerostephanos doodioides* (Copel.) Holttum, Guadalcanal, Solomon Islands, 2013 (TAIF); *Ranker 1460*, *Sphaerostephanos elatus* (Bojer) Holttum, Reunion, France, 1992 (UC 1610044); *Karger 2692*, *Sphaerostephanos* cf. *flavoviridis* Holttum, West Papua, Indonesia, 2011 (UC 2048193, Z); *Schuettpelz 890*, *Sphaerostephanos glandulosus* (Blume) S.E.Fawc. & A.R.Sm., Malaysia, (DUKE, KEP, S); *James SAJ082*, *Sphaerostephanos hastatopinnatus* (Brause) Holttum, New Britain, Papua New Guinea, 2011 (UC 2043793); *Fawcett 640*, *Sphaerostephanos heterocarpus* (Blume) Holttum, Viti Levu, Fiji, 2016 (UC 2049794, VT); *Fawcett 619*, *Sphaerostephanos heterocarpus* (Blume) Holttum, Viti Levu, Fiji, 2016 (UC 2049783, VT); *Cicuzza 495*, *Sphaerostephanos hirsutus* (Kunze ex Mett.) Holttum, Sulawesi, Pono, Indonesia, 2008 (UC, Z); *Anderson 4119*, *Sphaerostephanos hirtisorus* (C.Chr.) Holttum, Chiang Mai, Thailand, 1976 (UC 1432224); *Chen Wade3559*, *Sphaerostephanos hochreutineri* (Christ) Holttum, Vella Lavella, Solomon Islands, 2013 (TAIF 460030); *Karger 1406*, *Sphaerostephanos incisus* (Copel.) S.E.Fawc. & A.R.Sm., Bacan, Mauluku Utara, Indonesia, 2010 (UC 2048291, Z); *Karger 1071*, *Sphaerostephanos lamii* Holttum, Buru, Maluku, 2010 (UC 2048332, Z); *Kessler 13559*, *Sphaerostephanos larutensis* (Bedd.) C.Chr., Peninsular Malaysia, Malaysia, 2008 (GOET, UC 1951607); *Chen Wade3885*, *Sphaerostephanos lastreoides* (C.Presl) Holttum, Negros, Philippines, 2014 (TAIF 455400); *Chen Wade3979*, *Sphaerostephanos lastreoides* (C.Presl) Holttum, Negros, Philippines, 2014 (TAIF 455815, 455816); *Cicuzza 219*, *Sphaerostephanos latebrosus* (Kunze ex Mett.) Holttum, Sulawesi, Bariri, Indonesia, 2007 (UC, Z); *Wood 14100*, *Sphaerostephanos maemonensis* (W.H.Wagner & Grether) Holttum, Kosrae, Caroline Islands, 2010 (PTBG); *Chen Wade3957*, *Sphaerostephanos magnus* (Copel.) Holttum, Negros, Philippines, 2014 (TAIF 454834, 454835,454836, 454837); *Chen Wade3995-2*, *Sphaerostephanos* aff. *microlonchus* (Christ) S.E.Fawc. & A.R.Sm., Negros, Philippines, 2014 (TAIF 454807, 454808, 454809; VT 197691); *Karger 2663*, *Sphaerostephanos* aff. *mundus* (Rosenst.) Holttum, West Papua, Indonesia, 2011 (UC 2048196, Z); *Karger 2809*, *Sphaerostephanos novoguineensis* (Brause) Holttum, West Papua, Indonesia, 2011 (UC 2048203, Z); *Rothfels 4803*, *Sphaerostephanos oosorus* (Baker) Holttum, Mount Silam, Borneo, 2016 (UC 2048744); *Cicuzza 185*, *Sphaerostephanos oppositus* Holttum, Sulawesi, Bariri, Indonesia, 2007 (Z); *Chen Wade1806*, *Sphaerostephanos penniger* (Hook.) Holttum, Gunung Gede Pangrango National Park, Indonesia, 2011 (TAIF 388622, 388623, UC); *Chen Wade4839*, *Sphaerostephanos penniger* (Hook.) Holttum, Pahang, Peninsular Malaysia, 2017 (KLU, TAIF, UC); *Karger 2645*, *Sphaerostephanos pentaphyllus* (Rosenst.) S.E.Fawc. & A.R.Sm., West Papua, Indonesia, 2011 (UC 2048204, Z); *Karger 2859*, *Sphaerostephanos pilosquamatus* (Alderw.) Holttum, West Papua, Indonesia, 2011 (UC 2048191, Z); *Kessler 13709*, *Sphaerostephanos polycarpus* (Blume) Copel., Sulawesi, Indonesia, 2008 (GOET, UC); *Cicuzza 466*, *Sphaerostephanos polyotis* (C.Chr.) Holttum, Sulawesi, Pono, Indonesia, 2007 (UC, Z); *Chang 20100917-024*, *Sphaerostephanos productus* (Kaulf.) Holttum, Taitung, Taiwan, 2010 (TAIF); *Kluge 7448*, *Sphaerostephanos sarasinorum* Holttum, Sulawesi, Rorekatimbu, Indonesia, 2007 (BO, UC); *Chen Wade2965*, *Sphaerostephanos scandens* Holttum, Rendova, Solomon Islands, 2013 (TAIF 448614); *Kluge 9201*, *Sphaerostephanos scopulorum* (Holttum) S.E.Fawc. & A.R.Sm., West Papua, Indonesia, 2008 (UC 2048622); *Karger 247*, *Sphaerostephanos sessilipinna* (Copel.) Holttum, Panay, Philippines, 2009 (Z); *Chen Wade2027-1*, *Sphaerostephanos stipellatus* (Blume) Holttum, West Java, Halimum, Indonesia, 2011 (TAIF 388183, 388184); *Sundue 3752*, *Sphaerostephanos subappendiculatus* (Copel.) S.E.Fawc. & A.R.Sm., Madang, Papua New Guinea, 2014 (UC 2049167, VT); *Nitta 3025*, *Sphaerostephanos subpectinatus* (Copel.) Holttum, Moorea, Society Islands, 2013 (GH, UC); *Karger 2668*, *Sphaerostephanos superbus* (Brause) S.E.Fawc. & A.R.Sm., West Papua, Indonesia, 2011 (UC, Z); *Kuo 878*, *Sphaerostephanos taiwanensis* (C.Chr.) Holttum ex C.M.Kuo, Pingtung, Taiwan, 2010 (TAIF); *Karger 1586*, *Sphaerostephanos urdanatensis* (Copel.) Holttum, Mindanao, Philippines, 2010 (UC 2048235; Z 104920); *Chen Wade2816*, *Sphaerostephanos veitchii* Holttum, Ranongga, Solomon Islands, 2013 (TAIF 445062); *Grether 4202*, *Sphaerostephanos vestigiatus* (Copel.) Holttum, Los Negros, Admiralty Islands, 1945 (UC 732711); *Rinehart 21351*, *Sphaerostephanos warburgii* (Kuhn & Christ) Holttum, Guam, U.S.A., 1991 (UC 1734677); *Kessler 13952*, *Sphaerostephanos womersleyi* (Holttum) S.E.Fawc. & A.R.Sm., West Papua, Indonesia, 2008 (UC 2048619); *Kluge 9088*, *Sphaerostephanos* sp., West Papua, Indonesia, 2008 (UC 2048624); *Kluge 9071*, *Sphaerostephanos* sp., West Papua, Indonesia, 2008 (UC 2048584); *Karger 544*, *Sphaerostephanos* sp., Luzon, Philippines, 2009 (UC); *SITW11650*, *Sphaerostephanos* sp., Guadalcanal, Solomon Islands, 2016 (UC 2048648); *Chen Wade4923*, *Sphaerostephanos* sp., Negros, Philippines, 2017 (CMUH, PNH, TAIF); *Co 3474*, *Sphaerostephanos* sp., Luzon, Philippines, 1991 (MICH); *Karger 443*, *Sphaerostephanos* sp., Mindanao, Philippines, 2009 (Z); *Karger 2558*, *Sphaerostephanos* sp., West Papua, Indonesia, 2011 (UC, Z).

***Stegnogramma* Blume**—*Chen Wade1902*, *Stegnogramma aspidioides* Blume, Java, Indonesia, 2011 (TAIF); *Yu 655*, *Stegnogramma dictyoclinoides* Ching, Pingtung, Taiwan, (PE, TAIF); *Kuo 1885*, *Stegnogramma griffithii* (T.Moore) K.Iwats., Tam Dao, Vietnam, 2010 (TAIF); *Kuo 4240*, *Stegnogramma mingchegensis* (Ching) X.C.Zhang & L.J.He, Fukien, China, 2015 (TAIF); *Chang 20140714044*, *Stegnogramma sagittifolia* (Ching) L.J.He & X.C.Zhang, Guizhou, China, 2014 (TAIF); *Kuo 2368*, *Stegnogramma wilfordii* (Hook.) Seriz., Taipei, Taiwan, 2011 (TAIF); *Chen Wade4167*, *Stegnogramma* sp., Lam Dong, Vietnam, 2014 (TAIF); *WXP 149*, *Stegnogramma* sp., Yunnan, China, 2010 (PE).

***Steiropteris* (C.Chr.) Pic.Serm.**—*Fuentes 10972*, *Steiropteris buchtienii* (A.R.Sm.) Salino & T.E.Almeida, La Paz, Bolivia, 2006 (UC 1921877); *Christenhusz 2795*, *Steiropteris clypeolutata* (Desv.) Pic.Serm., Guadeloupe, 2003 (UC 1788485); *Fawcett 464*, *Steiropteris deltoidea* (Sw.) Pic.-Serm., Adjuntas, Puerto Rico, 2016 (VT); *Possley 215*, *Steiropteris deltoidea* (Sw.) Pic.Serm., Jayuya, Puerto Rico, 2016 (MAPR); *Meier 4771*, *Steiropteris fendleri* (D.C.Eaton) Pic.Serm., Yaracuy, Venezuela, 1999 (UC 1737148); *Jimenez 1061*, *Steiropteris gardneriana* (Baker) Pic.Serm., La Paz, Bolivia, 2001 (GOET, LPB, UC 1764496); *Hill 28047*, *Steiropteris glandulosa* (Desv.) Pic.Serm., St. Patrick, Dominica, 1996 (VT 197839); *Testo 1020*, *Steiropteris glandulosa* (Desv.) Pic.Serm. var. *brachyodus* (Kunze) Salino & T.E.Almeida, Puntarenas, Costa Rica, 2016 (VT); *Tuomisto 10697*, *Steiropteris glandulosa* (Desv.) Pic.Serm. var. *brachyodus* (Kunze) Salino & T.E.Almeida, Napo, Ecuador, 1997 (UC 1788318); *Gudino 1326*, *Steiropteris glandulosa* (Desv.) Pic.Serm. var. *longipilosa* (A.R.Sm.) Salino & T.E.Almeida, Pastaza, Ecuador, 1991 (UC 1597601); *Labiak 2993*, *Steiropteris hatschbachii* (A.R.Sm.) Salino & T.E.Almeida, Parana, Brazil, 2003 (UC 1926875); *Testo 1227*, *Steiropteris leprieurii* (Hook.) Pic.Serm. var. *subcostalis* (A.R.Sm.) A.R.Sm., Heredia, Costa Rica, 2017 (VT); *Churchill 3614*, *Steiropteris leprieurii* (Hook.) Pic.Serm. var. *subcostalis* (A.R.Sm.) A.R.Sm., Cartago, Costa Rica, 1980 (VT 197835); *Mexia 4904*, *Steiropteris mexiae* (Copel. ex C.Chr.) Salino & T.E.Almeida, Minas Gerais, Brazil, 1930 (UC 466421); *Salino 2003*, *Steiropteris mexiae* (Copel. ex C.Chr.) Salino & T.E.Almeida, Minas Gerais, Brazil, 2003 (UC); *Tuomisto 11636*, *Steiropteris pennellii* (A.R.Sm.) Salino & T.E.Almeida, Napo, Ecuador, 1998 (UC 1788328); *Holm-Nielsen 2912*, *Steiropteris polyphlebia* (C.Chr.) Salino & T.E.Almeida, Cotopaxi, Ecuador, 1973 (UC 1437100); *Salino 10229*, *Steiropteris polypodioides* (Raddi) Salino & T.E.Almeida, São Paulo, Brazil, 2005 (UC 2047328); *Nitta 2321*, *Steiropteris seemannii* (J.Sm.) Salino & T.E.Almeida, Alajuela, Costa Rica, 2013 (GH, UC); *Moran 3249*, *Steiropteris seemannii* (J.Sm.) Salino & T.E.Almeida, Alajuela, Costa Rica, 1983 (UC 1265902); *Grayum 3239*, *Steiropteris valdepilosa* (Baker) Pic.Serm., Heredia, Costa Rica, 1983 (UC 1490562); *Matos 1870*, *Steiropteris villosa* (Link) Salino & T.E.Almeida, 2010 (DUKE); *Testo 1442*, *Steiropteris* sp., Chocó, Colombia, 2017 (VT).

***Strophocaulon* S.E.Fawc. & A.R.Sm.**—*Fawcett 697*, *Strophocaulon invisum* (G.Forst.) S.E.Fawc. & A.R.Sm., Taveuni, Fiji, 2016 (UC 2049790, VT,); *Kluge 7791*, *Strophocaulon unitum* (L.) S.E.Fawc. &

A.R.Sm., Singani, Grand Comores, 2008 (UC 1924777); *Fawcett 641*, *Strophocaulon unitum* (L.) S.E.Fawc. & A.R.Sm., Viti Levu, Fiji, 2016 (UC 2049788, VT).

Thelypteris **Schmidel**—*Rothfels 4667*, *Thelypteris confluens* (Thunb.) C.V.Morton, Kwazulu-Natal, South Africa, 2015 (UC); *Fawcett 569*, *Thelypteris palustris* Schott, Michigan, U.S.A., 2016 (UC 2049130, VT); *Arsene 1*, *Thelypteris palustris* Schott, Michoacán, Mexico, 1910 (UC 477810); *Testo 1645*, *Thelypteris palustris* Schott, Florida, U.S.A., 2019 (FLAS).

Trigonospora **Holttum**—*Ballard 1393*, *Trigonospora obtusiloba* Sledge, Hedigala, Sri Lanka, 1951 (UC 1948787); *Ballard 1522*, *Trigonospora zeylanica* (Ching) Sledge, Sri Lanka, 1951 (UC 194876).