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Plastid Phylogenomic Analysis of Podostemaceae with an Emphasis on Neotropical Podostemoideae

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Abstract—Podostemaceae are a clade of aquatic flowering plants that form important components of tropical river ecosystems. Species in the family exhibit highly derived growth forms and high vegetative phenotypic plasticity, both of which contribute to taxonomic confusion. The backbone phylogeny of the family remains poorly resolved, many species remain to be included in a molecular phylogenetic analysis, and the monophyly of many taxa remains to be tested. To address these issues, we assembled sequence data for 73 protein-coding plastid genes from 132 samples representing 68 species (~23% of described species) that span the breadth of most major taxonomic, morphological, and biogeographic groups of Podostemaceae. With these data, we conducted the first plastid phylogenomic analysis of the family with broad taxon sampling. These analyses resolved most nodes with high support, including relationships not recovered in previous analyses. No evidence of widespread, well-supported conflict among individual plastid genes and the concatenated phylogeny was observed. We present new evidence that four genera (*Apinagia*, *Marathrum*, *Oserya*, and *Podostemum*), as well as four species, are not monophyletic. In particular, we show that *Podostemum flagelliforme* should not be included in *Podostemum* and is better recognized as *Devillea flagelliformis*, and that *Marathrum capillaceum* is embedded within *Lophogyne* s.l. and should be recognized as *Lophogyne capillacea*. We also place a previously unsampled and undescribed species that likely represents a new genus. In contrast to previous studies, the neotropical genera *Diamantina*, *Ceratolacis*, *Cipoia*, and *Podostemum* are resolved as successive sister groups to a clade of all paleotropical Podostemoideae taxa sampled, suggesting a single dispersal event from the neotropics to the paleotropics in the history of the subfamily. These results provide a strong basis for improving the classification of Podostemaceae and a framework for future phylogenomic studies of the clade employing data from the nuclear genome.

Keywords—Aquatic plants, chloroplast genome, Malpighiales, phylogenetic conflict, plastome, riverweeds.

Podostemaceae, the riverweed family, are a clade of flowering plants in the order Malpighiales (Koi et al. 2012; Xi et al. 2012; Ruhfel et al. 2016; Katayama et al. 2022). They are the largest strictly aquatic flowering plant family, with 51–54 genera and ~300 species (Ruhfel et al. 2011; Koi et al. 2012; Katayama et al. 2022; Bove et al. 2023; POWO 2023) and are circumscribed into three subfamilies: Podostemoideae, Tristichoideae, and Weddellinoideae. Each subfamily is well-supported by molecular and morphological evidence (Engler 1930; Cook and Rutishauser 2007; Ruhfel et al. 2011; Koi et al. 2012, 2022). Tristichoideae are characterized by tricarpellate ovaries and pantoporate pollen, in contrast to Podostemoideae and Weddellinoideae, which have bicarpellate ovaries and mostly tricolporate or tricolpate pollen. Podostemoideae are characterized by the presence of a spathella that encloses the flower bud prior to anthesis. Weddellinoideae differs from Podostemoideae by the absence of a spathella and the presence of a distinct perianth, which are likely plesiomorphic character states shared with Tristichoideae (Kita and Kato 2001; Cook and Rutishauser 2007; Ruhfel et al. 2011). Many genera in the family are monotypic (42%; Katayama et al. 2022).

The distribution of the family is primarily pantropical with a few species occurring in temperate areas of North America and Japan (Ruhfel et al. 2016). Species of Podostemaceae attach to solid substrates in swift flowing currents of river-rapids and waterfalls. These are unusual habitats for angiosperms and

form crucial elements of river biodiversity and ecology. Dense beds of riverweeds are dominant primary producers and important contributors to making river-rapids the most productive regions of rivers (Hynes 1970; Horn and Goldman 1994) while providing food and habitat for fish (Jégu et al. 2002; Chernoff et al. 2003) and invertebrates (Giller and Malmqvist 2002; Giller et al. 2004; Hutchens et al. 2004). Indeed, Podostemaceae are the dominant macrophyte in large stretches of tropical rivers and are often considered to be foundational species for river-rapid ecosystems (sensu Dayton 1972; Ellison et al. 2005; Wood and Freeman 2017). Currently, the construction of hydroelectric dams and the associated massive reservoirs is destroying river-rapid habitat along hundreds of kilometers of rivers at a time when many species of Podostemaceae are of conservation concern (Philbrick et al. 2010; Cheek et al. 2017, 2022; Bidault et al. 2023).

The vegetative plant body of Podostemaceae species is atypical compared to other angiosperms and interpretations of structural homology vary considerably (Jäger-Zürm 1997, 2005; Rutishauser 1997, 2015; Stevens 2001; Cook and Rutishauser 2007; Koi and Kato 2007, 2010; Sehgal et al. 2007). It has been suggested that “conventional morphology cannot cope with the family” (Stevens 2001) and that Podostemaceae be recognized in their own class, equal in rank to monocots and dicots (Cusset and Cusset 1988). Difficulty interpreting the various components of the plant body may be in part due

to the presence of organs of mixed shoot-leaf identity in species of Podostemoideae (Katayama et al. 2010; Rutishauser 2020). Another example of this difficulty is evident in an investigation by Jäger-Zürn et al. (2016) where they reinterpreted pinnately compound leaves as foliate roots. These highly derived growth forms along with vegetative phenotypic plasticity exhibited by species in the family (Rutishauser et al. 1999; Philbrick et al. 2010; Jäger-Zürn et al. 2016) contribute to taxonomic confusion.

Functional taxonomies do not exist for many genera of Podostemaceae, and their absence hinders meaningful assessment of species distributions and endemism important for conservation efforts (Philbrick et al. 2010; Bidault et al. 2023). For example, although van Royen's taxonomic monograph of neotropical species (Van Royen 1951, 1953, 1954) has been important to our understanding of some genera of these plants, his treatments of the largest neotropical genera, including *Apinagia*, are largely unworkable. Indeed, the most basic of taxonomic questions, 'What species does this specimen represent?' often remains difficult to answer, especially for members of Podostemoideae (Berry 2004; Philbrick et al. 2010; Bidault et al. 2023). This problem is also evident elsewhere in the literature. For example, 75% of accessions of two genera (*Apinagia* s.l. and *Rhyncholacis*) in an important molecular phylogenetic analysis of the family (Koi et al. 2012) were not identified to species. More than a decade later, taxonomic treatments of these genera remain absent, and researchers would not have greater success identifying these specimens today.

Understanding of the evolutionary relationships in Podostemaceae has improved considerably over the last several years due to molecular phylogenetic studies. Well-sampled phylogenies have relied primarily on plastid data, and particularly the *matK* region (e.g. Koi et al. 2012, 2019; Werukamkul et al. 2018; Wu et al. 2022). Other studies have utilized multiple genes, combining plastid data with the nuclear marker ITS (Tippery et al. 2011; Da Costa et al. 2018; Koi et al. 2022) or the mitochondrial gene *matR* (Ruhfel et al. 2011, 2016; Sun et al. 2016). Phylogenies based on plastid genome (plastome) datasets of Podostemaceae are becoming available as more plastomes are sequenced (Bedoya et al. 2019, 2020; Jin et al. 2020; Trad et al. 2021). However, to date, these plastome phylogenies of Podostemaceae have had limited taxonomic sampling. Furthermore, conflict between individual plastid gene trees and trees constructed using concatenated plastome data remains relatively unexplored at the family level (but see Trad et al. 2021 who included three Podostemaceae taxa in their analyses) and can be important to examine when inferring plastid phylogenies (Gonçalves et al. 2019; Walker et al. 2019). A single study using a large nuclear data set has been published (Katayama et al. 2022), but as in previous plastome-level studies, its taxon sampling is limited (< 10 taxa) and thus comparison to studies with more taxon-rich phylogenetic analyses is difficult. Hybridization has been reported in the family (Cheek et al. 2017; Bedoya et al. 2021) but it remains unclear how widespread this may be and if it impacts phylogenetic reconstruction.

Despite recent advances, several key areas of the Podostemaceae phylogeny remain unresolved, particularly in Podostemoideae, and many species remain to be sampled with molecular data. These issues inhibit our ability to assess their classification, elucidate patterns of character evolution, and infer their biogeography. For example, placement of the

monotypic *Diamantina*, a neotropical lineage in the subfamily, remains unclear and is weakly supported in all previous studies. *Diamantina* has been placed either as sister to all other Podostemoideae (Ruhfel et al. 2011; Koi et al. 2012; Sun et al. 2016), as sister to a clade containing the neotropical genera *Ceratolacis*, *Cipoia*, and *Podostemum* (Da Costa et al. 2018), or as sister to a strictly neotropical subclade (Ruhfel et al. 2016) that did not contain *Ceratolacis*, *Cipoia*, and *Podostemum*. Similarly, support remains weak for the relationships among several strongly-supported subclades, each of which are restricted to one of three main geographic areas (North and South America, Asia/Australia, and Africa/Madagascar; Koi et al. 2012; Ruhfel et al. 2016). Non-monophyletic genera are also common with many in need of further taxonomic adjustments and monographic work (e.g. *Apinagia* s.l., *Ledermannia* s.l., *Marathrum*, *Zeylanidium*; Philbrick et al. 2010, 2016, 2018; Koi et al. 2012, 2019; Schenk et al. 2015), and the circumscription of other genera remains to be tested with molecular data. For example, the monophyly of *Podostemum* sensu Philbrick and Novelo (2004) remains to be tested with molecular data, particularly regarding the inclusion of *Podostemum flagelliforme* (Tul. & Wedd.) C.T. Philbrick & Novelo, which was previously placed in the monotypic genus *Devillea*. This species was included in *Podostemum* based on phylogenetic analysis of morphological data, but has characteristics not seen in other members of the genus (Philbrick and Novelo 2004). Remaining questions such as these can be addressed with increased taxon and character sampling and thus a well-sampled plastid phylogenomic analysis may offer further insight.

In this study, we analyzed 73 coding regions of the plastome to conduct the first taxonomically well-sampled plastid phylogenomic analysis of Podostemaceae. The data analyzed comprised 132 samples, including eight publicly available plastomes and 124 samples newly sequenced for this study, obtained using a genome skimming approach. Our main goals were to 1) resolve backbone relationships within the family, 2) test the monophyly of several genera and species, and 3) examine conflict between individual plastid gene trees and a concatenated dataset of plastid coding regions. The results presented here allow for a better understanding of generic and species boundaries in Podostemaceae, provide evidence to support nomenclatural and taxonomic changes, and highlight areas of the phylogeny that need better sampling. The insights provided regarding the evolutionary history of the plastome in Podostemaceae will complement future phylogenomic studies of the clade using data from the nuclear genome.

MATERIALS AND METHODS

Taxon Sampling—Our sampling comprised 132 accessions including outgroups. Voucher information and GenBank numbers are provided in Appendix 1. Of these, 130 were Podostemaceae representing the three subfamilies, 31 genera, and 68 species (~23% of the described species diversity in the family; Ruhfel et al. 2011; Koi et al. 2012; Katayama et al. 2022; POWO 2023). Also included was one specimen that could not be placed in a recognized genus (*Philbrick et al. 6055*, [MICH]). All new specimens gathered for this study were collected legally with appropriate permits and permissions, where required. Following Tippery et al. (2011), *Apinagia nana* was retained as a distinct species, although Van Royen (1951) placed it in synonymy with *A. pilgeri* Mildbr. *Apinagia pilgeri* has since been transferred to *Oserya* as *O. pilgeri* by Philbrick et al. (2016). The name *Apinagia riedelii* (Bong.) Tul. has been widely used in the literature since 1849, but this species is more correctly referred to as *A. fucoides*

(Bove and Philbrick 2016; Philbrick et al. 2016). A proposal to conserve the more commonly used name (*A. riedelii*) was put forward (Bove and Philbrick 2016) but rejected (Wilson 2022). Thus, we use the name *Apinagia fucooides* here. This issue is particularly important to consider when comparing the results of this study to previous works that used the name *A. riedelii* (e.g. Tippery et al. 2011; Koi et al. 2012; Bove and Philbrick 2016 and references therein; Bedoya et al. 2019). Author citations for each name at the generic rank or below are listed in Appendix 1, if the name is not listed in the appendix, the authority is listed the first time the name is mentioned in the main text. Representatives of all major clades recovered in a densely sampled phylogenetic study using the plastid gene *matK* (clades A–M in Koi et al. 2012) are included here except *Saxicolella* p.p. (clade H in Koi et al. 2012; *Pohliella* Engl. sensu Cheek 2020). Sampling focused on neotropical taxa, and several species had more than one representative included to help test generic and species boundaries. Most genera not included in our sampling are from Africa/Madagascar (*Angolaea* Wedd., *Endocaulos* C.Cusset, *Lebbia* Cheek, *Leiothylax* Warm., *Letestuellia* G.Taylor, *Paleodicraea* C.Cusset, *Pohliella*, *Saxicolella* s.s., *Sphaerothylax* Bisch. ex C.Krauss, *Winklerella* Engl., and *Zehnderia* C.Cusset) or Asia/Australia (*Cussetia* M. Kato, *Farmeria* Willis ex Hook.f., *Griffithella* (Tul.) Warm, *Hanseniella* C.Cusset, *Hydrodiscus* Koi & M.Kato, *Indodalzellia* Koi & M. Kato, *Indotristicha* P. Royen, *Paradalzellia* Koi, P.L.Uniyal & M.Kato, *Thaumatococcus* M.Kato, Koi & Y.Kita, and *Willisia* Warm.). The only genus from the Americas not sampled was *Wettsteiniola* Suess., which may be closely related to *Rhyncholacis* (Da Costa et al. 2018). These missing genera were not sampled because specimens or tissues were not available, or extractions were unsuccessful. Many of the samples included here were sequenced for at most four gene regions in previous studies by the authors (Ruhfel et al. 2011, 2016; Tippery et al. 2011). Hypericaceae is the sister group to Podostemaceae (Koi et al. 2012; Xi et al. 2012; Ruhfel et al. 2016; Li et al. 2021; Katayama et al. 2022) and as such, *Cratoxylum cochinchinense* and *Vismia guianensis* were included as outgroups. Data from eight taxa were downloaded from GenBank including six species of Podostemaceae and the two outgroups (Xi et al. 2012; Bedoya et al. 2019; Jin et al. 2020).

DNA Extraction and Sequencing—Total genomic DNA (gDNA) was extracted from tissue from herbarium specimens or tissue preserved in silica gel or a saturated CTAB solution (Rogstad 1992) using the DNeasy Plant Mini Kit (Qiagen, Germantown, Maryland) following a modified protocol (Ruhfel et al. 2011). DNA quantification was performed with a Qubit Fluorometer 2.0 using a dsDNA BR Assay kit (Thermo Fisher, Waltham, Massachusetts) to ensure appropriate amounts of gDNA were available for high-throughput sequencing. DNA quantity and quality were also assessed using agarose gel electrophoresis. Samples of gDNA were submitted to Rapid Genomics (Gainesville, Florida) for library preparation and sequencing using a genome skimming approach (low-coverage shotgun-sequencing; Straub et al. 2012). Samples were sequenced either on the Illumina HiSeq 2500 Ultra-High-Throughput platform using single-end 100 bp reads (46 samples) or the Illumina HiSeq X platform (78 samples) using 150 bp paired-end reads (see Table S1).

Assembly of Plastid Exons—Demultiplexed reads were cleaned of adapters and trimmed using Trimmomatic 0.39 (Bolger et al. 2014) and quality checked with FastQC (Andrews 2010). During trimming, leading and trailing bases with a quality score less than 10 were removed and then reads were scanned with a 4-bp sliding window and cut when the average quality fell below 20. Reads less than 30 bp after cleaning were discarded.

Coding regions (exons only) from the plastid genome were assembled with HybPiper 1.3.1 (Johnson et al. 2016) using the Burrows-Wheeler alignment method (Li and Durbin 2009) to map reads to targets using the default coverage cutoff (–cov_cutoff = 8). The targets for gene assembly were plastid coding regions extracted from seven taxa of Podostemaceae available on GenBank: *Apinagia fucooides*, *Lophogyne capillacea* (syn. *Marathrum capillaceum* (Pulle) P.Royen), *Lophogyne royenella* (syn. *Monostylis capillacea* Tul.), *Marathrum foeniculaceum*, *Marathrum utile*, *Podostemum cerasophyllum*, and *Tristicha trifaria* (Xi et al. 2012; Bedoya et al. 2019; Jin et al. 2020). Paralogs were assessed using the method implemented in HybPiper which uses MAFFT (Katoh and Standley 2013) and FastTree (Price et al. 2009). Coding regions with an internal stop codon present were removed from further analysis and loci with fewer than 50% of the taxa present were not used in phylogenetic analyses.

Alignments and Phylogenetic Analyses—We aligned each gene with MUSCLE 3.8.425 (Edgar 2004) as implemented in Geneious 2022.2.1 (Biomatters, Ltd., Auckland, New Zealand) using the default options. Alignments were then manually inspected and adjusted by hand to retain the correct reading frame based on plastomes of Podostemaceae published in

Bedoya et al. (2019). Alignments were then trimmed of codons that were missing data in > 40% of the samples using pxclsq in Phyx (Brown et al. 2017).

All model testing, partition strategy selection, phylogenetic analyses, and branch support measurements were performed using IQ-TREE 1.6.12 (Nguyen et al. 2015). Maximum likelihood phylogenetic analyses of individual genes were conducted with standard model selection (–m TEST, Kalyaanamoorthy et al. 2017) using AICc followed by tree reconstruction with 20 independent runs and 1000 standard non-parametric bootstrap replicates. To analyze the full data set, we first concatenated the individual gene alignments and produced a partition file using pxcat in Phyx (Brown et al. 2017). Next, we determined the optimal partitioning scheme for the concatenated dataset with IQ-TREE and the “–m TESTMERGEONLY” option and reconstructed the phylogeny using the edge-linked proportional partition model (Chernomor et al. 2016) with 20 independent runs and 1000 standard non-parametric bootstrap replicates. To further examine branch support in the concatenated analyses we also calculated ultra-fast bootstrap support (UFBS; 1000 replicates, Hoang et al. 2017) and SH-aLRT support (1000 replicates, Guindon et al. 2010) using the optimized partition scheme and search strategy above. Each of these measures of support (BS, UFBS, and SH-aLRT) has its own strengths and weaknesses under various conditions (e.g. the presence of polytomies, model violations, and weak phylogenetic signal in the data; Hillis and Bull 1993; Guindon et al. 2010; Minh et al. 2013; Hoang et al. 2017). For this reason, we considered a branch to be well supported if the following three conditions were met: 1) BS value $\geq 80\%$; 2) SH-aLRT ≥ 80 ; and 3) UFBS value $\geq 95\%$.

Conflict Analysis—To examine conflict between individual gene trees and the concatenated phylogeny, we mapped the gene trees against the concatenated tree using the bipartition method implemented in PhyParts v. 0.0.1 (Smith et al. 2015) using either no support cutoff or a 70% BS support cutoff, representing moderate support (Hillis and Bull 1993). Prior to the PhyParts analysis, all trees were rooted on the outgroups using pxrr in Phyx (Brown et al. 2017). When no support cutoff is used, the node is evaluated as conflicting or concordant regardless of node support. When using a support cutoff, any node in the gene tree with support less than the value specified is considered uninformative. Using either approach, if a taxon is missing in the gene alignment, and is relevant to a particular node, that gene is considered uninformative for that node. PhyParts results were visualized using PhyPartsPieCharts (Johnson 2021).

RESULTS

Data Set Characteristics—One hundred and twenty-four accessions were newly sequenced for this study. The number of reads obtained and the proportion of the target gene length recovered for each accession are shown in Table S1 and Fig. S1, respectively. The final concatenated alignment contained 73 coding gene regions, 132 samples, and was 53,943 bps in length with 3.71% missing data (gaps and completely undetermined characters). Details on each individual coding region alignment, the concatenated alignment, and their best fit models can be found in Table S2.

Phylogenetic Analyses—Our maximum likelihood analysis of the concatenated dataset (Fig. 1, summary phylogeny; Figs. 2A, B, full phylogeny; Fig. S2, full phylogeny with branch lengths) recovered strong support for the monophyly of the family as well as relationships among major clades, genera, and species of Podostemaceae. Of the 129 internal branches of the phylogeny, only nine received < 70 BS with all but one of these between accessions of the same species. Of the 120 branches that received ≥ 70 BS, only eight were not also well-supported using our other measures of support (≥ 80 SH-aLRT; $\geq 95\%$ UFBS). Because most branches in the phylogeny (112/129; $\sim 87\%$) were well-supported by all metrics (i.e. ≥ 80 BS, ≥ 80 SH-aLRT, and ≥ 95 UFBS), we limit our discussion of branch support to BS values for well-supported branches and specifically mention SH-aLRT and UFBS values only if one or more of the three measures of support disagree. See Fig. S3 for SH-aLRT and UFBoot values.

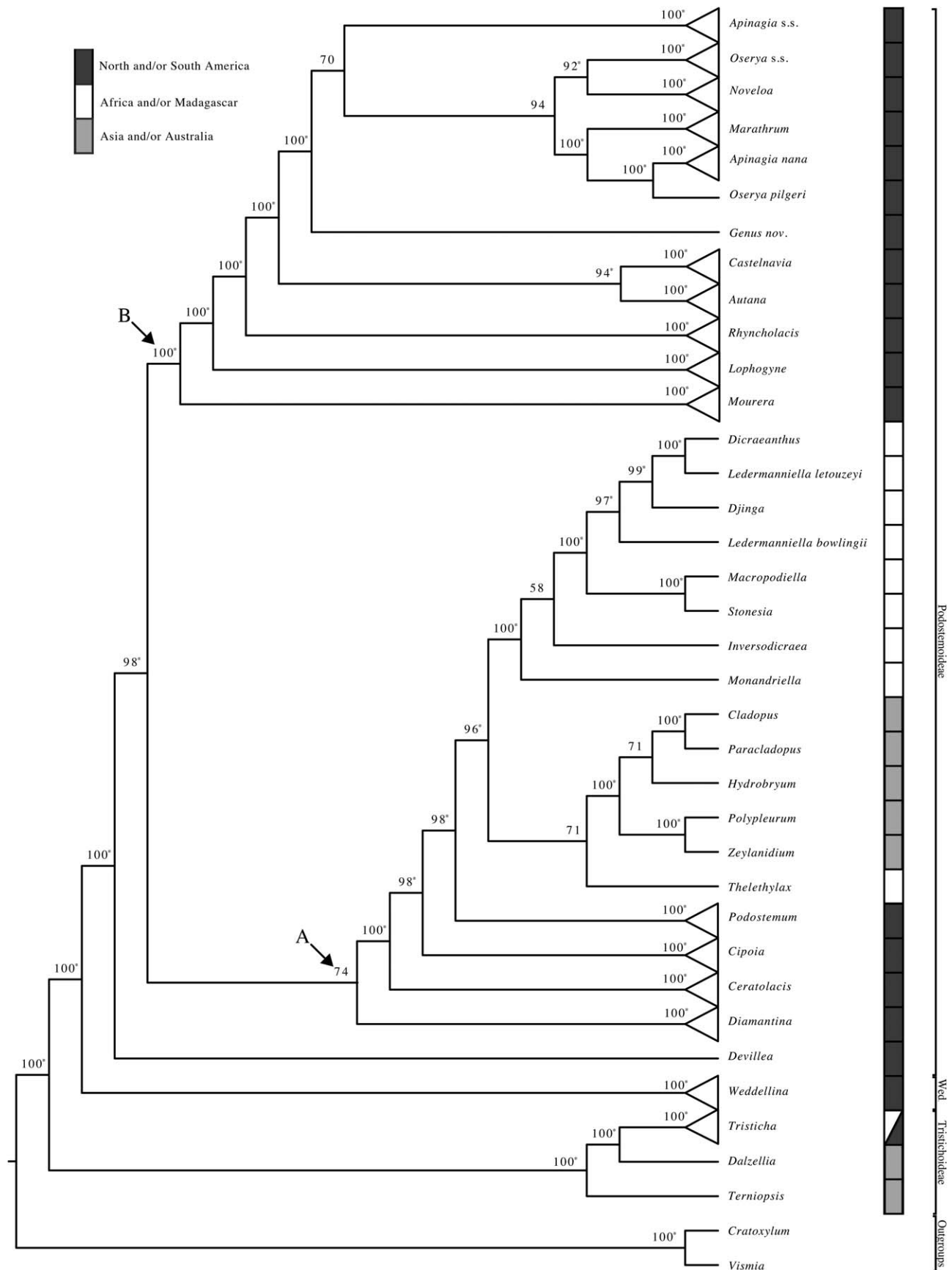


FIG. 1. Maximum likelihood summary phylogeny of Podostemaceae inferred from a concatenated dataset of 73 protein-coding genes of the plastid genome. Standard bootstrap support (BS) values $\geq 50\%$ are indicated above the branches. An asterisk (*) next to the BS value indicates that the branch was also supported by $\geq 95\%$ ultra-fast bootstrap support and ≥ 80 SH-aLRT branch tests. Clades labeled with "A" or "B" represent major subclades of Podostemoideae containing either both neotropical and paleotropical taxa or strictly neotropical taxa, respectively. See Figs. 2A and 2B for the complete tree. Shaded squares next to each terminal indicate their broad biogeographic distribution. Subfamilies of Podostemaceae and outgroups are indicated to the right of the phylogeny. Wed. = Weddellinoideae.

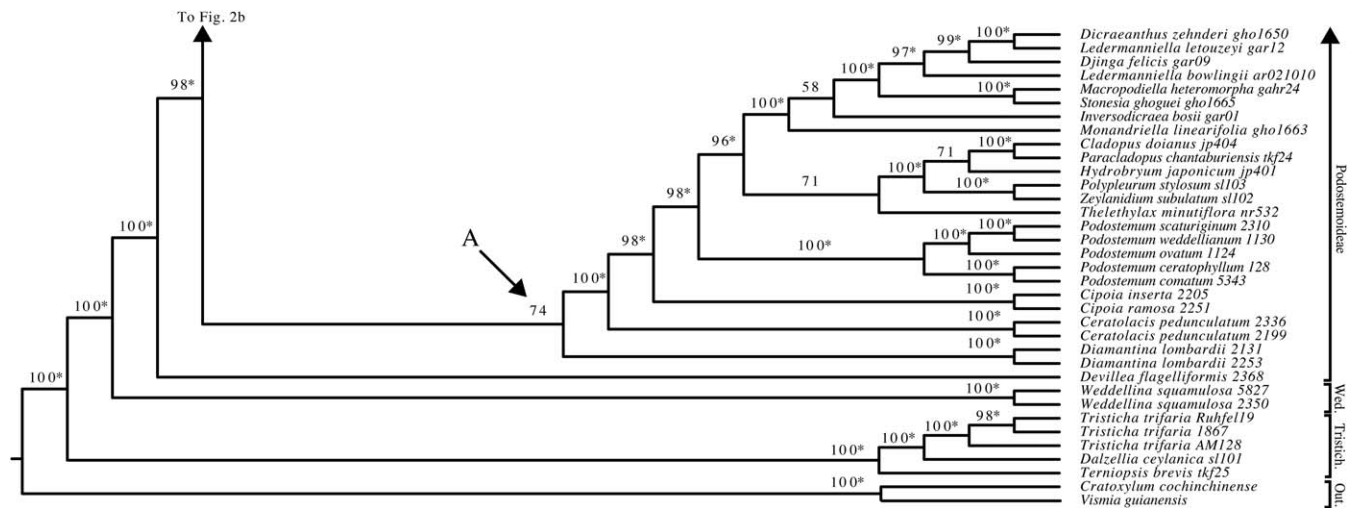


FIG. 2A. Maximum likelihood phylogeny of Podostemaceae inferred from a concatenated dataset of 73 protein-coding genes of the plastid genome. Voucher collection numbers are given after each species name. Standard bootstrap support (BS) values $\geq 50\%$ are indicated above the branches. An asterisk (*) next to the BS value indicates that the branch was also supported by $\geq 95\%$ ultra-fast bootstrap support and ≥ 80 SH-aLRT branch tests. The clade labeled with an "A" represents a major subclade of Podostemoideae containing both neotropical and paleotropical taxa. Subfamilies of Podostemaceae and outgroups are indicated to the right of the phylogeny. Out. = Outgroups; Tristich. = Tristichoideae; Wed. = Weddellinoideae. Phylogeny continues in Fig. 2B.

We recovered maximum support for the monophyly of the three subfamilies of Podostemaceae and the relationships among them. Tristichoideae was placed sister to Podostemoideae + Weddellinoideae. Within Tristichoideae, *Terniopsis brevis* and *Dalzellia ceylanica* were successive sister groups (100 BS) to a clade (100 BS) of three *Tristicha trifaria* samples. The two samples of *Weddellina squamulosa* formed a clade with 100 BS. Within Podostemoideae, *Devillea flagelliformis* (syn. *Podostemum flagelliforme*) was strongly supported (98 BS) as sister to the remaining taxa, which were separated into two major subclades. The first subclade of Podostemoideae (Fig. 1, clade A) was moderately supported (74 BS) by standard bootstrap methods but did not receive support from the other methods used (72.6 SH-aLRT, 77 UFBS) and is comprised of four neotropical genera (*Ceratolacis*, *Cipoia*, *Diamantina*, and *Podostemum*) and all sampled paleotropical taxa. The second major subclade of Podostemoideae (Fig. 1, clade B) was strictly comprised of neotropical taxa and received maximum support (100 BS).

In the first subclade, containing both neotropical and paleotropical Podostemoideae taxa (Fig. 1, clade A), neotropical *Diamantina* was sister to all other taxa which formed a strongly supported clade (100 BS). The neotropical genera *Ceratolacis*, *Cipoia*, and *Podostemum* (each monophyletic with 100 BS support), formed strongly supported (98 BS) successive sister groups to a strongly supported (96 BS) clade of all paleotropical taxa containing two subclades. The first, with Asian and Malagasy taxa (71 BS, not supported by other metrics: 68.6 SH-aLRT, 81 UFBS) and the second with African (100 BS) taxa. In the Asian/Malagasy clade, the Malagasy *Thelethylax minutiflora* was sister to a strongly supported (100 BS) clade of the Asian species. Here, *Zeylanidium subulatum* + *Polypleurum stylosum* (100 BS) was sister (71 BS, not supported by other metrics: 63 SH-aLRT, 83 UFBS) to a clade in which *Hydrobryum japonicum* was sister to *Cladopus doianus* + *Paracladopus chanthaburiensis* (100 BS). In the African clade, *Monandriella linearifolia* was sister to a poorly supported clade (58 BS) of the remaining African taxa. Among those,

Inversodicraea bosii was sister to a strongly supported clade (100 BS) containing *Stonesia ghoguei* + *Macropodiella heteromorpha* (100 BS) which was sister to a clade (97 BS) containing *Ledermanniella bowlingii*, *Djinga felixis*, *Ledermanniella letouzii*, and *Dicraeanthus zehnderi*. Relationships within this subclade of African taxa were all strongly supported (≥ 99 BS).

The strictly neotropical subclade of Podostemoideae (Fig. 1, clade B) is represented here by *Apinagia*, *Autana*, *Castelnavia*, *Lophogyne*, *Marathrum*, *Mourera*, *Noveloa*, *Oserya*, *Rhyncholacis*, and an undescribed species that likely represents a new genus (*Philbrick et al.* 6055, [MICH]). Within this clade, *Mourera*, *Lophogyne* s.l. (including *Marathrum capillaceum* [syn. *Lophogyne capillacea* Pulle]), and *Rhyncholacis* were each strongly supported as monophyletic (100 BS) and successive sister groups to the remaining neotropical taxa. Within *Lophogyne* s.l., two species, *L. fimbriata* and *L. royenella*, were strongly supported (100 BS) as not monophyletic. *Lophogyne fimbriata* was paraphyletic, with one sample supported (100 BS) as more closely related to a clade containing *L. wilsonii* and two samples of an unidentified *Lophogyne* species (*L.* sp. 2). Similarly, samples of *L. royenella* form a paraphyletic grade with one sample being strongly placed as sister to *L. ceratophylla* + an unidentified *Lophogyne* species (*L.* sp. 1). Among the remaining taxa, a strongly supported clade (94 BS) containing *Autana* (100 BS) + *Castelnavia* (100 BS), was sister to a clade (100 BS) containing three lineages whose relationships were not well supported (70 BS, not supported by other metrics: 71 SH-aLRT, 88 UFBS). The first of these three groups was an undescribed species ('Genus nov.') that likely represents a new genus. The second clade received strong support from standard bootstrapping (94 BS) and the SH-aLRT test (97.3) but fell just below the cutoff for the UFBS values representing a well-supported branch (94 UFBS). This clade contained subclades representing *Oserya* s.s., *Noveloa*, *Marathrum* and a clade of *Apinagia nana* + *Oserya pilgeri*, thus making *Apinagia* and *Oserya* non-monophyletic. Each of these four clades was supported with 100 BS. *Oserya perpusilla* + *Noveloa* is strongly supported (92 BS) and was sister to

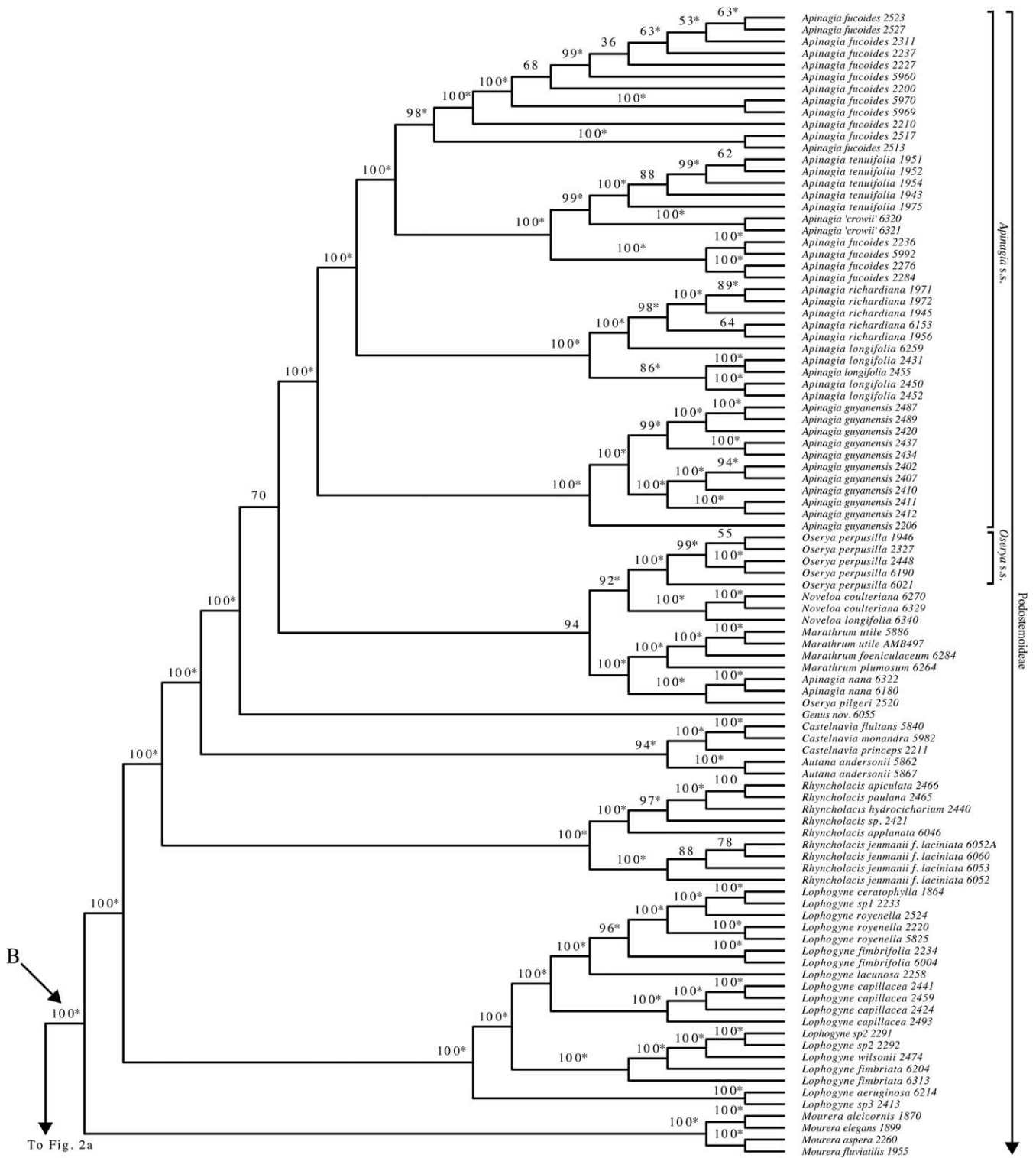


FIG. 2B. Continuation of Fig. 2A. Maximum likelihood phylogeny of Podostemaceae inferred from a concatenated dataset of 73 protein-coding genes of the plastid genome. The clade labeled with a "B" represents a major subclade of Podostemoideae containing only neotropical taxa. Subfamily Podostemoideae, *Apinagia* s.s., and *Oserya* s.s. are indicated to the right of the phylogeny.

Marathrum + (*Apinagia nana* + *Oserya pilgeri*) which received 100 BS. The third clade was strongly supported (100 BS) and represented *Apinagia* s.s. This clade contained samples from six species of *Apinagia* s.s., two of which were strongly supported (> 98 BS) as non-monophyletic. *Apinagia longifolia* was paraphyletic with regard to *A. richardiana* and *A. fucoides* was paraphyletic with *A. tenuifolia* + *A. 'crowii'* embedded within.

Conflict Analysis—When no support cutoff was used, we observed high levels of gene tree conflict throughout the phylogeny (Fig. S4). However, with the 70% BS cutoff (Fig. S5), the majority of individual genes were uninformative at most nodes and little conflict was evident. Of the 129 nodes of Podostemaceae in the 70% BS cutoff analysis (Fig. S5), 110 nodes (~85%) had from one to 68 (mean = 14.6) concordant

genes with BS support over 70%; 56 nodes (~43%) had from one to 15 (mean = 0.9) conflicting genes with support over 70%; and 14 nodes (~11%) had no conflicting or concordant genes. Of the 56 nodes with conflict present: 19 involved branches with near-zero lengths (Fig. S2, six nodes) and/or were within a clade representing a single species or closely related species (13 nodes). For example, within the clade of *Oserya perpusilla*, one internal node had five genes in conflict, and in the clade of *Tristicha trifaria* one internal node had 15 genes in conflict. Genes with the most conflict were *rps7* (471 bps, 17 conflicts) and *clpp* (687 bps, 15 conflicts). Four conflicts were observed involving *matK*, with each of these present within a clade representing a single species.

Alignments, partition files, and tree files are available in the Dryad Data Repository (Ruhfel et al. 2024).

DISCUSSION

Phylogenetic Relationships and Implications for Taxonomy, Nomenclature, Morphological Evolution, and Biogeography—The results presented here provide new insights on the evolutionary relationships of Podostemaceae using the largest plastome dataset for the family to date. We also provide the first examination of phylogenetic conflict of protein-coding genes within the plastome of the family. Previous plastome phylogenies of the family have included ≤ 5 species (Bedoya et al. 2019; Jin et al. 2020; Trad et al. 2021) while the most taxonomically well-sampled phylogeny of the clade (~132 species representing ~43 genera) was reconstructed using one plastid coding region (*matK*; Koi et al. 2012). In comparison to previous studies based on fewer genes and the current taxonomy of the group, the phylogeny presented here is mostly in agreement with notable exceptions discussed below. Our results strongly support the monophyly of the family as well as the three established subfamilies and agree with the relationships among them as recovered in previous analyses. However, we provide greater support for the backbone and relationships among genera, with the majority of the branches in the phylogeny being well supported, including many relationships that were unsupported in previous studies. In addition, our sampling includes several taxa that previously have not been included in molecular phylogenetic studies, which allows for important novel insights. We also show that four genera (*Apinagia* s.l., *Marathrum*, *Oserya*, and *Podostemum*) and four species are not monophyletic as currently circumscribed, and place an undescribed species that likely represents a new genus (*Philbrick et al. 6055*, [MICH]). Our phylogenetic results provide a strong foundation for reassessing the current classification of the family and set the stage for future monographic and molecular phylogenetic work. We discuss the most important implications of our results below.

Placement of *Podostemum flagelliforme* and the Non-Monophyly of *Podostemum*—Until the present study, the position of *Podostemum flagelliforme* (syn. *Devillea flagelliformis*) was untested with molecular data. Rediscovered in 2013 at a locality in the Balsas River in the Brazilian state of Tocantins approximately 120 km from the type locality, this species was previously known only from the type material collected over 175 yr ago from the Tocantins River also in the Brazilian state of Tocantins (Bove and Philbrick 2014). A phylogenetic analysis using morphological data (Philbrick and Novelo 2004)

determined that the species belonged within *Podostemum* s.l. (including *P. ceratophyllum*, the type species of the genus [Van Royen 1954; Philbrick and Novelo 2004]), due to three homoplasious synapomorphies recovered in their analysis: an anisobous ovary, a capsule at a 30–40° angle on the pedicel, and one deciduous capsule valve. However, the authors noted that it lacked morphological features (two stamens with an andropodium and pollen in dyads) shared by all other members of the genus *Podostemum*; *Podostemum flagelliforme* has one stamen per flower (thus no andropodium) and pollen in monads. Other treatments of the group (e.g. Moline et al. 2006; Cook and Rutishauser 2007) continued to recognize *Devillea* as a separate monotypic genus due to these differences in morphology. The strongly-supported placement of *Podostemum flagelliforme* as sister to all other Podostemoideae (Fig. 1; Fig. 2A as *Devillea flagelliformis*) indicates that *Podostemum* (sensu Philbrick and Novelo 2004) is not monophyletic and that *Devillea* should be recognized as a monotypic genus distantly related to *Podostemum* and that *Podostemum flagelliforme* is better recognized as *Devillea flagelliformis*.

Placement of *Diamantina*—Placement of *Diamantina* as sister to all other taxa in the mixed neotropical and paleotropical clade (Fig. 1, clade A) as recovered here agrees with the placement recovered in the molecular analysis of Da Costa et al. (2018) but contrasts with the results of previous phylogenetic analyses based on molecular (Ruhfel et al. 2011; Koi et al. 2012; Ruhfel et al. 2016; Sun et al. 2016) or morphological data (Philbrick and Novelo 2004; Philbrick et al. 2004). These studies variously placed *Diamantina* as sister to all other Podostemoideae, as sister to the strictly neotropical Podostemoideae clade (Fig. 1, clade B), or as a member of a paraphyletic grade of paleotropical taxa. Maximum likelihood bootstrap support for the placement presented here (74 BS) is higher than support for its placement in previous studies, however, our other two methods of support for this placement did not pass our threshold for being well supported (72.6 SH-aLRT; 77 UFBS). Morphological features of the pollen and silica bodies of *Diamantina* lend support to the phylogenetic position presented here and in Da Costa et al. (2018). *Diamantina* has previously been reported as the only genus within the family to produce pollen in tetrads (Philbrick et al. 2004; Rutishauser et al. 2005). However, those studies examined a limited number of specimens. Further examination of newly collected specimens, including one specimen included in this study (*Bove et al. 2253*) revealed that initial observations were based on underdeveloped anthers and that *Diamantina* regularly produces both tetrads and dyads (De Barros Marinho 2013; De Barros Marinho et al. 2014; C. T. Philbrick unpubl. data), a condition rare in angiosperms (Furness 2012). Most Podostemaceae in this mixed neotropical and paleotropical clade (Fig. 1, clade A) produce pollen in dyads, including all Asian, Australian, and many African taxa, as well as the neotropical genera *Ceratolacis*, *Cipoia*, and *Podostemum* (Philbrick et al. 2004; Cook and Rutishauser 2007). This suggests that dyad pollen may be a synapomorphy for this clade and has implications for reconstructing the evolutionary shift from monad to dyad pollen, or vice versa (De Barros Marinho et al. 2014) as some African taxa nested within this clade possess monad pollen (Thiv et al. 2009; Koi et al. 2012). The only known genus with dyad pollen that occurs outside of this clade is *Lophogyne* (Bove et al. 2011; De Barros Marinho 2013; De Barros Marinho et al. 2014) which suggests that dyad pollen has arisen independently at least

twice in the family. Morphology of silica bodies found in the vegetative tissues of some Podostemoaceae also supports the placement of *Diamantina* as a member of this mixed neotropical and paleotropical clade. Although only neotropical Podostemoideae taxa were included in the study by Da Costa et al. (2018), their recovered clade containing *Ceratolacis*, *Cipoia*, *Diamantina*, and *Podostemum* (here found to be the first several diverging lineages of the mixed neotropical and paleotropical clade [Fig. 1, clade A]) had a combination of silica body features not found elsewhere in neotropical Podostemoideae. These features include silica bodies present and located in the epidermis, undulate or perforated silica body morphology, and the presence of a lumen. An expanded investigation of silica bodies in the family, particularly including all paleotropical taxa (but see Ameka et al. 2002) and *Devillea flagelliformis*, is warranted.

In summary, the placement of *Diamantina* has not yet received strong support from phylogenetic analyses of molecular data. However, the shared morphological features of pollen and silica bodies with other taxa in the mixed neotropical and paleotropical clade (Fig. 1, clade A) provide additional evidence supporting the placement of *Diamantina* presented here. Nevertheless, a more comprehensive examination, including phylogenetic analysis of nuclear data and other morphological features, is warranted.

Relationships in the Mixed Neotropical and Paleotropical Clade—Relationships among the neotropical and paleotropical lineages within Podostemoideae have been unclear in previous studies. For example, in Koi et al. (2012) and Ruhfel et al. (2016), there were four paleotropical clades (2 African, 1 Malagasy, and 1 Asian/Australian), though relationships among those clades and the clades representing neotropical genera *Ceratolacis*, *Cipoia* (not included in Koi et al. 2012), and *Podostemum* were either weakly supported or in conflict with those presented here. In Ruhfel et al. (2016), *Ceratolacis*, *Cipoia*, and *Podostemum* were strongly supported (98 posterior probability) as members of a clade containing African and Malagasy taxa but excluding the Asian/Australian taxa. This conflict may be the result of Bayesian analyses providing inflated levels of support (Suzuki et al. 2002; Douady et al. 2003; Simmons et al. 2004) and/or issues with missing data (e.g. *Endocaulos*, *Pohliella*, and *Thelethylax* were each represented by only one of four genes included in that analysis). Here, support for the relationships among these clades is much improved. We found a strongly supported paleotropical clade embedded in a paraphyletic grade of neotropical taxa (Fig. 1, clade A; Fig. 2A, clade A). In addition to the neotropical *Diamantina* being placed as sister to all other taxa in this clade as discussed above, clades representing *Ceratolacis*, *Cipoia*, and *Podostemum* are strongly supported as successive sister groups to a strongly-supported clade containing all sampled paleotropical Podostemoideae taxa. Within that paleotropical clade, African and Asian/Australian taxa form strongly supported clades, and the Malagasy *Thelethylax* is moderately supported (71 BS) as sister to the Asian/Australian taxa. This set of relationships would likely alter biogeographic reconstructions of ancestral areas in the early history of the family as compared to those reconstructed in Koi et al. (2015) and Ruhfel et al. (2016). Here, in addition to the placement of the neotropical *Devillea* as sister to all other Podostemoideae, the first several lineages of the mixed neotropical and paleotropical clade are neotropical, suggesting a

single dispersal event from the neotropics to the paleotropics within Podostemoideae.

Before a formal reexamination of the biogeographic history of the family is conducted, genera missing in our sampling (see Materials and Methods) should be included in a plastid phylogenomic analysis. Particularly important to include are taxa that may help clarify the relationships between major subclades in the mixed neotropical and paleotropical clade. These taxa include two genera endemic to Africa (i.e. *Lebbiea* [Cheek and Lebbie 2018]; *Pohliella* [Cheek 2020]), one endemic to Madagascar (*Endocaulos*), and two that occur in both Africa and Madagascar (*Paleodicraea* and *Sphaerotherylax*, [Koi et al. 2012, R. Rutishauser unpubl. data]). *Lebbiea* is also important to include in a phylogenetic analysis as several aspects of its morphology are unique within the family (Cheek and Lebbie 2018). Though the Malagasy taxa *Endocaulos* and *Thelethylax* have been included in previous studies, *Paleodicraea* and *Sphaerotherylax* have never been included in a molecular analysis and thus it is not known if the four Podostemoideae genera that occur in Madagascar form a monophyletic group. In previous studies, a clade containing *Endocaulos* + *Thelethylax* has been variously placed as 1) sister to a clade of Asian and Australian taxa (Koi et al. 2012), 2) sister to a clade comprised of *Cipoia*, *Ceratolacis*, and *Podostemum* (Ruhfel et al. 2016), or 3) sister to other African species (Moline et al. 2006; Schenk et al. 2015). Finally, it is important to sample *Pohliella* in future plastid phylogenomic analyses, as Cheek (2020) stated that *Cipoia* and *Pohliella* are identical morphologically and recommended that they be included in a future molecular phylogenetic analysis to determine if taxa in these genera should be recognized as one amphi-Atlantic genus. However, initial investigations of the morphology of *Cipoia* and *Pohliella* by R. Rutishauser (unpubl. data) have revealed that the similarities between these two genera may be the result of shared plesiomorphic or convergent character states common in other Podostemoideae taxa such as thread-like roots, a single stamen per flower, presence of a gynophore, and bilocular ovaries (Ameka et al. 2002; Philbrick and Novelo 2004; Philbrick et al. 2004; Cook and Rutishauser 2007). Furthermore, Ruhfel et al. (2016) included samples representing both *Cipoia* and *Pohliella* (i.e. *Pohliella amicorum* [J.B.Hall] Cheek, syn. *Saxicolella amicorum* J.B. Hall) in their molecular phylogenetic analysis, the results of which suggest that *Cipoia* and *Pohliella* are not closely related. Given that the placement of *Cipoia* presented here conflicts with its position in Ruhfel et al. (2016), and that data for only one gene were available for *Pohliella* in that study, the relationship of *Cipoia* and *Pohliella* should be reexamined when additional plastome-level data are available. Other taxa missing in our sampling (e.g. *Saxicolella* s.s., Koi et al. 2012; Cheek et al. 2022) are likely embedded in more nested subclades of Asian or African taxa and while important to include in future studies, are less so for determining major relationships and biogeographic patterns in the family.

Relationships in the Strictly Neotropical Clade—Relationships within the strictly neotropical clade of Podostemoideae (Fig. 1, clade B; Fig. 2B, clade B) are much improved compared to previous studies, with most sampled, currently recognized genera strongly supported as monophyletic. Particularly with the nomenclatural changes suggested below, some of which include changes to be made in future publications, taxonomy at the genus level in the neotropical clade is moving closer to reflecting evolutionary history. In contrast, work below the genus level is needed to define species

boundaries and relationships, particularly in the genera *Apinagia* s.s., the recently expanded *Lophogyne* s.l., and *Rhyncholacis*. For example, in *Apinagia* s.s. and *Rhyncholacis* initial investigations for monographic work (C. T. Philbrick unpubl. data) suggest that there are many fewer species than currently accepted names in these genera. This is likely because extreme variation in vegetative form has led to the over-description of species (Philbrick et al. 2010). This reduction in species number has occurred in previously published monographs of (e.g. *Ceratolacis*, Philbrick et al. 2009; *Podostemum*, Philbrick and Novelo 2004) and other nomenclatural adjustments (Philbrick et al. 2010, 2016).

Lophogyne* s.l. and the Non-Monophyly of *Marathrum—

Our results support broadening the circumscription of *Lophogyne* as proposed by Philbrick and Bove (2019) and recover strongly-supported relationships within the clade. Along with the previously recognized *Lophogyne* species (Bove et al. 2011), *Lophogyne* s.l. now includes taxa that were formerly placed in the genera *Apinagia*, *Jenmaniella* Engl., *Marathrum*, and *Monostylis* Tul. Philbrick and Bove (2019) list four morphological characters that define *Lophogyne* s.l.: 1) the ovary is oriented vertically or obliquely at anthesis, 2) the flower projects from the ruptured spathella, 3) stamens and tepals occur on only one side of the ovary, and 4) silica bodies are absent from the leaves. For the first time, we present evidence that the South American species currently recognized as *Marathrum capillaceum* (Pulle) P.Royen is embedded within *Lophogyne* s.l. and should be recognized as *Lophogyne capillacea* Pulle as originally described (see Bove et al. 2019 regarding the illegitimate later homonym *Lophogyne capillacea* (Tul.) C.T.Philbrick & C.P.Bove). This species possesses the three floral features of *Lophogyne* s.l. given by Philbrick and Bove (2019). However, the presence of silica bodies needs further study. Schnell (1967) reports the presence of silica bodies in the petiole but does not mention their presence elsewhere in the leaf. Philbrick and Bove (2019) cite Da Costa et al. (2018) regarding the absence of silica bodies in the leaves of *Lophogyne* s.l. species, but *L. capillacea* was not included in that study. For those species they did examine, their methods state that they sampled “apical, medial and basal portions of fully developed leaves,” thus it is unclear if they sampled the same portion of the leaf that Schnell (1967) refers to as the petiole. Initial investigations (C. T. Philbrick unpubl. data) suggest that *Marathrum* s.s., including the type species of the genus, *M. foeniculaceum* (Van Royen 1951; Tippery et al. 2011), is found in Mexico, Central America, Columbia, and Cuba; other species once placed in *Marathrum* that are found outside of those areas have been transferred to other genera (Philbrick et al. 2018). Our results also strongly support that two *Lophogyne* species, *L. fimbriata* and *L. royenella*, are not monophyletic. *Lophogyne ceratophylla* and an unidentified *Lophogyne* species (*L. sp1*) are embedded within a paraphyletic *L. royenella* while *L. wilsonii* (paratype sampled here, Bove and Philbrick 2474; Bove et al. 2020) and another unidentified *Lophogyne* species (*L. sp2*) are embedded within a paraphyletic *L. fimbriata*. Paraphyletic species are not uncommon in molecular phylogenetic studies of Podostemaceae and may be attributed to allopatric speciation (e.g. Koi et al. 2012; Kato et al. 2019). Paraphyletic or non-monophyletic species may also be the result of misidentifications due the challenge of placing names on poorly known taxa, such as some species of *Lophogyne* s.l., that lack information regarding their morphological variability combined with a limited understanding of

species distributions (Bidault et al. 2023). Monographic work in *Lophogyne* s.l. is clearly needed.

Possible New Genus—We place an undescribed species collected in Venezuela in 2007 (Philbrick et al. 6055, [MICH]). As far as we are aware, this species has been collected at only one locality. Initial attempts by C. T. Philbrick to identify this specimen to genus based on morphology were inconclusive and given its placement in the phylogeny, it likely represents a new genus. This species is strongly placed within a clade containing two other subclades, the first representing *Apinagia* s.s. (100 BS) and the second (94 BS) containing several taxa, including *Oserya* s.s., *Noveloa*, *Marathrum* s.s., and *Apinagia nana* and *Oserya pilgeri*. Relationships among these three lineages are not well supported (70 BS). Initial investigations by C. T. Philbrick (unpubl. data) suggest this undescribed taxon has prostrate stems divided into two regions including disklike hold-fasts from which leaves do not arise, and a region where the leaves arise. Thus the stems of this taxon are not similar to those in *Apinagia* s.s. which has upright stems (Tippery et al. 2011). Species of the second subclade have either upright or prostrate stems (Tippery et al. 2011). Morphological investigations, including comparisons to other closely related taxa, are ongoing and a formal description of this taxon will be presented in a future publication.

***Oserya* is Not Monophyletic**—Our results place the genera *Oserya* s.s. and *Noveloa* as strongly supported sister taxa. Tippery et al. (2011) separated two species from *Oserya* s.l. and placed them in the new genus *Noveloa* based on their phylogenetic results and differences in morphology and biogeographic distribution (*Noveloa coulteriana*; *N. longifolia*). *Oserya* s.s. has pinnate leaf divisions, unistaminate flowers, five nonsuture ribs per capsule valve, and is distributed in South America, while *Noveloa* has dichotomous or subdichotomous leaf divisions, stamens numbering 1–3, three nonsuture ribs per capsule valve, and is distributed in Central America and Mexico (Tippery et al. 2011). While our results suggest that *Oserya* s.s. and *Noveloa* could be circumscribed into a broad *Oserya* s.l., we prefer to recognize these two genera separately due to their morphological and biogeographic differences. Our results also provide evidence that the recent transfer of *Apinagia pilgeri* Mildbr. into *Oserya* s.s. as *Oserya pilgeri* by Philbrick et al. (2016) is not warranted and would make *Oserya* s.s. nonmonophyletic. *Oserya pilgeri* is strongly supported as sister to *Apinagia nana*, and that clade is strongly supported as sister to *Marathrum*. As *Apinagia nana* and *Oserya pilgeri* are clearly not at home in either *Oserya* s.s. or *Apinagia* s.s., they should either be transferred to a new genus or into *Marathrum*. We defer these taxonomic changes pending further sampling from *Marathrum*. These two species are morphologically quite different from *Marathrum* species, so if this clade remains sister to *Marathrum* in future studies we suggest creating a new genus. An additional nomenclatural issue remains unaddressed as Philbrick et al. (2016) considered *Oserya flabellifera* Tul. & Wedd., the type species of *Oserya* (Van Royen 1954), and *Castelnavia monandra* synonyms. They did not propose combinations in *Castelnavia* for other names in *Oserya* s.s. (e.g. *O. perpusilla*, sampled here). Based on our results, *O. perpusilla* (and perhaps other species still included in *Oserya* s.s. [Tippery et al. 2011]) is not closely related to *Castelnavia*. We will address the necessary nomenclatural adjustments in a future publication.

***Apinagia* s.s.**—The taxonomic impediment in Podostemaceae is especially acute in *Apinagia* s.l., the largest (34–37 spp.)

and most taxonomically troublesome genus of neotropical Podostemaceae (Van Royen 1951; Berry 2004; Philbrick et al. 2010, 2016; POWO 2023). The genus is also of special conservation concern as over 50% of its species are documented from only one or two rivers, yet taxonomic uncertainty severely clouds the understanding of species distributions. Two factors contribute to this taxonomic uncertainty. First is the application of a largely typological species concept (cf. Cracraft 2000) by many previous workers, where idealized types represent a species and population level variation is disregarded. Second is the heavy reliance by previous workers on vegetative characters (e.g. leaf form) to distinguish species. Highly plastic vegetative forms, common in aquatic macrophytes and in Podostemaceae in particular (e.g. Sculthorpe 1967; Philbrick and Novelo 2004), combined with species delineations that emphasize vegetative features, have resulted in a taxonomy of dubious utility. The solution, we believe, rests on the use of characters that do not exhibit phenotypic plasticity (e.g. reproductive characters) for species recognition. Initial investigations by C. T. Philbrick suggest that characters important for species recognition in *Apinagia* include stamen arrangement around the ovary, tepal form, pedicel apex shape, and features of the mature capsules including the number and form of ribs that occur on capsule valves.

Results presented here agree with Tippery et al. (2011) who revealed that *Apinagia* s.l. is not monophyletic. Only *Apinagia* s.l. species with upright stems (one attachment point), as opposed to prostrate stems (multiple attachment points) should be included in *Apinagia* s.s. as the type for *Apinagia*, *A. fucoides* (Van Royen 1951; Tippery et al. 2011; Bove and Philbrick 2016), is a member of this upright-stem clade. Upright stems are not unique to *Apinagia* s.s., and are also present in species of *Castelnavia*, *Oserya*, and *Lophogyne* (Tippery et al. 2011). Many *Apinagia* species with prostrate stems have been transferred to other genera (Philbrick and Bove 2019) or will be in the future (e.g. *Apinagia nana*; Ruhfel et al. in prep), and other names have been placed into synonymy (Philbrick et al. 2016). Furthermore, preliminary investigations based on more than 20 yr of field work and hundreds of specimens collected by C. T. Philbrick and colleagues along with inspection of type material suggest that many fewer species exist than the number of accepted names (Philbrick et al. 2016). Preliminary work by C. T. Philbrick (unpubl. data) suggests that *Apinagia* s.s. contains ~15 species, at least two of which are undescribed, though we defer making any taxonomic revisions until more species can be sampled and nuclear data can be examined. Two species of *Apinagia* s.s. are strongly supported as not monophyletic in our results. *Apinagia richardiana* is embedded within *Apinagia longifolia* and *Apinagia tenuifolia* and the undescribed species *A. 'crowii'* are embedded within *A. fucoides*. While no morphological differences were found between the two clades of *A. fucoides*, there is a difference in their geographic distribution. The clade containing *A. fucoides* specimens C.P. Bove et al. 2236, 2276, and 2284, and C.T. Philbrick et al. 5992 is distributed in the northeast of Brazil (Piauí, Tocantins) while the other *A. fucoides* clade is distributed in central Brazil (Tocantins, Goiás, Mato Grosso, Mato Grosso do Sul). Overall, further work is needed on species boundaries within *Apinagia*. Results presented here provide critical information for developing a functional taxonomy for this genus to be included in an upcoming monograph, necessary for implementing conservation strategies to

save these threatened species. Clarified species boundaries will allow for critically needed evaluation of local species endemism and the impact of expanding hydroelectric generation capacity (Philbrick et al. 2010).

Phylogenetic Conflict and the Use of Concatenated Plastid Genes for Phylogenetic Reconstruction in Podostemaceae—We observed very little supported conflict between individual plastid gene trees and the concatenated phylogeny. Furthermore, most individual gene trees lacked strong support for the majority of branches (Fig. S5), indicating that concatenation of the plastid coding regions was appropriate for inferring the species phylogeny. Most supported conflict was within clades corresponding to single species or closely related groups of species, suggesting that there was no evidence of widespread conflict among plastid gene trees in Podostemaceae due to biological causes (e.g. heteroplasmic recombination) or systematic and stochastic error (see Walker et al. 2019 and references therein). There were four nodes where the gene tree for *matK*, the gene region most often used to infer the phylogeny of this family in previous publications, conflicted with the concatenated tree. However, each of these conflicts was within a clade representing a single species and thus not relevant to relationships among genera and species in the family. This suggests that individual plastid gene regions such as *matK* may continue to be useful for placing taxa within the Podostemaceae phylogeny, provided they contain sufficient phylogenetic information. Hybridization has been suggested in *Inversodicraea* based on morphology (Cheek et al. 2017) and demonstrated in *Marathrum* with molecular data (Bedoya et al. 2021) and thus it is possible that introgression as well as incomplete lineage sorting could cause phylogenetic conflict among nuclear genes and the plastome. In such a scenario, plastome data may or may not reflect the overall species divergence history. The extent to which this is an issue for phylogenetic inference in Podostemaceae remains to be tested with broadly sampled, nuclear phylogenomic data.

Conclusions and Future Directions—The phylogeny presented here is the first well-sampled plastid phylogenomic analysis of the family and provides novel insights on Podostemaceae evolutionary history and plastome evolution. Our analyses resolve several recalcitrant nodes compared to previous studies, provide evidence for taxonomic and nomenclatural adjustments, place a previously unsampled and undescribed taxon that likely represents a new genus and, in contrast to previously published results, suggest that there has been only one dispersal event from the neotropics to the paleotropics within Podostemoideae. Additionally, we show that there is no evidence of widespread conflict among plastid genes and the concatenated phylogeny. While taxon sampling here was adequate to address several important questions, expanded sampling is needed to complete an assessment of phylogenetic relationships of all described taxa of Podostemaceae. Particularly important to include in future studies are representatives of genera not sampled here, and an expanded sampling of large and taxonomically confusing genera such as *Apinagia* s.s., *Inversodicraea*, *Ledermannia*, *Lophogyne* s.l., and *Rhyncholacis*, all of which are greatly in need of monographic work. Particularly needed are more comparative morphological studies on several populations per species in order to evaluate the range of phenotypic plasticity (e.g. Bidault et al. 2023). Now that the phylogenetic history of the Podostemaceae plastome is becoming clear, a

more complete understanding of the evolutionary history of the family will require analyses using nuclear genomic data.

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AUTHOR CONTRIBUTIONS

BRR and CTP conceived and designed the study. BRR was the primary author of the manuscript. BRR, CPB, CTP, and RR provided important samples and vouchers. BRR and NK extracted the gDNA and prepared it for sequencing. BRR and DAL developed and utilized the pipeline to trim, filter, assemble, and organize the raw data. BRR analyzed the final datasets and produced the figures. All authors contributed to the final manuscript.

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APPENDIX 1. Voucher information and GenBank accessions for sequences used in this study. Data produced for this study have GenBank numbers beginning with “OR” or “PP”. Data for species not sequenced in this study list the GenBank numbers for each coding region or the full plastome accession number. An em dash (—) indicates that the sequence was not available. Herbarium acronyms follow Index Herbariorum (Thiers 2023). Order of data in the appendix below is as follows, except for those with only a full plastome accession number: **Family. Genus. Species**: voucher (herbarium), GenBank accessions: *atpA*, *atpB*, *atpE*, *atpF*, *atpH*, *atpI*, *ccsA*, *cema*, *clpP*, *matK*, *ndhA*, *ndhB*, *ndhC*, *ndhD*, *ndhE*, *ndhF*, *ndhG*, *ndhH*, *ndhI*, *ndhJ*, *ndhK*, *petA*, *petB*, *petD*, *petG*, *petL*, *petN*, *psaA*, *psaB*, *psaC*, *psaI*, *psaJ*, *psbA*, *psbB*, *psbC*, *psbD*, *psbE*, *psbF*, *psbH*, *psbI*, *psbJ*, *psbK*, *psbL*, *psbM*, *psbN*, *psbT*, *psbZ*, *rbcL*, *rpl2*, *rpl14*, *rpl16*, *rpl20*, *rpl22*, *rpl32*, *rpl33*, *rpl36*, *rpoA*, *rpoB*, *rpoC1*, *rpoC2*, *rps11*, *rps12*, *rps14*, *rps15*, *rps18*, *rps19*, *rps2*, *rps3*, *rps4*, *rps7*, *rps8*, *ycf3*, and *ycf4*.

Hypericaceae (outgroup). *Cratogeomys* Blume. *C. cochinchinense* (Lour.) Blume: unknown CNShis0047329 (CNS), MK995180.

Vismia Vand. *V. guianensis* (Aubl.) Pers.: A. M. Amorim 7659 (CEPEC), JX662421, JX663828, JX663747, JX664444, JX662935, JX665032, JX662304, JX664834, —, JX661967, JX663657, JX664325, JX661839, JX664366, JX664647, JX662779, JX663435, JX662826, JX662090, JX662735, JX664561, JX664114, JX663943, JX663015, JX662454, JX662486, —, JX664235, JX662981, JX663129, JX664189, JX664679, JX663305, JX662222, JX662603, JX662343, JX664515, JX663861, JX663222, JX663895, JX664030, JX661926, JX662262, —, JX662648, JX664606, JX664149, JX664076, JX664280, JX663393, JX663990, JX662567, JX662863, —, —, JX663059, JX662048, JX663504, JX664967, JX662692, JX664799, JX663610, JX661885, JX663534, —, JX662384, JX663177, JX663787, JX664877, —, JX663349, JX664482, JX663262.

Podostemaceae (ingroup). *Apinagia* Tul. A. ‘crowii’: C. T. Philbrick et al. 6320 (MICH, VEN), PP242918, PP245408, PP246237, PP244218, PP242314, PP242798, PP242195, PP243494, PP241351, PP245884, PP244816, PP241110, PP244098, PP243041, PP242078, PP245170, PP245291, PP246603, PP244697, PP241720, PP243611, PP244458,

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- Cipoia* C.T.Philbrick, **Novelo, and Irgang.** *C. inserta* C.T.Philbrick, **Novelo & Irgang:** C. P. Bove *et al.* 2205 (MICH, R), PP242927, PP245417, PP246246, PP244227, PP242323, PP242807, PP242204, PP243503, PP241360, PP245893, PP244825, PP241119, PP244107, PP243050, PP242087, PP245179, PP245300, PP246612, PP244706, PP241729, PP243620, PP244467, PP241606, PP242567, PP245779, PP243286, PP245062, PP248289, PP247457, PP247699, PP248412, PP247222, PP246858, PP243741, PP241482, PP242444, PP242685, PP245658, PP244944, PP246010, PP243864, PP241242, PP241849, PP243391, PP245538, PP247940, PP247339, OR885185, PP246980, PP240998, PP246367, PP249115, PP247104, PP248642, PP248528, PP248175, PP244347, PP246489, PP248055, PP249347, PP246124, PP243984, PP241966, PP243170, PP244587, PP246735, PP247579, PP247819, PP249470, PP249235, PP248873, PP248993, PP248752. *C. ramosa* C.P.Bove: C.T.Philbrick & **Novelo:** C. P. Bove *et al.* 2251 (MICH, R), PP242928, PP245418, PP246247, PP244228, PP242324, PP242808, PP242205, PP243504, PP241361, PP245894, PP244826, PP241120, PP244108, PP243051, PP242088, PP245180, PP245301, PP246613, PP244707, PP241730, PP243621, PP244468, PP241607, PP242568, PP245780, PP243287, PP245063, PP248290, PP247458, PP247700, PP248413, PP247223, PP246859, PP243742, PP241483, PP242445, PP242686, PP245659, PP244945, PP246011, PP243865, PP241243, PP241850, PP243392, PP245539, PP247941, PP247340, OR885186, PP246981, PP240999, PP246368, PP249116, PP247105, —,
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- Cladopus* H.A.Möller. *C. doianus* (Koidz.) Koriba: S. Koi & N. Katayama *jp404* (TNS), PP242929, PP245419, PP246248, PP244229, PP242325, PP242809, PP242206, PP243505, PP241362, PP245895, —, PP241121, PP244109, PP243052, PP242089, PP245181, —, PP246614, PP244708, PP241731, PP243622, PP244469, PP241608, PP242569, —, —, PP245064, PP248291, PP247459, PP247701, —, PP247224, PP246860, PP243743, PP241484, PP242446, PP242687, PP245660, PP244946, PP246012, PP243866, PP241244, PP241851, —, PP245540, —, PP247341, OR885187, PP246982, PP241000, PP246369, PP249117, PP247106, —, PP248530, —, PP244349, PP246491, PP248057, PP249349, PP246126, PP243986, PP241968, —, PP244589, PP246737, PP247581, PP247821, PP249472, PP249237, PP248875, PP248995, PP248754.
- Dalzellia* Wight. *D. ceylanica* (Gardner) Wight: M. Kato & N. Katayama *sl101* (TNS), PP242930, PP245420, PP246249, PP244230, PP242326, PP242810, PP242207, —, PP241363, —, PP244827, PP241122, PP244110, —, PP242090, —, —, PP246615, PP244709, PP241732, PP243623, PP244470, PP241609, —, —, —, —, PP248292, PP247460, PP247702, —, —, PP246861, PP243744, PP241485, PP242447, PP242688, PP245661, PP244947, —, —, —, —, —, —, —, —, —, PP247342, OR885188, PP246983, PP241001, PP246370, —, —, —, —, —, —, —, —, —, PP246492, PP248058, PP249350, PP246127, PP243987, PP241969, —, —, PP246738, —, —, PP247822, PP249473, PP249238, —, —, PP248996, PP248755.
- Devillea* Tul. & Wedd. *D. flagelliformis* Tul. & Wedd.: C. P. Bove *et al.* 2368 (MICH, R), PP242973, PP245462, PP246291, PP244273, PP242368, PP242853, PP242248, PP243547, PP241405, PP245938, PP244870, PP241166, PP244152, PP243095, PP242132, PP245225, PP245343, PP246659, PP244751, PP241774, PP243664, PP244512, PP241653, PP242611, PP245821, PP243323, PP245106, PP248336, PP247503, PP247744, PP248456, PP247266, PP246903, PP243788, PP241529, PP242491, PP242731, PP245704, PP244988, PP246053, PP243909, PP241286, PP241893, PP243431, PP245582, PP247983, PP247385, OR885232, PP247027, PP241043, PP246413, PP249160, PP247149, PP248682, PP248570, PP248217, PP244392, PP246535, PP248101, PP249393, PP246170, PP244031, PP242011, PP243214, PP244632, PP246782, PP247623, PP247865, PP249516, PP249273, PP248918, PP249039, PP248798.
- Diamantina* **Novelo, C.T.Philbrick & Irgang.** *D. lombardii* **Novelo, C.T.Philbrick & Irgang:** C. P. Bove *et al.* 2131 (R), PP242931, PP245421, PP246250, PP244231, PP242327, PP242811, PP242208, PP243506, PP241364, PP245896, PP244828, PP241123, PP244111, PP243053, PP242091, PP245183, PP245302, PP246616, PP244710, PP241733, PP243624, PP244471, PP241610, PP242570, PP245781, PP243288, PP245065, PP248293, PP247461, PP247703, PP248414, PP247225, PP246862, PP243745, PP241486, PP242448, PP242689, PP245662, PP244948, PP246013, PP243867, PP241245, PP241852, PP243393, PP245541, PP247942, PP247343, OR885189, PP246984, PP241002, PP246371, PP249118, PP247107, PP248643, PP248531, PP248177, PP244350, PP246493, PP248059, PP249351, PP246128, PP243988, PP241970, PP243172, PP244590, PP246739, PP247582, PP247823, PP249474, —, PP248876, PP248997, PP248756; C. P. Bove *et al.* 2253 (MICH, R), PP242932, PP245422, PP246251, PP244232, PP242812, PP242209, PP243507, PP241365, PP245897, PP244829, PP241124, PP244112, PP243054, PP242092, PP245184, PP245303, PP246617, PP244711, PP241734, PP243625, PP244472, PP241611, PP242571, PP245782, PP243289, PP245066, PP248294, PP247462, PP247704, PP248415, PP247226, PP246863, PP243746, PP241487, PP242449, PP242690, PP245663, PP244949, PP246014, PP243868, PP241246, PP241853, PP243394, PP245542, PP247943, PP247344, OR885190, PP246985, PP241003, PP246372, PP249119, PP247108, PP248644, PP248532, PP248178, PP244351, PP246494, PP248060, PP249352, PP246129, PP243989, PP241971, PP243173, PP244591, PP246740, PP247583, PP247824, PP249475, —, PP248877, PP248998, PP248757.
- Dicraeanthus* Engl. *D. zehnderi* H.Hess: J. Ghogue *gho1650* (YA, Z/ ZT), PP242933, PP245423, PP246252, PP244233, PP242329, PP242813, PP242210, PP243508, PP241366, PP245898, PP244830, PP241125, PP244113, PP243055, PP242093, PP245185, PP245304, PP246618,

- PP244712, PP241735, PP243626, PP244473, PP241612, PP242572, PP245783, PP243290, PP245067, PP248295, PP247463, PP247705, PP248416, PP247227, PP246864, PP243747, PP241488, PP242450, PP242691, PP245664, PP244950, PP246015, PP243869, PP241247, PP241854, PP243395, PP245543, PP247944, PP247345, OR885191, PP246986, PP241004, PP246373, PP249120, PP247109, PP248645, PP248533, PP248179, PP244352, PP246495, PP248061, PP249353, PP246130, PP243990, PP241972, PP243174, PP244592, PP246741, PP247584, PP247825, PP249476, PP249239, PP248878, PP248999, PP248758.
- Djinga C.Cusset. D. felicis C.Cusset:** *J. Ghogue et al. gar09* (YA, Z/ZT), PP242934, PP245424, PP246253, PP244234, PP242330, PP242814, PP242211, PP243509, PP241367, PP245899, PP244831, PP241126, PP244114, PP243056, PP242094, PP245186, PP245305, PP246619, PP244713, PP241736, PP243627, PP244474, PP241613, PP242573, PP245784, —, PP245068, PP248296, PP247464, PP247706, PP248417, PP247228, PP246865, PP243748, PP241489, PP242451, PP242692, PP245665, PP244951, PP246016, PP243870, PP241248, PP241855, PP243396, PP245544, PP247945, PP247346, OR885192, PP246987, PP241005, PP246374, PP249121, PP247110, PP248646, PP248534, PP248180, PP244353, PP246496, PP248062, PP249354, PP246131, PP243991, PP241973, PP243175, PP244593, PP246742, PP247585, PP247826, PP249477, PP249240, PP248879, PP249000, PP248759.
- Genus nov.:** *C. T. Philbrick et al. 6055* (MICH), PP242970, PP245458, PP246287, PP244269, PP242365, PP242849, PP242244, PP243544, PP241402, PP245934, PP244866, PP241162, PP244149, PP243091, PP242129, PP245221, PP245340, PP246655, PP244748, PP241771, PP243660, PP244509, PP241649, PP242608, PP245819, PP243321, PP245103, PP248332, PP247499, PP247741, PP248452, PP247263, PP246900, PP243784, PP241525, PP242487, PP242727, PP245701, PP244985, PP246051, PP243905, PP241283, PP241890, PP243427, PP245579, PP247980, PP247381, OR885228, PP247023, PP241040, PP246409, PP249156, PP247145, —, PP248567, PP248213, PP244388, PP246531, PP248097, PP249389, PP246166, PP244027, PP242008, PP243210, PP244628, PP246778, PP247620, PP247861, PP249512, PP249270, PP248914, PP249035, PP248794.
- Hydrobryum Endl. H. japonicum Imamura:** *S. Koi & N. Katayama jp401* (TNS), PP242935, PP245425, PP246254, PP244235, PP242331, PP242815, PP242212, PP243510, PP241368, PP245900, PP244832, PP241127, PP244115, PP243057, PP242095, PP245187, PP245306, PP246620, PP244714, PP241737, PP243628, PP244475, PP241614, PP242574, PP245785, PP243291, PP245069, PP248297, PP247465, PP247707, PP248418, PP247229, PP246866, PP243749, PP241490, PP242452, PP242693, PP245666, PP244952, PP246017, PP243871, PP241249, PP241856, PP243397, PP245545, PP247946, PP247347, OR885193, PP246988, PP241006, PP246375, PP249122, PP247111, PP248647, PP248535, PP248181, PP244354, PP246497, PP248063, PP249355, PP246132, PP243992, PP241974, PP243176, PP244594, PP246743, PP247586, PP247827, PP249478, —, PP248880, PP249001, PP248760.
- Inversodicraea Engl. ex R.E.Fr. I. bosii (C.Cusset) Rutish. & Thiv:** *J. Ghogue et al. gar01* (YA, Z/ZT), PP242936, PP245426, PP246255, PP244236, PP242332, PP242816, PP242213, PP243511, PP241369, PP245901, PP244833, PP241128, PP244116, PP243058, PP242096, PP245188, PP245307, PP246621, PP244715, PP241738, PP243629, PP244476, PP241615, PP242575, PP245786, PP243292, PP245070, PP248298, PP247466, PP247708, PP248419, PP247230, PP246867, PP243750, PP241491, PP242453, PP242694, PP245667, PP244953, PP246018, PP243872, PP241250, PP241857, PP243398, PP245546, PP247947, PP247348, OR885194, PP246989, PP241007, PP246376, PP249123, PP247112, PP248648, PP248536, PP248182, PP244355, PP246498, PP248064, PP249356, PP246133, PP243993, PP241975, PP243177, PP244595, PP246744, PP247587, PP247828, PP249479, PP249241, PP248881, PP249002, PP248761.
- Ledermannia Engl. L. bowlingii (J.B.Hall) C.Cusset:** *G. Ameka and R. Rutishauser ar021010* (GC, Z/ZT), PP242945, PP245434, PP246264, PP244245, PP242341, PP242825, PP242221, PP243520, PP241378, PP245910, PP244842, PP241137, PP244125, PP243067, PP242105, PP245197, PP245316, PP246630, PP244724, PP241747, PP243638, PP244485, PP241624, PP242584, PP245795, —, PP245079, PP248307, PP247475, PP247717, PP248428, PP247239, PP246876, PP243759, PP241500, PP242462, PP242703, PP245676, PP244961, PP246027, PP243881, PP241259, PP241866, —, PP245555, PP247956, PP247357, OR885203, PP246998, PP241016, PP246385, PP249132, PP247121, PP248657, PP248544, PP248190, PP244364, PP246507, PP248073, PP249365, PP246142, PP244002, PP241984, PP243186, PP244604, PP246753, PP247596, PP247837, PP249488, PP249250, PP248890, PP249011, PP248770. **L. letouzeyi C.Cusset:** *J. Ghogue et al. gar12* (YA, Z/ZT), PP242946, PP245435, PP246265, PP244246, PP242342, PP242826, PP242222, PP243521, PP241379, PP245911, PP244843, PP241138, PP244126, PP243068, PP242106, PP245198, PP245317, PP246631, PP244725, PP241748, PP243639, PP244486, PP241625, PP242585, PP245796, —, PP245080, PP248308, PP247476, PP247718, PP248429, PP247240, PP246877, PP243760, PP241501, PP242463, PP242704, PP245677, PP244962, PP246028, PP243882, PP241260, PP241867, —, PP245556, PP247957, PP247358, OR885204, PP246999, PP241017, PP246386, PP249133, PP247122, —, PP248545, —, PP244365, PP246508, PP248074, PP249366, PP246143, PP244003, PP241985, PP243187, PP244605, PP246754, PP247597, PP247838, PP249489, PP249251, PP248891, PP249012, PP248771.
- Lophogyne Tul. L. aeruginosa (P.Royen) C.T.Philbrick & C.P.Bove:** *C. T. Philbrick and S. Jairam-Doerga 6214* (BBS, MICH), PP242949, PP245438, PP246268, PP244249, PP242345, PP242829, PP242225, PP243524, PP241382, PP245914, PP244846, PP241141, PP244129, PP243071, PP242109, PP245201, PP245320, PP246634, PP244728, PP241751, PP243642, PP244489, PP241628, PP242588, PP245799, PP243302, PP245083, PP248311, PP247479, PP247721, PP248432, PP247243, PP246880, PP243763, PP241504, PP242466, PP242707, PP245680, PP244965, PP246031, PP243885, PP241263, PP241870, —, PP245559, PP247960, PP247361, OR885207, PP247002, PP241020, PP246389, PP249136, PP247125, PP248660, PP248548, PP248193, PP244368, PP246511, PP248077, PP249369, PP246146, PP244006, PP241988, PP243190, PP244608, PP246757, PP247600, PP247841, PP249492, PP249253, PP248894, PP249015, PP248774. **L. capillacea Pule:** *C. P. Bove and C. T. Philbrick 2424* (MICH, R), PP242950, PP245439, PP246269, PP244250, PP242346, PP242830, PP242226, PP243525, PP241383, PP245915, PP244847, PP241142, PP244130, PP243072, PP242110, PP245202, PP245321, PP246635, PP244729, PP241752, PP243643, PP244490, PP241629, PP242589, PP245800, PP243303, PP245084, PP248312, PP247480, PP247722, PP248433, PP247244, PP246881, PP243764, PP241505, PP242467, PP242708, PP245681, PP244966, PP246032, PP243886, PP241264, PP241871, PP243408, PP245560, PP247961, PP247362, OR885208, PP247003, PP241021, PP246390, PP249137, PP247126, PP248661, PP248549, PP248194, PP244369, PP246512, PP248078, PP249370, PP246147, PP244007, PP241989, PP243191, PP244609, PP246758, PP247601, PP247842, PP249493, PP249254, PP248895, PP249016, PP248775; *C. P. Bove and C. T. Philbrick 2441* (MICH, R), PP242951, PP245440, PP246270, PP244251, PP242347, PP242831, PP242227, PP243526, PP241384, PP245916, PP244848, PP241143, PP244131, PP243073, PP242111, PP245203, PP245322, PP246636, PP244730, PP241753, PP243644, PP244491, PP241630, PP242590, PP245801, PP243304, PP245085, PP248313, PP247481, PP247723, PP248434, PP247245, PP246882, PP243765, PP241506, PP242468, PP242709, PP245682, PP244967, PP246033, PP243887, PP241265, PP241872, PP243409, PP245561, PP247962, PP247363, OR885209, PP247004, PP241022, PP246391, PP249138, PP247127, PP248662, PP248550, PP248195, PP244370, PP246513, PP248079, PP249371, PP246148, PP244008, PP241990, PP243192, PP244610, PP246759, PP247602, PP247843, PP244944, PP249255, PP248896, PP249017, PP248776; *C. P. Bove and C. T. Philbrick 2459* (MICH, R), PP242952, PP245441, PP246271, PP244252, PP242348, PP242832, PP242228, PP243527, PP241385, PP245917, PP244849, PP241144, PP244132, PP243074, PP242112, PP245204, PP245323, PP246637, PP244731, PP241754, PP243645, PP244492, PP241631, PP242591, PP245802, PP243305, PP245086, PP248314, PP247482, PP247724, PP248435, PP247246, PP246883, PP243766, PP241507, PP242469, PP242710, PP245683, PP244968, PP246034, PP243888, PP241266, PP241873, PP243410, PP245562, PP247963, PP247364, OR885210, PP247005, PP241023, PP246392, PP249139, PP247128, PP248663, PP248551, PP248196, PP244371, PP246514, PP248080, PP249372, PP246149, PP244009, PP241991, PP243193, PP244611, PP246760, PP247603, PP247844, PP249495, PP249256, PP248897, PP249018, PP248777; *C. P. Bove et al. 2493* (R), MN165813. **L. ceratophylla (Engl.) C.T.Philbrick & C.P.Bove:** *C. P. Bove and C. T. Philbrick 1864* (MICH, R), PP242937, PP245427, PP246256, PP244237, PP242333, PP242817, PP242214, PP243512, PP241370, PP245902, PP244834,

- PP248445, PP247256, PP246893, PP243777, PP241518, PP242480, PP242720, PP245694, PP244978, PP246044, PP243898, PP241276, PP241883, PP243420, PP245572, PP247973, PP247374, OR885221, PP247016, PP241033, PP246402, PP249149, PP247138, PP248673, PP248561, PP248206, PP244381, —, PP248090, PP249382, PP246159, PP244020, PP242001, PP243203, PP244621, PP246771, PP247613, PP247854, PP249505, PP249267, PP248907, PP249028, PP248787. *N. longifolia* (Novelo & C.T.Philbrick) C.T.Philbrick: *C. T. Philbrick* 6340 (MICH, UAT), PP242965, PP245453, PP246283, PP244264, PP242360, PP242844, PP242240, PP243539, PP241397, PP245929, PP244861, PP241157, PP244144, PP243086, PP2442124, PP245216, PP245335, PP246650, PP244743, PP241766, PP243657, PP244504, PP241644, PP242603, PP245814, PP243316, PP245098, PP248327, PP247494, PP247736, PP248447, PP247258, PP246895, PP243779, PP241520, PP242482, PP242722, PP245696, PP244980, PP246046, PP243900, PP241278, PP241885, PP243422, PP245574, PP247975, PP247376, OR885223, PP247018, PP241035, PP246404, PP249151, PP247140, PP248675, PP248563, PP248208, PP244383, PP246526, PP248092, PP249384, PP246161, PP244022, PP242003, PP243205, PP244623, PP246773, PP247615, PP247856, PP249507, PP249269, PP248909, PP249030, PP248789.
- Oserya* Tul & Wedd. *O. perpusilla* (Went) P.Royen: *C. P. Bove and C. T. Philbrick* 2448 (MICH, R), PP242966, PP245454, PP246284, PP244265, PP242361, PP242845, PP242241, PP243540, PP241398, PP245930, PP244862, PP241158, PP244145, PP243087, PP242125, PP245217, PP245336, PP246651, PP244744, PP241767, PP243658, PP244505, PP241645, PP242604, PP245815, PP243317, PP245099, PP248328, PP247495, PP247737, PP248448, PP247259, PP246896, PP243780, PP241521, PP242483, PP242723, PP245697, PP244981, PP246047, PP243901, PP241279, PP241886, PP243423, PP245575, PP247976, PP247377, OR885224, PP247019, PP241036, PP246405, PP249152, PP247141, PP248676, PP248564, PP248209, PP244384, PP246527, PP248093, PP249387, PP246162, PP244023, PP242004, PP243206, PP244624, PP246774, PP247616, PP247857, PP249508, —, PP248910, PP249031, PP248790; *C. P. Bove et al.* 1946 (MICH, R), PP242967, PP245455, PP246285, PP244266, PP242362, PP242846, PP242242, PP243541, PP241399, PP245931, PP244863, PP241159, PP244146, PP243088, PP242126, PP245218, PP245337, PP246652, PP244745, PP241768, —, PP244506, PP241646, PP242605, PP245816, PP243318, PP245100, PP248329, PP247496, PP247738, PP248449, PP247260, PP246897, PP243781, PP241522, PP242484, PP242724, PP245698, PP244982, PP246048, PP243902, PP241280, PP241887, PP243424, PP245576, PP247977, PP247378, OR885225, PP247020, PP241037, PP246406, PP249153, PP247142, PP248677, PP248565, PP248210, PP244385, PP246528, PP248094, PP249385, PP246163, PP244024, PP242005, PP243207, PP244625, PP246775, PP247617, PP247858, PP249509, —, PP248911, PP249032, PP248791; *C. P. Bove et al.* 2327 (R), PP242971, PP245459, PP246288, PP244270, PP242366, PP242850, PP242245, PP243545, PP241403, PP245935, PP244867, PP241163, PP244150, PP243092, PP242130, PP245222, PP245341, PP246656, PP244749, PP241772, PP243661, PP244510, PP241650, PP242609, PP245820, PP243322, PP245104, PP248333, PP247500, PP247472, PP248453, PP247264, PP246901, PP243785, PP241526, PP242488, PP242728, PP245702, PP244986, PP246052, PP243906, PP241284, PP241891, PP243428, PP245580, PP247981, PP247382, OR885229, PP247024, PP241041, PP246410, PP249157, PP247146, PP248680, PP248568, PP248214, PP244389, PP246532, PP248098, PP249390, PP246167, PP244028, PP242009, PP243211, PP244629, PP246779, PP247621, PP247622, PP249513, —, PP248915, PP249036, PP248795; *C. T. Philbrick* 6190 (BBS, MICH), PP242969, PP245457, PP246286, PP244268, PP242364, PP242848, PP242243, PP243543, PP241401, PP245933, PP244865, PP241161, PP244148, PP243090, PP242128, PP245220, PP245339, PP246654, PP244747, PP241770, PP243659, PP244508, PP241648, PP242607, PP245818, PP243320, PP245102, PP248331, PP247498, PP247740, PP248451, PP247262, PP246899, PP243783, PP241524, PP242486, PP242726, PP245700, PP244984, PP246050, PP243904, PP241282, PP241889, PP243426, PP245578, PP247979, PP247380, OR885227, PP247022, PP241039, PP246408, PP249155, PP247144, PP248679, PP248566, PP248212, PP244387, PP246530, PP248096, PP249388, PP246165, PP244026, PP242007, PP243209, PP244627, PP246777, PP247619, PP247860, PP249511, —, PP248913, PP249034, PP248793; *C. T. Philbrick et al.* 6021 (MICH, VEN), PP242968, PP245456, —, PP244267, PP242363, PP242847, —, PP243542, PP241400, PP245932, PP244864, PP241160, PP244147, PP243089, PP242127, PP245219, PP245338, PP246653, PP244746, PP241769, —, PP244507, PP241647, PP242606, PP245817, PP243319, PP245101, PP248330, PP247497, PP247739, PP248450, PP247261, PP246898, PP243782, PP241523, PP242485, PP242725, PP245699, PP244983, PP246049, PP243903, PP241281, PP241888, PP243425, PP245577, PP247978, PP247379, OR885226, PP247021, PP241038, PP246407, PP249154, PP247143, PP248678, —, PP248211, PP244386, PP246529, PP248095, PP249386, PP246164, PP244025, PP242006, PP243208, PP244626, PP246776, PP247618, PP247859, PP249510, —, PP248912, PP249033, PP248792. *O. pilgeri* (Mildbr.) C.T. Philbrick & C.P. Bove: *C. P. Bove et al.* 2520 (MICH, R), PP242902, PP245391, PP246220, PP244201, PP242297, PP242781, PP242178, PP243477, PP241334, PP245867, PP244799, PP241093, PP244081, PP243024, PP242061, PP245153, PP245274, PP246586, PP244680, PP241703, PP243594, PP244441, PP241580, PP242541, PP245753, PP243261, PP245036, PP248263, PP247431, PP247673, PP244386, PP247196, PP246832, PP243715, PP241456, PP242418, PP242659, PP245632, PP244918, PP245984, PP243838, PP241216, PP241823, PP243365, PP245512, PP247914, PP247313, OR885159, PP246954, PP240972, PP246341, PP249089, PP247078, PP248617, PP248502, PP248150, PP244321, PP246463, PP248029, PP249321, PP246098, PP243958, PP241940, PP243144, PP244561, PP246709, PP247553, PP247793, PP249444, PP249209, PP248847, PP248967, PP248726.
- Paracladopus* M.Kato. *P. chantaburiensis* Koi & M.Kato: *S. Koi et al.* *tkj24* (TNS), PP242972, PP245460, PP246289, PP244271, PP242367, PP242851, PP242246, —, PP241404, PP245936, PP244868, PP241164, PP244151, PP243093, PP242131, PP245233, PP245342, PP246657, PP244750, PP241773, PP243662, PP244511, PP241651, PP242610, —, —, PP245105, PP248334, PP247501, PP247743, PP248454, PP247265, PP246902, PP243786, PP241527, PP242489, PP242729, PP245703, PP244987, —, PP243907, PP241285, PP241892, PP243429, PP245581, PP247982, PP247383, OR885230, PP247025, PP241042, PP246411, PP249158, PP247147, —, PP248569, PP248215, PP244390, PP246533, PP248099, PP249391, PP246168, PP244029, PP242010, PP243212, PP244630, PP246780, PP247622, PP247863, PP249514, PP249271, PP248916, PP249037, PP248796.
- Podostemum* Michx. *P. ceratophyllum* Michx.: *B. Ruhfel and Z. Xi* 128 (A), JX662415, JX663820, JX663738, JX664438, JX662930, JX665023, JX662296, JX664827, JX662893, JX661961, JX663649, JX664316, JX661833, JX664358, JX664639, JX662770, JX663427, JX662818, JX662082, JX662728, JX664553, JX664107, JX663934, JX663008, JX662449, JX662482, JX663558, JX664226, JX662972, JX663121, JX664181, JX664674, JX663298, JX662213, JX662596, JX662336, JX664510, JX663856, JX663213, JX663889, JX664022, JX661920, JX662254, JX661794, JX662639, JX664597, JX664143, JX664067, JX663981, JX664271, JX663384, JX662558, JX662857, JX663455, —, JX663050, JX662039, JX663495, JX664958, JX662683, JX664790, JX663601, JX661876, JX663530, JX663085, JX662377, JX663168, JX663781, JX664870, JX664913, JX663340, JX664475, JX663254. *P. comatum* Hicken: *C. T. Philbrick et al.* 5343 (MICH, R), —, PP245461, PP246290, PP244272, —, PP242852, PP242247, PP243546, —, PP245937, PP244869, PP241165, —, PP243094, —, PP245224, —, PP246658, —, —, PP243663, —, PP241652, —, —, —, PP248335, PP247502, —, PP248455, —, —, PP243787, PP241528, PP242490, PP242730, —, —, —, PP243908, —, —, PP243430, —, —, PP247384, OR885231, PP247026, —, PP246412, PP249159, PP247148, PP248681, —, PP248216, PP244391, PP246534, PP248100, PP249392, PP246169, PP244030, —, PP243213, PP244631, PP246781, —, PP247864, PP249515, PP249272, PP248917, PP249038, PP248797. *P. ovatum* C.T.Philbrick & Novelo: *Bove et al.* 1124 (R), PP242974, PP245463, PP246292, PP244274, PP242369, PP242854, PP242249, PP243548, PP241406, PP245939, PP244871, PP241167, PP244153, PP243096, PP242133, PP245226, PP245344, PP246660, PP244752, PP241775, PP243665, PP244513, PP241654, PP242612, PP245822, PP243324, PP245107, PP248337, PP247504, PP247745, PP248457, PP247267, PP246904, PP243789, PP241530, PP242492, PP242732, PP245705, PP244989, PP246054, PP243910, PP241287, PP241894, PP243432, PP245583, PP247984, PP247386, OR885233, PP247028, PP241044, PP246414, PP249161, PP247150, PP248683, PP248571, PP248218, PP244393, PP246536, PP248102, PP249394, PP246171, PP244032, PP242012, PP243215, PP244633, PP246783, PP247624, PP247866, PP249517, PP249274, PP248919, PP249040, PP248799. *P. scaturiginum* (Mart.) C.T.Philbrick & Novelo: *C. P. Bove and C. T. Philbrick* 2310 (MICH, R), PP242975, PP245464, PP246293, PP244275, PP242370, PP242855, PP242250, PP243549, PP241407, PP245940, PP244872, PP241168, PP244154, PP243097, PP242134, PP245227, PP245345, PP246661, PP244753, PP241776, PP243666, PP244514, PP241655,

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PP248684, PP248572, PP248219, PP244394, PP246537, PP248103,
PP249395, PP246172, PP244033, PP242013, PP243216, PP244634,
PP246784, PP247625, PP247867, PP249518, PP249275, PP248920,
PP249041, PP248800. **P. weddellianum** (Tul.) C.T.Philbrick & Novelo:
C. P. Bove 1130 (R), PP242976, PP245465, PP246294, —, PP242371,
PP242856, PP242251, —, PP241408, —, PP244873, PP241169, PP244155,
PP243098, —, PP245228, PP245346, PP246662, —, PP241777, PP243667,
PP244515, PP241656, —, —, —, PP248339, PP247506, PP247747, —,
—, PP246906, PP243791, PP241532, PP242494, PP242734, PP245707, —,
—, —, PP241289, —, —, PP245585, —, —, OR885235, PP247030,
PP241046, PP246416, PP249163, —, —, —, —, PP246538, PP248104,
PP249396, —, PP244034, PP242014, PP243217, —, PP246785, PP247626,
PP247868, PP249519, PP249276, PP248921, PP249042, PP248801.
- Polypleurum** (Tul.) Warm. **P. stylosum** (Wight) J.B.Hall: M. Kato &
N. Katayama *si103* (TNS), PP242977, PP245466, PP246295, PP244276,
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—, PP245229, —, PP246663, PP244754, PP241778, PP243668, PP244516,
PP241657, —, —, —, —, PP248340, PP247507, PP247748, —, —,
PP246907, PP243792, PP241533, PP242495, PP242735, PP245708,
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PP247031, PP241047, PP246417, —, PP247152, —, —, PP244395,
PP246539, PP248105, PP249397, PP246173, PP244035, PP242015, —, —,
PP246786, PP247627, PP247869, PP249520, PP249277, —, PP249043,
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- Rhyncholacis** Tul. **R. apiculata** P.Royen: C. P. Bove and C. T. Phil-
brick 2466 (MICH, R), PP242983, PP245472, PP246301, PP244282,
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PP247393, OR885242, PP247037, PP241053, PP246423, PP249169,
PP247158, PP248690, PP248578, PP248225, PP244401, PP246545,
PP248111, PP249403, PP246179, PP244041, PP242021, PP243223,
PP244640, PP246792, PP247633, PP247875, PP249526, PP249283,
PP248927, PP249049, PP248808. **R. applanata** K.I. Goebel: C. T. Phil-
brick et al. 6046 (MICH, VEN), PP242982, PP245471, PP246300,
PP244281, PP242377, PP242861, PP242257, PP243554, PP241414,
PP245945, PP244878, PP244117, PP244160, PP243104, PP242139,
PP245234, PP245351, PP246668, PP244759, PP241783, PP243673,
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PP248345, PP247512, PP247753, PP248463, PP247273, PP246912,
PP243797, PP241538, PP242750, PP242740, PP245713, PP244996,
PP246060, PP243917, PP241294, PP241900, PP243438, PP245591,
PP247990, PP247392, OR885241, PP247036, PP241052, PP246422,
PP249168, PP247157, PP248689, PP248577, PP248224, PP244400,
PP246544, PP248110, PP249402, PP246178, PP244024, PP242020,
PP243222, PP244639, PP246791, PP247632, PP247874, PP249525,
PP249282, PP248926, PP249048, PP248807. **R. hydrocichorium** Tul.: C.
P. Bove and C. T. Philbrick 2440 (MICH, R), PP242984, PP245473,
PP246302, PP244283, PP242379, PP242863, PP242259, PP243556,
PP241416, PP245947, PP244880, PP241177, PP244162, PP243106,
PP242141, PP245236, PP245353, PP246670, PP244761, PP241785,
PP243675, PP244523, PP241664, PP242620, PP245830, PP243332,
PP245115, PP248347, PP247514, PP247755, PP248465, PP247275,
PP246914, PP243799, PP241540, PP242502, PP242742, PP245715,
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PP242022, PP243224, PP244641, PP246793, PP247634, PP247876,
PP249527, PP249284, PP248928, PP249050, PP248809. **R. jenmanii** Engl.
forma laciniata P. Royen: C. T. Philbrick et al. 6052 (MICH, VEN),
PP242978, PP245467, PP246296, PP244277, PP242373, PP242857,
PP242253, PP243550, PP241410, PP245941, PP244874, PP241171,
PP244156, PP243100, PP242135, PP245230, PP245347, PP246664,
PP244755, PP241779, PP243669, PP244517, PP241658, PP242614,
PP245824, PP243326, PP245109, PP248341, PP247508, PP247749,
PP248459, PP247269, PP246908, PP243793, PP241534, PP242496,
PP242736, PP245709, PP244992, PP246056, PP243913, PP241290,
PP241896, PP243434, PP245587, PP247986, PP247388, OR885237,
PP247032, PP241048, PP246418, PP249164, PP247153, PP248685,
PP248573, PP248220, PP244396, PP246540, PP248106, PP249398,
PP246174, PP244036, PP242016, PP243218, PP244635, PP246787,
PP247628, PP247870, PP249521, PP249278, PP248922, PP249044,
PP248803; C. T. Philbrick et al. 6052A (MICH, VEN), PP242979,
PP245468, PP246297, PP244278, PP242374, PP242858, PP242254,
PP243551, PP241411, PP245942, PP244875, PP241172, PP244157,
PP243101, PP242136, PP245231, PP245348, PP246665, PP244756,
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PP243327, PP245110, PP248342, PP247509, PP247750, PP248460,
PP247270, PP246909, PP243794, PP241535, PP242497, PP247387,
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PP248221, PP244397, PP246541, PP248107, PP249399, PP246175,
PP244037, PP242017, PP243219, PP244636, PP246788, PP247629,
PP247871, PP249522, PP249279, PP248923, PP249045, PP248804; C. T.
Philbrick et al. 6053 (MICH, VEN), PP242980, PP245469, PP246298,
PP244279, PP242375, PP242859, PP242255, PP243552, PP241412,
PP245943, PP244876, PP241173, PP244158, PP243102, PP242137,
PP245232, PP245349, PP246666, PP244757, PP241781, PP243671,
PP244519, PP241660, PP242616, PP245826, PP243328, PP245111,
PP248343, PP247510, PP247751, PP248461, PP247271, PP246910,
PP243795, PP241536, PP242498, PP242738, PP245711, PP244994,
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PP247988, PP247390, OR885239, PP247034, PP241050, PP246420,
PP249166, PP247155, PP248687, PP248575, PP248222, PP244398,
PP246542, PP248108, PP249400, PP246176, PP244038, PP242018,
PP243220, PP244637, PP246789, PP247630, PP247872, PP249523,
PP249280, PP248924, PP249046, PP248805; C. T. Philbrick et al. 6060
(MICH, R), PP242981, PP245470, PP246299, PP244280, PP242377,
PP242860, PP242256, PP243553, PP241413, PP245944, PP244877,
PP241174, PP244159, PP243103, PP242138, PP245233, PP245350,
PP246667, PP244758, PP241782, PP243672, PP244520, PP241661,
PP242617, PP245827, PP243329, PP245112, PP248344, PP247511,
PP247752, PP248462, PP247272, PP246911, PP243796, PP241537,
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PP241293, PP241899, PP243437, PP245590, PP247989, PP247391,
OR885240, PP247035, PP241051, PP246421, PP249167, PP247156,
PP248688, PP248576, PP248223, PP244399, PP246543, PP248109,
PP249401, PP246177, PP244039, PP242019, PP243221, PP244638,
PP246790, PP247631, PP247873, PP249524, PP249281, PP248925,
PP249047, PP248806. **R. paulana** C.T. Philbrick & C.P. Bove: C. P.
Bove and C. T. Philbrick 2465 (MICH, R), PP242986, PP245475, PP246304,
PP244285, PP242381, PP242865, PP242261, PP243558, PP241418,
PP245949, PP244882, PP241179, PP244164, PP243108, PP242143,
PP245238, PP245355, PP246672, PP244763, PP241787, PP243677,
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PP246064, PP243921, PP241298, PP241904, PP243442, PP245595,
PP247994, PP247396, PP2485245, PP247040, PP241056, PP246426,
PP249172, PP247161, PP248693, PP248581, PP248228, PP244404,
PP246548, PP248114, PP249406, PP246182, PP244044, PP242024,
PP243226, PP244643, PP246795, PP247636, PP247878, PP249529,
PP249286, PP248930, PP249052, PP248811. **R. sp.:** C. P. Bove and C. T.
Philbrick 2421 (MICH, R), PP242985, PP245474, PP246303, PP244284,
PP242380, PP242864, PP242260, PP243557, PP241417, PP245948,
PP244881, PP241178, PP244163, PP243107, PP242142, PP245237,
PP245354, PP246671, PP244762, PP244786, PP243676, PP244524,
PP241665, PP242621, PP245831, PP243333, PP245116, PP248348,
PP247515, PP247756, PP248466, PP247276, PP246915, PP243800,
PP241541, PP242503, PP242743, PP245716, PP244999, PP246063,
PP243920, PP241297, PP241903, PP243441, PP245594, PP247993,
PP247395, OR885244, PP247039, PP241055, PP246425, PP249171,
PP247160, PP248692, PP248580, PP248227, PP244403, PP246547,
PP248113, PP249405, PP246181, PP244043, PP242023, PP243225,
PP244642, PP246794, PP247635, PP247877, PP249528, PP249285,
PP248929, PP249051, PP248810.
- Stonesia** G.Taylor. **S. ghoguei** E.Pfeifer & Rutish.: J. Ghogue *gho1665*
(YA, Z/GT), PP242987, PP245476, PP246305, PP244286, PP242382,

TABLE S1. Sequencing platform, number of reads, coding region assembly information, and proportion of missing data for each sample.

Species	Family/Subfamily or Tribe	Country, Second Division	Collector and Voucher Number	Sequencing Technology	Total Reads	Reads Mapped	Proportion Reads On Target	Estimated Average CDS Sequencing Depth	Proportion Missing Data in Concatenated Alignment
<i>Apiiagia 'crowii'</i>	Podostemaceae/ Podostemoideae	Venezuela, Amazonas	C. T. Philbrick et al. 6320	Illumina HiSeq X, paired-end, 150bp	8509957	320271	0.038	862.24	< 0.001
<i>Apiiagia 'crowii'</i>	Podostemaceae/ Podostemoideae	Venezuela, Amazonas	C. T. Philbrick et al. 6321	Illumina HiSeq X, paired-end, 150bp	7396299	300756	0.041	809.70	< 0.001
<i>Apiiagia fucoides</i> (Mart.) Tul.	Podostemaceae/ Podostemoideae	Brazil, Mato Grosso	C. T. Philbrick et al. 5960	Illumina HiSeq 2500, single end, 100bp	1699160	170947	0.101	306.82	< 0.001
<i>Apiiagia fucoides</i> (Mart.) Tul.	Podostemaceae/ Podostemoideae	Brazil, Minas Gerais	C. P. Bove et al. 2200	Illumina HiSeq X, paired-end, 150bp	9158465	266331	0.029	717.02	< 0.001
<i>Apiiagia fucoides</i> (Mart.) Tul.	Podostemaceae/ Podostemoideae	Brazil, Goias	C. P. Bove et al. 2210	Illumina HiSeq X, paired-end, 150bp	7485324	347986	0.046	936.86	< 0.001
<i>Apiiagia fucoides</i> (Mart.) Tul.	Podostemaceae/ Podostemoideae	Brazil, Tocantins	C. P. Bove et al. 2227	Illumina HiSeq X, paired-end, 150bp	10497995	232350	0.022	625.54	< 0.001
<i>Apiiagia fucoides</i> (Mart.) Tul.	Podostemaceae/ Podostemoideae	Brazil, Tocantins	C. P. Bove et al. 2236	Illumina HiSeq X, paired-end, 150bp	8040783	411494	0.051	1107.83	< 0.001
<i>Apiiagia fucoides</i> (Mart.) Tul.	Podostemaceae/ Podostemoideae	Brazil, Goias	C. P. Bove et al. 2237	Illumina HiSeq X, paired-end, 150bp	9598952	113817	0.012	306.42	0.004
<i>Apiiagia fucoides</i> (Mart.) Tul.	Podostemaceae/ Podostemoideae	Brazil, Piauí	C. P. Bove et al. 2276	Illumina HiSeq X, paired-end, 150bp	5854743	443546	0.076	1194.13	< 0.001
<i>Apiiagia fucoides</i> (Mart.) Tul.	Podostemaceae/ Podostemoideae	Brazil, Piauí	C. P. Bove et al. 2284	Illumina HiSeq X, paired-end, 150bp	10064493	486719	0.048	1310.36	< 0.001
<i>Apiiagia fucoides</i> (Mart.) Tul.	Podostemaceae/ Podostemoideae	Brazil, Minas Gerais	C. P. Bove et al. 2311	Illumina HiSeq X, paired-end, 150bp	11048528	164332	0.015	442.42	< 0.001
<i>Apiiagia fucoides</i> (Mart.) Tul.	Podostemaceae/ Podostemoideae	Brazil, Mato Grosso	C. P. Bove et al. 2517	Illumina HiSeq X, paired-end, 150bp	8012540	185943	0.023	500.60	< 0.001
<i>Apiiagia fucoides</i> (Mart.) Tul.	Podostemaceae/ Podostemoideae	Brazil, Mato Grosso	C. P. Bove et al. 2523	Illumina HiSeq X, paired-end, 150bp	11562816	477220	0.041	1284.78	0.005
<i>Apiiagia fucoides</i> (Mart.) Tul.	Podostemaceae/ Podostemoideae	Brazil, Mato Grosso	C. P. Bove et al. 2527	Illumina HiSeq X, paired-end, 150bp	8025010	155453	0.019	418.51	< 0.001
<i>Apiiagia fucoides</i> (Mart.) Tul.	Podostemaceae/ Podostemoideae	Brazil, Mato Grosso do Sul	C. T. Philbrick et al. 5969	Illumina HiSeq X, paired-end, 150bp	7521180	166354	0.022	447.86	0.030
<i>Apiiagia fucoides</i> (Mart.) Tul.	Podostemaceae/ Podostemoideae	Brazil, Mato Grosso	C. T. Philbrick et al. 5970	Illumina HiSeq X, paired-end, 150bp	9899266	218034	0.022	587.00	0.002
<i>Apiiagia fucoides</i> (Mart.) Tul.	Podostemaceae/ Podostemoideae	Brazil, Tocantins	C. T. Philbrick et al. 5992	Illumina HiSeq X, paired-end, 150bp	10051353	352383	0.035	948.69	< 0.001
<i>Apiiagia fucoides</i> (Mart.) Tul.	Podostemaceae/ Podostemoideae	Brazil, Mato Grosso	C. P. Bove et al. 2513	NA - not sequenced in this study	NA	NA	NA	NA	< 0.001
<i>Apiiagia guyanensis</i> (Pulle) P. Royen	Podostemaceae/ Podostemoideae	Brazil, Goias	C. P. Bove et al. 2206	Illumina HiSeq X, paired-end, 150bp	12158897	229289	0.019	617.30	< 0.001
<i>Apiiagia guyanensis</i> (Pulle) P. Royen	Podostemaceae/ Podostemoideae	Brazil, Para	C. P. Bove and C. T. Philbrick 2402	Illumina HiSeq X, paired-end, 150bp	9374143	240029	0.026	646.21	< 0.001
<i>Apiiagia guyanensis</i> (Pulle) P. Royen	Podostemaceae/ Podostemoideae	Brazil, Amapá	C. P. Bove and C. T. Philbrick 2407	Illumina HiSeq X, paired-end, 150bp	7268716	153142	0.021	412.29	< 0.001
<i>Apiiagia guyanensis</i> (Pulle) P. Royen	Podostemaceae/ Podostemoideae	Brazil, Para	C. P. Bove and C. T. Philbrick 2410	Illumina HiSeq X, paired-end, 150bp	11426515	506213	0.044	1362.84	< 0.001
<i>Apiiagia guyanensis</i> (Pulle) P. Royen	Podostemaceae/ Podostemoideae	Brazil, Para	C. P. Bove and C. T. Philbrick 2411	Illumina HiSeq X, paired-end, 150bp	7649470	115867	0.015	311.94	0.078
<i>Apiiagia guyanensis</i> (Pulle) P. Royen	Podostemaceae/ Podostemoideae	Brazil, Para	C. P. Bove and C. T. Philbrick 2412	Illumina HiSeq X, paired-end, 150bp	8434291	266753	0.032	718.16	< 0.001

(Continued)

TABLE S1. (CONTINUED).

Species	Family/Subfamily or Tribe	Country, Second Division	Collector and Voucher Number	Sequencing Technology	Total Reads	Reads Mapped	Proportion Reads On Target	Estimated Average Sequencing Depth	Proportion Missing Data in Concatenated Alignment
<i>Apinagia guyanensis</i> (Pulle)	Podostemaceae/ Podostemoideae	Brazil, Amapá	C. P. Bove and C. T. Philbrick 2420	Illumina HiSeq X, paired-end, 150bp	7525819	176068	0.023	474.01	0.042
<i>Apinagia guyanensis</i> (Pulle)	Podostemaceae/ Podostemoideae	Brazil, Amapá	C. P. Bove and C. T. Philbrick 2434	Illumina HiSeq X, paired-end, 150bp	7516786	328763	0.044	885.10	< 0.001
<i>Apinagia guyanensis</i> (Pulle)	Podostemaceae/ Podostemoideae	Brazil, Amapá	C. P. Bove and C. T. Philbrick 2437	Illumina HiSeq X, paired-end, 150bp	6475028	241779	0.037	650.92	0.002
<i>Apinagia guyanensis</i> (Pulle)	Podostemaceae/ Podostemoideae	Brazil, Amapá	C. P. Bove and C. T. Philbrick 2487	Illumina HiSeq X, paired-end, 150bp	8553012	131261	0.015	353.38	0.006
<i>Apinagia guyanensis</i> (Pulle)	Podostemaceae/ Podostemoideae	Brazil, Amapá	C. P. Bove and C. T. Philbrick 2489	Illumina HiSeq X, paired-end, 150bp	11029542	163738	0.015	440.82	0.044
<i>Apinagia longifolia</i> (Tul.)	Podostemaceae/ Podostemoideae	Suriname, Sipaliwini	C. T. Philbrick 6259	Illumina HiSeq 2500, single end, 100bp	310077	6340	0.02	11.38	0.373
<i>Apinagia longifolia</i> (Tul.)	Podostemaceae/ Podostemoideae	Brazil, Amapá	C. P. Bove and C. T. Philbrick 2431	Illumina HiSeq X, paired-end, 150bp	7991831	127815	0.016	344.11	< 0.001
<i>Apinagia longifolia</i> (Tul.)	Podostemaceae/ Podostemoideae	Brazil, Amapá	C. P. Bove and C. T. Philbrick 2450	Illumina HiSeq X, paired-end, 150bp	7444616	197537	0.027	531.81	< 0.001
<i>Apinagia longifolia</i> (Tul.)	Podostemaceae/ Podostemoideae	Brazil, Amapá	C. P. Bove and C. T. Philbrick 2452	Illumina HiSeq X, paired-end, 150bp	8576683	179042	0.021	482.02	< 0.001
<i>Apinagia longifolia</i> (Tul.)	Podostemaceae/ Podostemoideae	Brazil, Amapá	C. P. Bove and C. T. Philbrick 2455	Illumina HiSeq X, paired-end, 150bp	9602788	158993	0.017	428.04	< 0.001
<i>Apinagia nana</i> Went	Podostemaceae/ Podostemoideae	Venezuela, Amazonas	C. T. Philbrick et al. 6322	Illumina HiSeq 2500, single end, 100bp	3762588	137072	0.036	246.02	0.043
<i>Apinagia nana</i> Went	Podostemaceae/ Podostemoideae	Suriname, Sipaliwini	C. T. Philbrick et al. 6180	Illumina HiSeq X, paired-end, 150bp	8883844	133915	0.015	360.53	0.006
<i>Apinagia richardiana</i> (Tul.)	Podostemaceae/ Podostemoideae	Brazil, Roraima	C. P. Bove et al. 1945	Illumina HiSeq X, paired-end, 150bp	7561980	220873	0.029	594.64	< 0.001
<i>Apinagia richardiana</i> (Tul.)	Podostemaceae/ Podostemoideae	Brazil, Roraima	C. P. Bove et al. 1956	Illumina HiSeq X, paired-end, 150bp	7626355	136987	0.018	368.80	< 0.001
<i>Apinagia richardiana</i> (Tul.)	Podostemaceae/ Podostemoideae	Brazil, Roraima	C. P. Bove et al. 1971	Illumina HiSeq X, paired-end, 150bp	7814905	314360	0.04	846.33	< 0.001
<i>Apinagia richardiana</i> (Tul.)	Podostemaceae/ Podostemoideae	Brazil, Roraima	C. P. Bove et al. 1972	Illumina HiSeq X, paired-end, 150bp	7681782	176542	0.023	475.29	< 0.001
<i>Apinagia richardiana</i> (Tul.)	Podostemaceae/ Podostemoideae	Suriname, Sipaliwini	C. T. Philbrick et al. 6153	Illumina HiSeq X, paired-end, 150bp	7532390	190382	0.025	512.55	< 0.001
<i>Apinagia tenuifolia</i> P. Royen	Podostemaceae/ Podostemoideae	Brazil, Roraima	C. P. Bove et al. 1943	Illumina HiSeq X, paired-end, 150bp	9850534	553108	0.056	1489.09	< 0.001
<i>Apinagia tenuifolia</i> P. Royen	Podostemaceae/ Podostemoideae	Brazil, Roraima	C. P. Bove et al. 1951	Illumina HiSeq X, paired-end, 150bp	10380372	381795	0.037	1027.88	< 0.001
<i>Apinagia tenuifolia</i> P. Royen	Podostemaceae/ Podostemoideae	Brazil, Roraima	C. P. Bove et al. 1952	Illumina HiSeq X, paired-end, 150bp	6973489	241219	0.035	649.42	0.005
<i>Apinagia tenuifolia</i> P. Royen	Podostemaceae/ Podostemoideae	Brazil, Roraima	C. P. Bove et al. 1954	Illumina HiSeq X, paired-end, 150bp	8826994	285984	0.032	769.93	< 0.001
<i>Apinagia tenuifolia</i> P. Royen	Podostemaceae/ Podostemoideae	Brazil, Roraima	C. P. Bove et al. 1975	Illumina HiSeq X, paired-end, 150bp	7188166	277023	0.039	745.81	< 0.001
<i>Autana andersonii</i>	Podostemaceae/ Podostemoideae	Venezuela, Amazonas	C. T. Philbrick et al. 5862	Illumina HiSeq 2500, single end, 100bp	2782850	110802	0.04	198.87	0.004
<i>Autana andersonii</i>	Podostemaceae/ Podostemoideae	Venezuela, Amazonas	C. T. Philbrick et al. 5867	Illumina HiSeq X, paired-end, 150bp	8207232	314976	0.038	847.99	0.002

(Continued)

TABLE S1. (CONTINUED).

Species	Family/Subfamily or Tribe	Country, Second Division	Collector and Voucher Number	Sequencing Technology	Total Reads	Reads Mapped	Proportion Reads On Target	Estimated Average CDS Sequencing Depth	Proportion Missing Data in Concatenated Alignment
<i>Costelhaevia fruitians</i> Tul. & Wedd.	Podostemaceae/ Podostemoideae	Brazil, Para	C. T. Philbrick <i>et al.</i> 5840	Illumina HiSeq X, paired-end, 150bp	8301972	49352	0.006	132.87	0.003
<i>Costelhaevia monandra</i> Tul. & Wedd.	Podostemaceae/ Podostemoideae	Brazil, Para	C. T. Philbrick <i>et al.</i> 5982	Illumina HiSeq 2500, single end, 100bp	3215297	54446	0.017	97.72	0.002
<i>Costelhaevia princeps</i> Tul. & Wedd.	Podostemaceae/ Podostemoideae	Brazil, Goias	C. P. Bove <i>et al.</i> 2211	Illumina HiSeq 2500, single end, 100bp	1689879	13609	0.008	24.43	0.013
<i>Ceratolacis pedunculatum</i> C.T.Philbrick, Novelo & Irgang	Podostemaceae/ Podostemoideae	Brazil, Minas Gerais	C. P. Bove <i>et al.</i> 2199	Illumina HiSeq 2500, single end, 100bp	3000923	180179	0.06	323.39	0.011
<i>Ceratolacis pedunculatum</i> C.T.Philbrick, Novelo & Irgang	Podostemaceae/ Podostemoideae	Brazil, Pernambuco	C. P. Bove <i>and</i> C. T. Philbrick 2336	Illumina HiSeq 2500, single end, 100bp	2580975	207415	0.08	372.27	0.008
<i>Cipicia inserta</i> C.T.Philbrick, Novelo & Irgang	Podostemaceae/ Podostemoideae	Brazil, Goias	C. P. Bove <i>et al.</i> 2205	Illumina HiSeq 2500, single end, 100bp	3043108	310169	0.102	556.70	0.009
<i>Cipicia ramosa</i> C.P.Bove, C.T.Philbrick & Novelo	Podostemaceae/ Podostemoideae	Brazil, Minas Gerais	C. P. Bove <i>et al.</i> 2251	Illumina HiSeq 2500, single end, 100bp	2624755	59696	0.023	107.14	0.017
<i>Cladopus doianus</i> (Koidz.) Kõrba	Podostemaceae/ Podostemoideae	Japan, Kagoshima	S. Koi & N. Katsuyama jp404	Illumina HiSeq 2500, single end, 100bp	1025807	25025	0.024	44.92	0.161
<i>Drevillea flagelliformis</i> Tul. & Wedd.	Podostemaceae/ Podostemoideae	Brazil, Tocantins	C. P. Bove <i>et al.</i> 2368	Illumina HiSeq 2500, single end, 100bp	13690876	389739	0.028	699.51	0.007
<i>Diamantina lombardii</i> Novelo, C.T.Philbrick & Irgang	Podostemaceae/ Podostemoideae	Brazil, Minas Gerais	C. P. Bove <i>et al.</i> 2131	Illumina HiSeq 2500, single end, 100bp	1344893	87979	0.065	157.91	0.014
<i>Diamantina lombardii</i> Novelo, C.T.Philbrick & Irgang	Podostemaceae/ Podostemoideae	Brazil, Minas Gerais	C. P. Bove <i>et al.</i> 2253	Illumina HiSeq X, paired-end, 150bp	10217942	186058	0.018	500.91	0.013
<i>Dicrananthus zehnderi</i> H.Hess	Podostemaceae/ Podostemoideae	Cameroon	J. Ghogue gh01650	Illumina HiSeq 2500, single end, 100bp	1193041	79992	0.067	143.57	0.016
<i>Djinga felicitis</i> C.Cusset	Podostemaceae/ Podostemoideae	Cameroon	J. Ghogue <i>et al.</i> gar09	Illumina HiSeq 2500, single end, 100bp	4192918	121708	0.029	218.44	0.029
<i>Genus nov.</i>	Podostemaceae/ Podostemoideae	Venezuela, Bolivar	C. T. Philbrick <i>et al.</i> 6055	Illumina HiSeq 2500, single end, 100bp	3278987	35078	0.011	62.96	0.008
<i>Hydrobryum japonicum</i> Imamura	Podostemaceae/ Podostemoideae	Japan, Kagoshima	S. Koi & N. Katsuyama jp401	Illumina HiSeq 2500, single end, 100bp	3274813	36360	0.011	65.26	0.025
<i>Inversodicraea bosii</i> (C.Cusset) Rutish. & Thiv	Podostemaceae/ Podostemoideae	Cameroon	J. Ghogue <i>et al.</i> gar01	Illumina HiSeq 2500, single end, 100bp	900620	37610	0.042	67.50	0.011
<i>Lederermanniella bowlingii</i> (J.B.Hall) C.Cusset	Podostemaceae/ Podostemoideae	Ghana	G. Ameka <i>and</i> R. Rutishauser ar021010	Illumina HiSeq 2500, single end, 100bp	1608416	62257	0.039	111.74	0.018
<i>Lederermanniella letonzeyi</i> C.Cusset	Podostemaceae/ Podostemoideae	Cameroon	J. Ghogue <i>et al.</i> gar12	Illumina HiSeq 2500, single end, 100bp	1467443	25611	0.017	45.97	0.030
<i>Lophogyne aegrinosa</i> (P.Royer) C.T.Philbrick & C.P.Bove	Podostemaceae/ Podostemoideae	Suriname, Sipaliwini	C. T. Philbrick <i>and</i> S. Jairam-Doerga 6214	Illumina HiSeq 2500, single end, 100bp	3487916	717069	0.206	1287.01	0.004
<i>Lophogyne capillacea</i> Pulle	Podostemaceae/ Podostemoideae	Brazil, Amapá	C. P. Bove <i>and</i> C. T. Philbrick 2424	Illumina HiSeq X, paired-end, 150bp	9599332	150685	0.016	405.68	0.002
<i>Lophogyne capillacea</i> Pulle	Podostemaceae/ Podostemoideae	Brazil, Amapá	C. P. Bove <i>and</i> C. T. Philbrick 2441	Illumina HiSeq X, paired-end, 150bp	7341516	159180	0.022	428.55	0.014

(Continued)

TABLE S1. (CONTINUED).

Species	Family/Subfamily or Tribe	Country, Second Division	Collector and Voucher Number	Sequencing Technology	Total Reads	Reads Mapped	Proportion Reads On Target	Estimated Average Sequencing Depth	Proportion Missing Data in Concatenated Alignment
<i>Lophogyne capillacea</i> Pulle	Podostemaceae/ Podostemoideae	Brazil, Amapá	C. P. Bove and C. T. Philbrick 2459	Illumina HiSeq X, paired- end, 150bp	8843269	240829	0.027	648.37	0.014
<i>Lophogyne capillacea</i> Pulle	Podostemaceae/ Podostemoideae	Brazil, Goiás	C. P. Bove et al. 2493	NA - not sequenced in this study	NA	NA	NA	NA	0.002
<i>Lophogyne ceratophylla</i> (Engl.) C.T.Philbrick & C.P.Bove	Podostemaceae/ Podostemoideae	Brazil, Para	C. P. Bove and C. T. Philbrick 1864	Illumina HiSeq X, paired- end, 150bp	8690609	364452	0.042	981.19	< 0.001
<i>Lophogyne fimbriata</i> (P.Royen) C.T.Philbrick & C.P.Bove	Podostemaceae/ Podostemoideae	Suriname, Sipaliwini	C. T. Philbrick et al. 6204	Illumina HiSeq 2500, single end, 100bp	1946508	80354	0.041	144.22	0.003
<i>Lophogyne fimbriata</i> (P.Royen) C.T.Philbrick & C.P.Bove	Podostemaceae/ Podostemoideae	Venezuela, Amazonas	C. T. Philbrick et al. 6313	Illumina HiSeq X, paired- end, 150bp	8257608	106904	0.013	287.81	0.002
<i>Lophogyne fimbriifolia</i> (P.Royen) C.T.Philbrick & C.P.Bove	Podostemaceae/ Podostemoideae	Brazil, Tocantins	C. P. Bove et al. 2234	Illumina HiSeq 2500, single end, 100bp	5066773	67389	0.013	120.95	0.003
<i>Lophogyne fimbriifolia</i> (P.Royen) C.T.Philbrick & C.P.Bove	Podostemaceae/ Podostemoideae	Brazil, Tocantins	C. T. Philbrick et al. 6004	Illumina HiSeq X, paired- end, 150bp	11820970	843599	0.071	2271.16	0.001
<i>Lophogyne lacunosa</i> (Gardner) C.P.Bove & C.T.Philbrick	Podostemaceae/ Podostemoideae	Brazil, Minas Gerais	C. P. Bove and C. T. Philbrick 2258	Illumina HiSeq 2500, single end, 100bp	2834144	161275	0.057	289.46	0.001
<i>Lophogyne royenella</i> C.P.Bove & C.T.Philbrick	Podostemaceae/ Podostemoideae	Brazil, Goiás	C. P. Bove et al. 2220	Illumina HiSeq 2500, single end, 100bp	2129189	88415	0.042	158.69	0.003
<i>Lophogyne royenella</i> C.P.Bove & C.T.Philbrick	Podostemaceae/ Podostemoideae	Brazil, Tocantins	C. T. Philbrick et al. 5825	Illumina HiSeq X, paired- end, 150bp	3275619	63841	0.019	171.87	< 0.001
<i>Lophogyne royenella</i> C.P.Bove & C.T.Philbrick	Podostemaceae/ Podostemoideae	Brazil, Mato Grosso	C. P. Bove et al. 2524	NA - not sequenced in this study	NA	NA	NA	NA	< 0.001
<i>Lophogyne</i> sp. 1	Podostemaceae/ Podostemoideae	Brazil, Tocantins	C. P. Bove et al. 2233	Illumina HiSeq X, paired- end, 150bp	10956475	527223	0.048	1419.40	< 0.001
<i>Lophogyne</i> sp. 2	Podostemaceae/ Podostemoideae	Brazil, Piauí	C. P. Bove et al. 2291	Illumina HiSeq X, paired- end, 150bp	8734201	165509	0.019	445.59	0.077
<i>Lophogyne</i> sp. 2	Podostemaceae/ Podostemoideae	Brazil, Piauí	C. P. Bove et al. 2292	Illumina HiSeq X, paired- end, 150bp	9308508	309386	0.033	832.94	0.004
<i>Lophogyne</i> sp. 3	Podostemaceae/ Podostemoideae	Brazil, Para	C. P. Bove and C. T. Philbrick 2413	Illumina HiSeq X, paired- end, 150bp	8978861	266596	0.03	717.74	< 0.001
<i>Lophogyne wilsonii</i> C.P.Bove & C.T.Philbrick	Podostemaceae/ Podostemoideae	Brazil, Amapá	C. P. Bove and C. T. Philbrick 2474	Illumina HiSeq X, paired- end, 150bp	7708793	247882	0.032	667.35	0.029
<i>Macropodiella heteromorpha</i> (Baill.) C.Cusset	Podostemaceae/ Podostemoideae	Cameroon	J. Glogue et al. <i>gahn</i> 24	Illumina HiSeq 2500, single end, 100bp	3167301	27416	0.009	49.21	0.038
<i>Marathrum foeniculaceum</i> Bonpl.	Podostemaceae/ Podostemoideae	Honduras, Comayagua	C. T. Philbrick and Raney 6284	Illumina HiSeq X, paired- end, 150bp	9609321	532042	0.055	1432.38	< 0.001
<i>Marathrum plumosum</i> (Novelo & C.T.Philbrick) C.T.Philbrick & C.P.Bove	Podostemaceae/ Podostemoideae	Mexico, Jalisco	C. T. Philbrick 6264	Illumina HiSeq 2500, single end, 100bp	1237282	103897	0.084	186.48	< 0.001
<i>Marathrum utile</i> Tul.	Podostemaceae/ Podostemoideae	Venezuela, Zulia	C. T. Philbrick et al. 5886	Illumina HiSeq X, paired- end, 150bp	5077105	190495	0.038	512.86	< 0.001

(Continued)

TABLE S1. (CONTINUED).

Species	Family/Subfamily or Tribe	Country, Second Division	Collector and Voucher Number	Sequencing Technology	Total Reads	Reads Mapped	Proportion Reads On Target	Estimated Average Sequencing Depth	Proportion Missing Data in Concatenated Alignment
<i>Maranthrum utile</i> Tul.	Podostemaceae/ Podostemoideae	Columbia, La Guajira	A. M. Bedoya AMB497	NA - not sequenced in this study	NA	NA	NA	NA	< 0.001
<i>Monandriella linearifolia</i> Engl.	Podostemaceae/ Podostemoideae	Cameroon	J. Choque gho1663	Illumina HiSeq 2500, single end, 100bp	381161	4313	0.011	7.74	0.771
<i>Mouriera alcornis</i> (Tul.) P.Royen	Podostemaceae/ Podostemoideae	Brazil, Para	C. P. Bove and C. T. Philbrick 1870	Illumina HiSeq 2500, single end, 100bp	1971231	235054	0.119	421.88	0.009
<i>Mouriera aspera</i> (Raeusch.) Tul.	Podostemaceae/ Podostemoideae	Brazil, Minas Gerais	C. P. Bove et al. 2260	Illumina HiSeq 2500, single end, 100bp	1299721	131072	0.101	235.25	0.008
<i>Mouriera elegans</i> (Tul.) Bailion	Podostemaceae/ Podostemoideae	Brazil, Matto Grosso	C. P. Bove and C. T. Philbrick 1899	Illumina HiSeq X, paired-end, 150bp	9339958	363889	0.039	979.67	0.003
<i>Mouriera fluviatilis</i> Aubl.	Podostemaceae/ Podostemoideae	Brazil, Roraima	C. P. Bove et al. 1955	Illumina HiSeq X, paired-end, 150bp	5980570	195900	0.033	527.41	0.014
<i>Noveloa coulteriana</i> (Tul.) C.T.Philbrick	Podostemaceae/ Podostemoideae	Mexico, Jalisco	C. T. Philbrick et al. 6270	Illumina HiSeq 2500, single end, 100bp	2461793	172936	0.07	310.39	0.066
<i>Noveloa coulteriana</i> (Tul.) C.T.Philbrick	Podostemaceae/ Podostemoideae	Mexico, Nayarit	C. T. Philbrick 6329	Illumina HiSeq X, paired-end, 150bp	7037535	388580	0.055	1046.14	0.009
<i>Noveloa longifolia</i> (Novelo & C.T.Philbrick)	Podostemaceae/ Podostemoideae	Mexico, Jalisco	C. T. Philbrick 6340	Illumina HiSeq X, paired-end, 150bp	8531504	910624	0.107	2451.60	0.025
<i>Oserjya perpusilla</i> (Went) P.Royen	Podostemaceae/ Podostemoideae	Brazil, Roraima	C. P. Bove et al. 1946	Illumina HiSeq X, paired-end, 150bp	7393306	469120	0.063	1262.98	0.023
<i>Oserjya perpusilla</i> (Went) P.Royen	Podostemaceae/ Podostemoideae	Brazil, Bahia	C. P. Bove et al. 2327	Illumina HiSeq X, paired-end, 150bp	10878110	403235	0.037	1085.60	0.010
<i>Oserjya perpusilla</i> (Went) P.Royen	Podostemaceae/ Podostemoideae	Brazil, Amapá	C. P. Bove and C. T. Philbrick 2448	Illumina HiSeq X, paired-end, 150bp	10658363	178630	0.017	480.91	0.013
<i>Oserjya perpusilla</i> (Went) P.Royen	Podostemaceae/ Podostemoideae	Venezuela, Bolivar	C. T. Philbrick et al. 6021	Illumina HiSeq X, paired-end, 150bp	7842778	174724	0.022	470.40	0.060
<i>Oserjya perpusilla</i> (Went) P.Royen	Podostemaceae/ Podostemoideae	Suriname, Sipaliwini	C. T. Philbrick 6190	Illumina HiSeq X, paired-end, 150bp	7872044	230064	0.029	619.38	0.013
<i>Oserjya pilgeri</i> (Mildbr.) C.T. Philbrick & C.P. Bove	Podostemaceae/ Podostemoideae	Brazil, Mato Grosso	C. P. Bove et al. 2520	Illumina HiSeq X, paired-end, 150bp	9615790	166329	0.017	447.80	0.007
<i>Paracladopus chantaburiensis</i> Koi & M. Kato	Podostemaceae/ Podostemoideae	Thailand, Chanthaburi	S. Koi et al. #424	Illumina HiSeq 2500, single end, 100bp	638726	19651	0.031	35.27	0.037
<i>Podostemum ceratophyllum</i> Michx.	Podostemaceae/ Podostemoideae	USA, Massachusetts	B. Rutliff and Z. Xi 128	NA - not sequenced in this study	NA	NA	NA	NA	0.018
<i>Podostemum comatum</i> Hicken	Podostemaceae/ Podostemoideae	Brazil, Rio Grande do Sul	C. T. Philbrick et al. 5343	Illumina HiSeq X, paired-end, 150bp	13600472	6486	0.0005	17.46	0.340
<i>Podostemum ovatum</i> C.T.Philbrick & Novelo	Podostemaceae/ Podostemoideae	Brazil, Rio de Janeiro	Bove et al. 1124	Illumina HiSeq 2500, single end, 100bp	1331433	30118	0.023	54.06	0.011
<i>Podostemum scaturiginum</i> (Mart.) C.T.Philbrick & Novelo	Podostemaceae/ Podostemoideae	Brazil, Minas Gerais	C. P. Bove and C. T. Philbrick 2310	Illumina HiSeq 2500, single end, 100bp	4150301	113104	0.027	203.00	0.009
<i>Podostemum weddellianum</i> (Tul.) C.T.Philbrick & Novelo	Podostemaceae/ Podostemoideae	Brazil, Rio de Janeiro	C. P. Bove 1130	Illumina HiSeq 2500, single end, 100bp	2484989	9286	0.004	16.67	0.190
<i>Polylepium stilosum</i> (Wright) J.B.Hall	Podostemaceae/ Podostemoideae	Sri Lanka, Central Province	M. Kato & N. Katayama s1103	Illumina HiSeq 2500, single end, 100bp	462988	7952	0.017	14.27	0.340

(Continued)

TABLE S1. (CONTINUED).

Species	Family/Subfamily or Tribe	Country, Second Division	Collector and Voucher Number	Sequencing Technology	Total Reads	Reads Mapped	Proportion Reads On Target	Estimated Average CDS Sequencing Depth	Proportion Missing Data in Concatenated Alignment
<i>Rhynchosolacis apiculata</i> P. Royen	Podostemaceae/ Podostemoideae	Brazil, Amapa	C. P. Bove and C. T. Philbrick 2466	Illumina HiSeq X, paired-end, 150bp	7128011	103919	0.015	279.77	0.002
<i>Rhynchosolacis appianata</i> K.I. Goebel	Podostemaceae/ Podostemoideae	Venezuela, Bolivar	C. T. Philbrick et al. 6046	Illumina HiSeq X, paired-end, 150bp	9639140	530148	0.055	1427.28	0.003
<i>Rhynchosolacis hydrochloriorum</i> Tul.	Podostemaceae/ Podostemoideae	Brazil, Amapa	C. P. Bove and C. T. Philbrick 2440	Illumina HiSeq X, paired-end, 150bp	7520743	126449	0.017	340.43	< 0.001
<i>Rhynchosolacis jennmanii</i> Engl. forma <i>lactiniata</i> P. Royen	Podostemaceae/ Podostemoideae	Venezuela, Bolivar	C. T. Philbrick et al. 6052	Illumina HiSeq 2500, single end, 100bp	1766238	45254	0.026	81.22	0.010
<i>Rhynchosolacis jennmanii</i> Engl. forma <i>lactiniata</i> P. Royen	Podostemaceae/ Podostemoideae	Venezuela, Bolivar	C. T. Philbrick et al. 6052A	Illumina HiSeq X, paired-end, 150bp	7475088	186770	0.025	502.83	0.002
<i>Rhynchosolacis jennmanii</i> Engl. forma <i>lactiniata</i> P. Royen	Podostemaceae/ Podostemoideae	Venezuela, Bolivar	C. T. Philbrick et al. 6053	Illumina HiSeq X, paired-end, 150bp	9681520	240590	0.025	647.72	0.003
<i>Rhynchosolacis jennmanii</i> Engl. forma <i>lactiniata</i> P. Royen	Podostemaceae/ Podostemoideae	Venezuela, Bolivar	C. T. Philbrick et al. 6060	Illumina HiSeq X, paired-end, 150bp	8810844	264735	0.03	712.73	0.003
<i>Rhynchosolacis paulana</i> C.T. Philbrick & C.P. Bove	Podostemaceae/ Podostemoideae	Brazil, Amapa	C. P. Bove and C. T. Philbrick 2465	Illumina HiSeq X, paired-end, 150bp	8698433	107729	0.012	290.03	0.005
<i>Rhynchosolacis</i> sp.	Podostemaceae/ Podostemoideae	Brazil, Amapa	C. P. Bove and C. T. Philbrick 2421	Illumina HiSeq X, paired-end, 150bp	7885988	131605	0.017	354.31	0.004
<i>Stonesia ghogueti</i> E.Pfeifer & Rutish.	Podostemaceae/ Podostemoideae	Cameroon	J. Ghoguet <i>gho1665</i>	Illumina HiSeq 2500, single end, 100bp	3609339	58326	0.016	104.68	0.028
<i>Thelethylax minutiflora</i> (Tul.) C.Cusset	Podostemaceae/ Podostemoideae	Madagascar, Toamasina	N. Rakotonirina <i>nr532</i>	Illumina HiSeq 2500, single end, 100bp	2358410	416449	0.177	747.45	0.008
<i>Zeylanidium subulatum</i> (Gardner) C.Cusset	Podostemaceae/ Podostemoideae	Sri Lanka, Central Province	M. Kato & N. Katayama <i>s1102</i>	Illumina HiSeq 2500, single end, 100bp	4615327	25450	0.006	45.68	0.249
<i>Dalzellia ceylanica</i> (Gardner) Wight	Podostemaceae/ Tristichoidae	Sri Lanka, Central Province	M. Kato & N. Katayama <i>s1101</i>	Illumina HiSeq 2500, single end, 100bp	5148406	7835	0.002	14.06	0.348
<i>Terniopsis brevis</i> M.Kato	Podostemaceae/ Tristichoidae	Thailand, Nakhon Nayok	S. Koi et al. <i>tk25</i>	Illumina HiSeq 2500, single end, 100bp	449405	3544	0.008	6.36	0.728
<i>Tristicha trifaria</i> (Bory ex Willd.) Spreng.	Podostemaceae/ Tristichoidae	Brazil, Para	C. P. Bove and C. T. Philbrick 1867	Illumina HiSeq 2500, single end, 100bp	3016276	178400	0.059	320.20	0.004
<i>Tristicha trifaria</i> (Bory ex Willd.) Spreng.	Podostemaceae/ Tristichoidae	Costa Rica	B. Rutifl 19	Illumina HiSeq 2500, single end, 100bp	1691875	56293	0.033	101.04	0.100
<i>Tristicha trifaria</i> (Bory ex Willd.) Spreng.	Podostemaceae/ Tristichoidae	Mali	A. Mesterhazy <i>am128</i>	NA - not sequenced in this study	NA	NA	NA	NA	0.002
<i>Weddellina squamulosa</i> Tul.	Podostemaceae/ Weddellinoideae	Brazil, Bahia	C. P. Bove et al. 2350	Illumina HiSeq 2500, single end, 100bp	4563752	43416	0.01	77.92	0.037
<i>Weddellina squamulosa</i> Tul.	Podostemaceae/ Weddellinoideae	Brazil, Tocantins	C. T. Philbrick et al. 5827	Illumina HiSeq 2500, single end, 100bp	1747225	31379	0.018	56.32	0.058
<i>Cratoxylum cochinchinense</i> (Lour.) Blume.	Hypericaceae/ Cratoxyleae	China, Yunnan	unknown	NA - not sequenced in this study	NA	NA	NA	NA	0.010
<i>Vismia guianensis</i> (Aubl.) Pers.	Hypericaceae/ Hypericeae	Brazil, Bahia	A. M. Amorim 7659	NA - not sequenced in this study	NA	NA	NA	NA	0.060

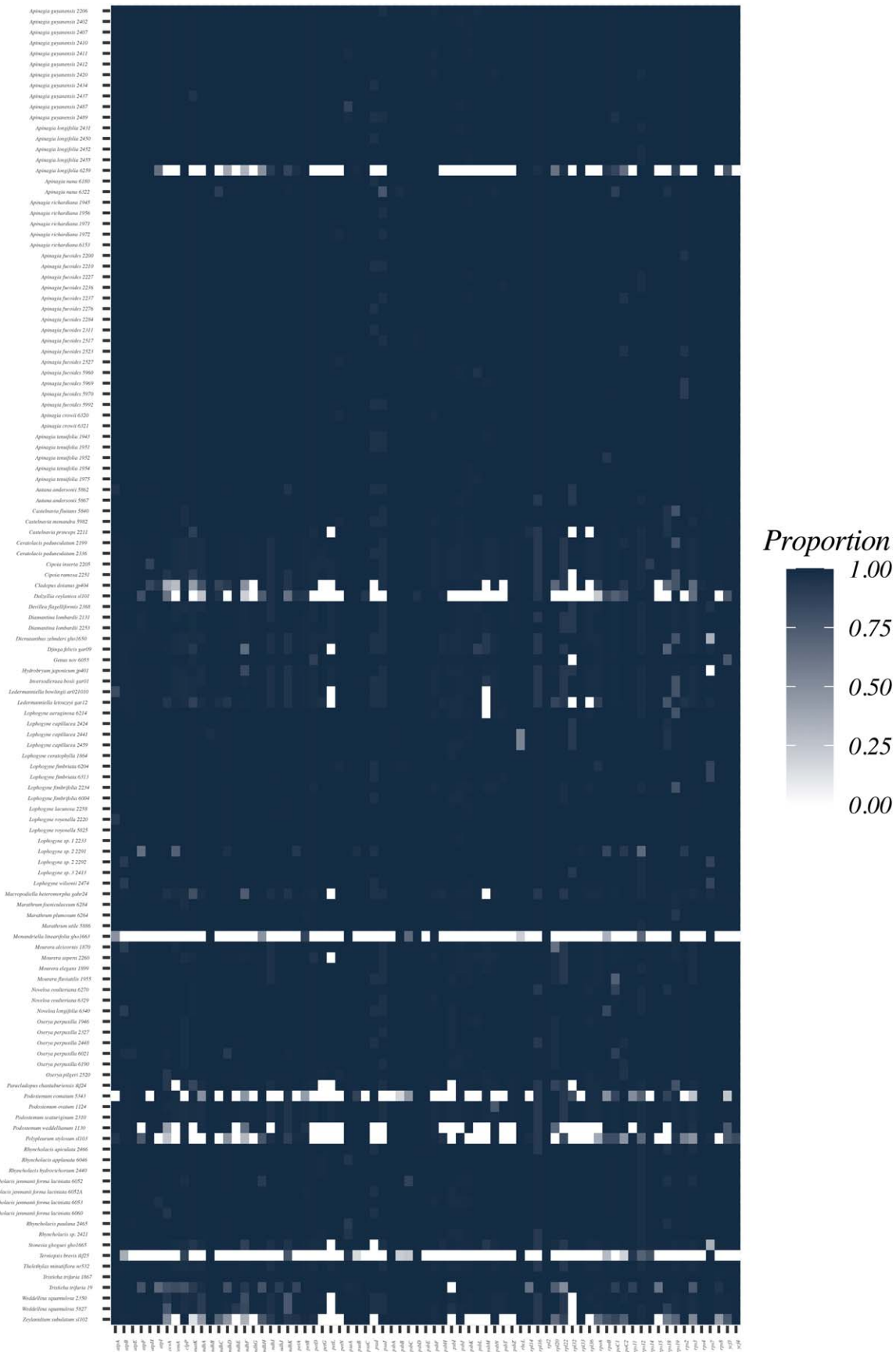


FIG. S1. Heatmap plot showing proportion of the target gene length recovered for each accession. Columns represent plastid genes and rows represent samples of Podostemaceae.

TABLE S2. Dataset Characteristics. Best fit models of sequence evolution were chosen by AICc using ModelFinder as implemented in IQ-TREE 1.6.12.

Alignment	Sequences	Characters	Constant/ Invariable Sites	Parsimony Sites	Distinct Site Patterns	Proportion Missing Data	Best Fit Model	Partitions
<i>atpA</i>	130	1515	1101	308	434	0.0083016	TVM+F+I+G4	1
<i>atpB</i>	130	1488	1068	331	431	0.0110267	GTR+F+I+G4	1
<i>atpE</i>	129	402	257	103	138	0.00364457	K3Pu+F+G4	1
<i>atpF</i>	129	555	336	149	241	0.00913472	TPM3 + F+G4	1
<i>atpH</i>	129	246	199	32	57	0.00491586	JC	1
<i>atpI</i>	129	744	548	158	223	0.00731433	TVM+F+G4	1
<i>ccsA</i>	126	951	526	315	481	0.0287166	GTR+F+G4	1
<i>cemA</i>	124	672	411	197	251	0.00960061	TVM+F+G4	1
<i>clpP</i>	130	687	342	242	329	0.0228306	TVM+F+G4	1
<i>matK</i>	125	1527	704	615	808	0.0223183	TVM+F+G4	1
<i>ndhA</i>	127	1110	719	331	391	0.0201107	GTR+F+I+G4	1
<i>ndhB</i>	132	1479	1364	71	114	0.000722232	GTR+F+I	1
<i>ndhC</i>	127	363	272	73	112	0.006117	TPM3 + F+G4	1
<i>ndhD</i>	129	1503	997	404	512	0.0181652	TVM+F+I+G4	1
<i>ndhE</i>	125	306	223	72	91	0.00235294	JC+G4	1
<i>ndhF</i>	130	2244	1241	783	1003	0.0480872	GTR+F+I+G4	1
<i>ndhG</i>	124	531	361	133	145	0.00100237	GTR+F+G4	1
<i>ndhH</i>	131	1182	869	247	309	0.0166815	TVM+F+I+G4	1
<i>ndhI</i>	128	498	357	106	139	0.012613	K3Pu+F+G4	1
<i>ndhJ</i>	129	477	336	114	146	0.00199893	K3Pu+F+G4	1
<i>ndhK</i>	129	753	481	214	298	0.0417555	GTR+F+I+G4	1
<i>petA</i>	129	969	676	217	307	0.00381597	TVM+F+I+G4	1
<i>petB</i>	131	642	499	117	163	0.00716987	GTR+F+G4	1
<i>petD</i>	125	477	387	65	106	0.00367296	K3Pu+F+I+G4	1
<i>petG</i>	122	114	91	18	30	0.00280414	JC	1
<i>petL</i>	113	96	60	26	40	0.00359513	JC	1
<i>petN</i>	124	90	76	6	19	0.00994624	JC	1
<i>psaA</i>	131	2253	1743	374	462	0.00415731	TVM+F+I+G4	1
<i>psaB</i>	130	2205	1724	379	426	0.00846677	TVM+F+I+G4	1
<i>psaC</i>	129	246	205	29	54	0.00113443	JC	1
<i>psaI</i>	123	114	85	23	32	0.0145486	JC	1
<i>psaJ</i>	124	135	104	30	41	0.0179211	JC	1
<i>psbA</i>	130	1062	867	150	183	0.00065189	TVM+F+I+G4	1
<i>psbB</i>	132	1527	1165	283	357	0.013172	GTR+F+I+G4	1
<i>psbC</i>	132	1422	1118	229	318	0.0141606	GTR+F+I+G4	1
<i>psbD</i>	132	1062	878	133	182	0.00132683	K3Pu+F+I+G4	1
<i>psbE</i>	130	252	216	26	42	0.000641026	JC	1
<i>psbF</i>	130	120	101	14	24	0.00576923	JC	1
<i>psbH</i>	126	222	161	50	69	0.00439725	JC	1
<i>psbI</i>	122	111	88	18	33	0.00620292	JC	1
<i>psbJ</i>	127	123	98	20	30	0.00902631	JC	1
<i>psbK</i>	125	186	141	30	48	0.00580645	JC	1
<i>psbL</i>	124	117	102	11	24	0.00310174	JC	1
<i>psbM</i>	119	105	87	15	26	0.0158463	JC	1
<i>psbN</i>	127	132	114	14	27	0.00697924	JC	1
<i>psbT</i>	123	102	87	13	21	0.00167384	JC	1
<i>psbZ</i>	126	189	148	33	45	0.00176367	JC	1
<i>rbcl</i>	132	1428	1095	266	325	0.0135759	GTR+F+I+G4	1
<i>rpl2</i>	129	369	263	76	116	0.00485284	K2P+G4	1
<i>rpl14</i>	130	423	291	85	131	0.0206219	K3P+G4	1
<i>rpl16</i>	132	825	726	63	94	0.00121212	TVM+F+G4	1
<i>rpl20</i>	128	348	207	97	167	0.0202721	K3P+G4	1
<i>rpl22</i>	128	369	188	144	191	0.0261052	TPM3 + F+G4	1
<i>rpl32</i>	117	171	115	42	67	0.0203929	JC	1
<i>rpl33</i>	123	198	138	45	62	0.00813008	JC	1
<i>rpl36</i>	121	114	83	20	35	0.00565463	JC	1
<i>rpoA</i>	127	1017	601	295	419	0.0163519	TVM+F+I+G4	1
<i>rpoB</i>	131	3213	2217	693	946	0.0302421	GTR+F+I+G4	1
<i>rpoC1</i>	129	2034	1325	463	689	0.0154124	GTR+F+I+G4	1
<i>rpoC2</i>	130	4143	2426	1290	1628	0.0318665	GTR+F+I+G4	1
<i>rps11</i>	129	417	245	120	178	0.00658078	K2P+G4	1
<i>rps12</i>	132	369	304	33	70	0.0133038	K3P+G4	1
<i>rps14</i>	130	303	198	80	118	0.00426504	JC+G4	1
<i>rps15</i>	125	273	190	53	82	0.00518681	JC	1
<i>rps18</i>	126	417	269	90	180	0.033516	K3Pu+F+G4	1
<i>rps19</i>	131	282	209	41	92	0.025337	JC	1
<i>rps2</i>	127	714	512	135	210	0.00942897	TVM+F+I+G4	1
<i>rps3</i>	129	666	383	216	311	0.0284587	TVM+F+I+G4	1
<i>rps4</i>	130	606	353	180	229	0.00129474	GTR+F+G4	1
<i>rps7</i>	121	471	388	50	117	0.0295836	K3Pu+F+G4	1

(Continued)

TABLE S2. (CONTINUED).

Alignment	Sequences	Characters	Constant/ Invariable Sites	Parsimony Sites	Distinct Site Patterns	Proportion Missing Data	Best Fit Model	Partitions
<i>rps8</i>	127	411	240	131	183	0.00718432	K3Pu+F+G4	1
<i>ycf3</i>	130	501	395	78	118	0.0183326	TPM3u+F+I+G4	1
<i>ycf4</i>	129	555	340	162	216	0.00280746	TVM+F+G4	1
73-gene	132	53943	37434	12269	16156	0.0370654	See partition file for statistics and model for each partition	34

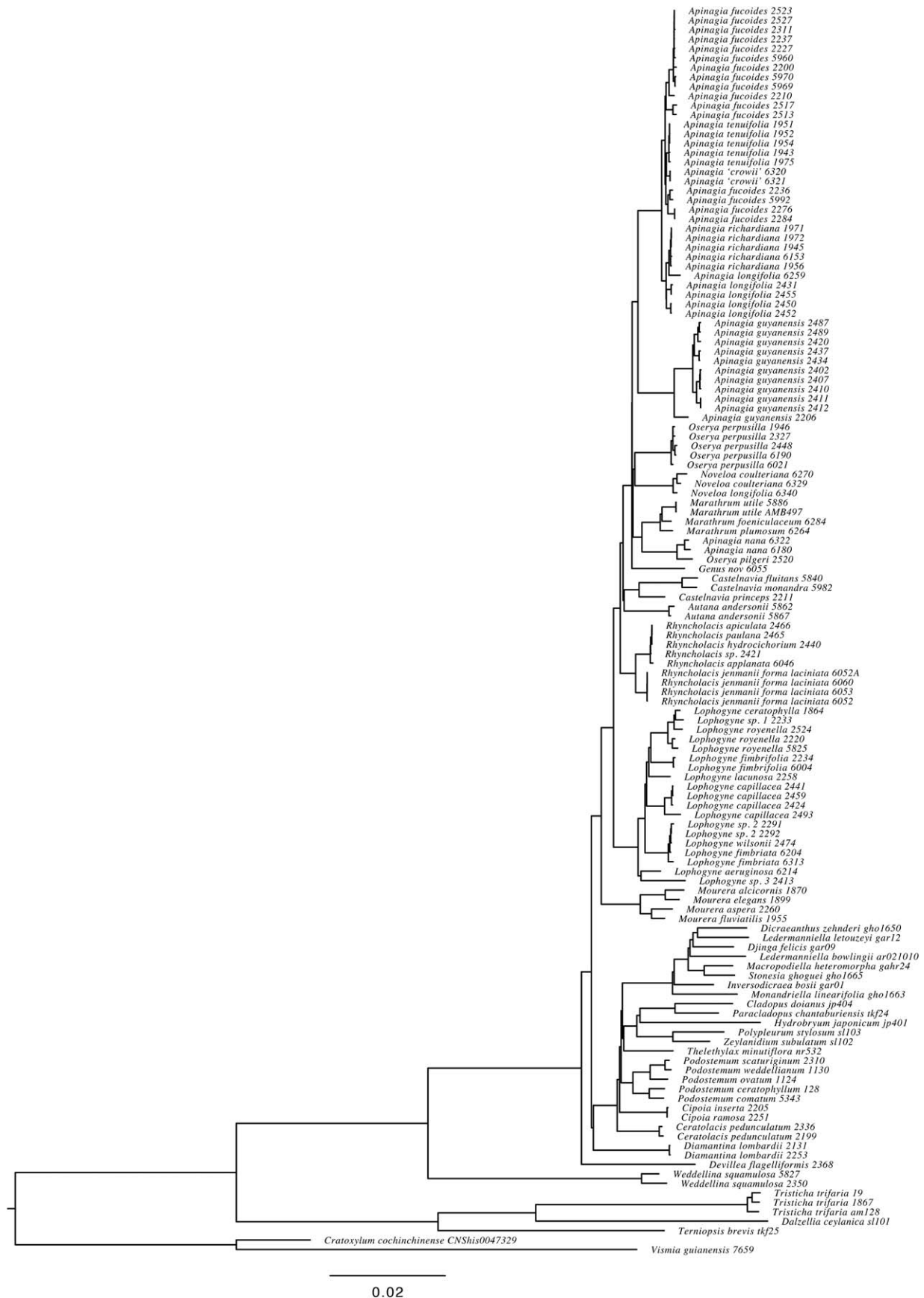


FIG. S2. Phylogram of the maximum likelihood phylogeny of Podostemaceae inferred from a concatenated dataset of 73 protein-coding genes of the plastid genome. Voucher collection numbers are given after each species name. Branch lengths are in units of estimated substitutions per site.

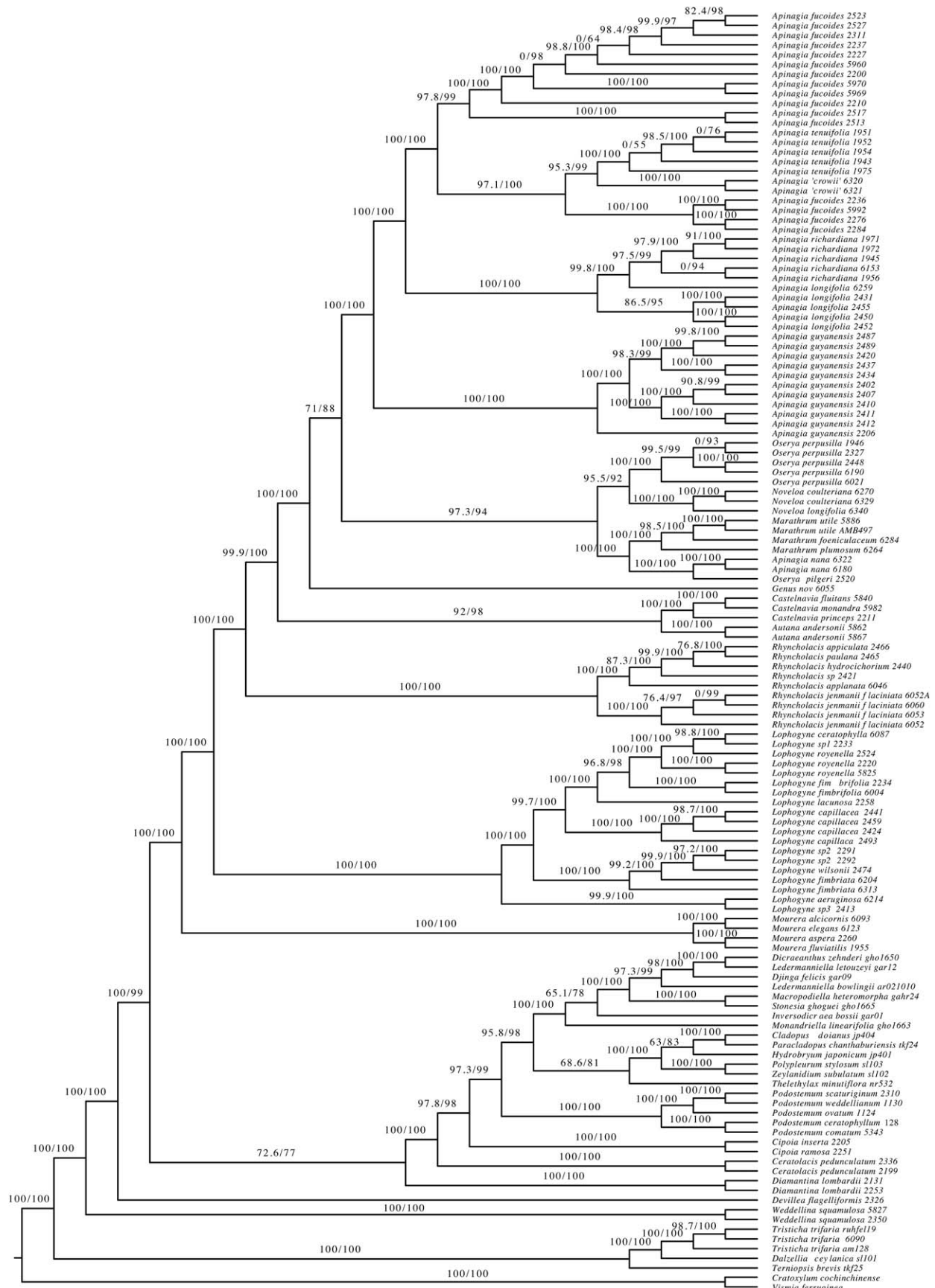


FIG. S3. Maximum likelihood phylogeny of Podostemaceae inferred from a concatenated dataset of 73 protein-coding genes of the plastid genome. Voucher collection numbers are given after each species name. SH-aLRT (left) and ultra-fast bootstrap support (right) values are indicated above the branches.

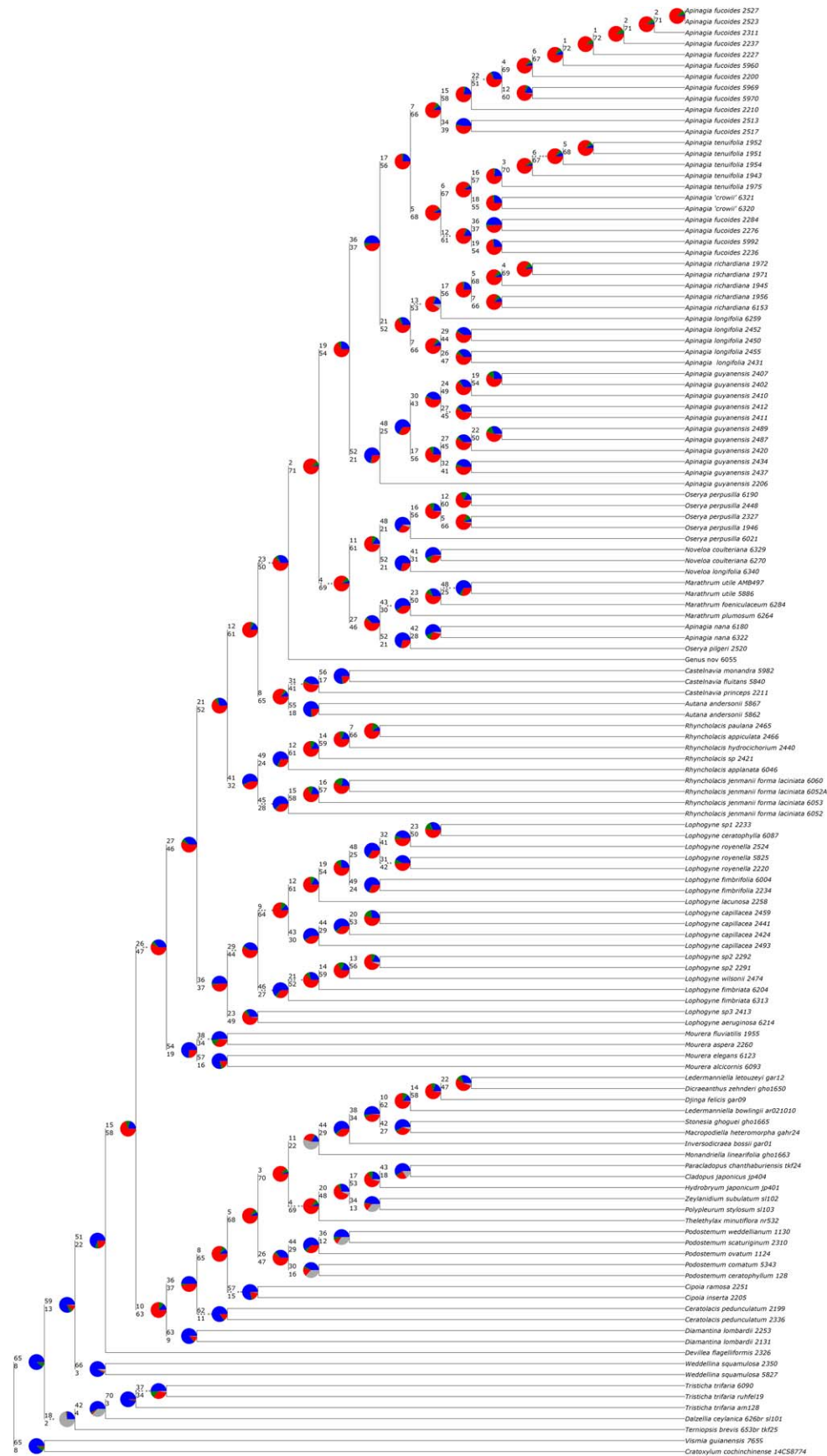


FIG. S4. PhyParts conflict analysis with no bootstrap support cutoff, showing 73 gene trees mapped against the maximum likelihood phylogeny from the concatenated analysis. Numbers above branches equal the number of genes concordant with that bipartition, while the numbers below each branch represent the number of conflicting genes. Pie charts at nodes represent the proportion of gene tree concordance (blue slices), the proportion of the most common conflicting bipartition (green), the proportion of all other conflicting bipartitions (red), and the proportion that are uninformative (grey).

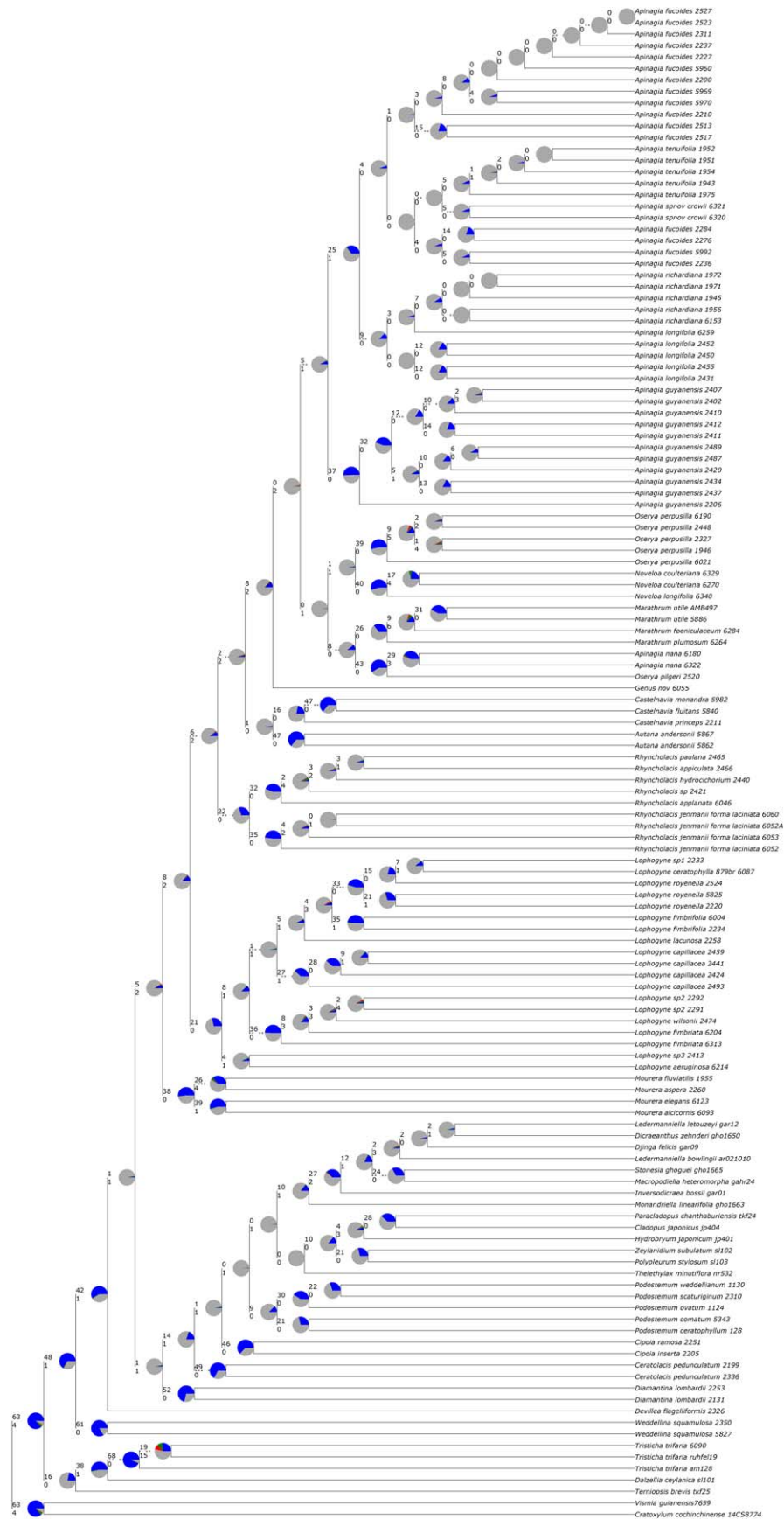


FIG. S5. PhyParts Conflict analysis with a 70% bootstrap support cutoff, showing 73 gene trees mapped against the maximum likelihood phylogeny from the concatenated analysis. Numbers above branches equal the number of genes concordant with that bipartition, while the numbers below each branch represent the number of conflicting genes. Pie charts at nodes represent the proportion of gene tree concordance (blue slices), the proportion of the most common conflicting bipartition (green), the proportion of all other conflicting bipartitions (red), and the proportion that are uninformative given a 70% bootstrap support cutoff (grey).