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Authors: Tippery, Nicholas P., Philbrick, C. Thomas, Bove, Claudia P., and Les, Donald H.

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Systematics and Phylogeny of Neotropical Riverweeds (Podostemaceae: Podostemoideae)

Nicholas P. Tippery,[1,4] C. Thomas Philbrick,[2] Claudia P. Bove,[3] and Donald H. Les[1]

[1]Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269-3043, U. S. A.
[2]Department of Biological and Environmental Sciences, Western Connecticut State University, Danbury, Connecticut 06810, U. S. A.
[3]Departamento de Botânica, Museu Nacional, Universidade Federal do Rio de Janeiro, Quinta da Boa Vista, Rio de Janeiro 20940-040, Brazil
[4]Author for correspondence (nicholas.tippery@uconn.edu)

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Abstract—New World Podostemaceae (riverweeds) comprise approximately 135 species in 21 genera, most of which are of tropical distribution, shed pollen in monads, and belong to subfamily Podostemoideae. We undertook a phylogenetic study of Neotropical Podostemoideae using molecular (ITS, *rbcL*, *trnL*) and morphological data, to assess the monophyly of genera and their interrelationships. Extensive taxon sampling (38 taxa in 15 genera) revealed that the large genera *Apinagia* and *Marathrum* are not monophyletic as currently circumscribed, although several species of the former comprised a clade that could be delimited morphologically by the shared character of upright stems (i.e. anchored to the substrate only basally). *Marathrum* species were split geographically, with Central and South American taxa resolving in different clades. *Oserya* also comprised two geographically disparate clades, with the type species belonging to the South American clade. To establish the monophyly of *Oserya*, we erected a new genus ***Noveloa*** to accommodate the Central American species ***N. coulteriana*** and ***N. longifolia***. The Central American *Marathrum* clade included the monotypic *Vanroyenella*, which we transferred to that genus as ***Marathrum plumosum***. The genera *Castelnavia* and *Rhyncholacis* were monophyletic in our analyses; *C. multipartita* f. *pendulosa* was elevated to species rank as ***Castelnavia pendulosa***. The monotypic *Lonchostephus* resolved within *Mourera*, with which it shares a number of morphological features that are found also in *Tulasneantha* (also monotypic), but which otherwise are unique in Podostemaceae. We recommend that *Lonchostephus* and *Tulasneantha* be merged with *Mourera* and provide the new combination ***Mourera monadelpha*** for the latter. Finally, an unexpected clade of morphologically diverse genera, including members of *Apinagia*, *Jenmaniella*, *Lophogyne*, *Marathrum*, and *Monostylis*, resolved with strong support but uncertain morphological integrity, as sister to all ingroup taxa except *Mourera*. However, nomenclatural changes in this group have not been made, pending additional taxon sampling and procurement of further molecular and morphological evidence.

Keywords—Aquatic plants, ITS, Malpighiales, river-rapids, taxonomy, *trnL.*

Resumo—As Podostemaceae (flor-da-cachoeira) do Novo Mundo compreendem cerca de 135 espécies em 21 gêneros, a maioria de distribuição tropical, com pólen em mônades, pertencentes à subfamília Podostemoideae. Realizamos o estudo filogenético de Podostemaceae Neotropicais utilizando dados moleculares (ITS, *rbcL*, *trnL*) e morfológicos, a fim de avaliar o monofiletismo dos gêneros e suas relações filogenéticas. Uma extensa amostragem de táxons (38 táxons de 15 gêneros) revelou que os amplos gêneros *Apinagia* e *Marathrum*, não são monofiléticos com a atual circunscrição, embora diversas espécies do primeiro, formem um clado que pode ser delimitado morfologicamente por compartilhar o caráter presença de caule ereto (i.e. ancorado ao substrato apenas na base). Espécies de *Marathrum* foram separadas geograficamente, com os táxons da América Central e do Sul agrupadas em clados diferentes. *Oserya* também compreende dois clados distintos geograficamente, com a espécie tipo pertencente ao clado da América do Sul. Com o intuito de estabelecer o monofiletismo em *Oserya*, nós elegemos um novo gênero (***Noveloa***) para acomodar as espécies da América Central (***N. coulteriana*** e ***N. longifolia***). O clado *Marathrum* da América Central, incluiu o gênero monotípico *Vanroyenella*, que nós transferimos para aquele gênero como ***Marathrum plumosum***. Os gêneros *Castelnavia* e *Rhyncholacis* são monofiléticos em nossa análise; *C. multipartita* f. *pendulosa* foi elevada à posição de espécie como ***Castelnavia pendulosa***. O gênero monotípico *Lonchostephus* foi incluído em *Mourera*, com o qual compartilha diversos caracteres morfológicos também encontrados em *Tulasneantha* (também monotípico), que, no entanto, são únicos em Podostemaceae. Recomendamos que *Lonchostephus* e *Tulasneantha* sejam unidos com *Mourera* e propomos a nova combinação: ***Mourera monadelpha*** para esta última. Finalmente, um clado inesperado de gêneros morfologicamente distintos, incluindo membros de *Apinagia*, *Jenmaniella*, *Lophogyne*, *Marathrum* e *Monostylis*, uniram-se com forte suporte, mas de integridade morfológica incerta, como grupo irmão de todo o grupo interno, exceto *Mourera*. Entretanto, mudanças nomenclaturais neste grupo não foram realizadas, dependendo de uma amostragem de táxons adicionais e maiores evidências moleculares e morfológicas.

Podostemaceae are a morphologically complex group of modified aquatic plants, comprising approximately 50 genera that are distributed predominantly in tropical latitudes (Cook and Rutishauser 2007). Recent analyses of molecular and morphological data have resolved the family within the clusioid clade of Malpighiales (e.g. Savolainen et al. 2000; Soltis et al. 2000; Gustafsson et al. 2002; Wurdack and Davis 2009). Podostemaceae are anomalous ecologically, in that they occur exclusively in river-rapids and waterfalls, where they attach firmly to the rocky substrate.

Engler (1930) divided Podostemaceae into three subfamilies: Podostemoideae (35 genera), Tristichoideae (three genera), and Weddellinoideae (monotypic), which molecular data support as independent lineages (Kita and Kato 2001; Moline et al. 2007). The primarily Old World Tristichoideae are sister to the rest of Podostemaceae, within which Weddellinoideae (Neotropics) and Podostemoideae (cosmopolitan) are sister groups (Kita and Kato 2001; Moline et al. 2007). Molecular phylogenetic analyses have resolved Podostemoideae clades that correspond to geographic regions, with taxa from Africa, Asia/Australia, the Americas (except *Podostemum*), and the genus *Podostemum* all comprising independent lineages (Kita and Kato 2001; Moline et al. 2007). *Podostemum* and several other genera differ from most Neotropical Podostemoideae in having dyad or tetrad pollen, whereas the latter have monad pollen (Philbrick et al. 2004a). In addition to *Podostemum* (dyad pollen), molecular data also resolve *Ceratolacis* Wedd. (dyad pollen) and *Diamantina* Novelo, C. T. Philbrick & Irgang (tetrad pollen) outside of the major New World clade (Ruhfel et al. in press).

Twenty-one genera (ca. 135 species) of Podostemaceae are documented from the Americas (Table 1). Nineteen genera are members of subfamily Podostemoideae, excluding only *Tristicha* (Tristichoideae) and *Weddellina* (Weddellinoideae). All New World species except one (*Podostemum ceratophyllum*) are tropical to subtropical, ranging from central Mexico to northern Argentina (Table 1). Phylogenetic analyses of morphological (Philbrick and Novelo 2004) and molecular (Moline et al. 2006) data have indicated that species previously recognized in the genera *Crenias* Spreng. (Cook and Rutishauser 2001)

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Table 1. The 20 genera of Neotropical Podostemaceae, with total number of species, number of species included in this study, geographic range, and reference source for each. All genera are members of subfamily Podostemoideae except *Tristicha* (Tristichoideae) and *Weddellina* (Weddellinoideae). Arg. - Argentina, Brz. - Brazil, c. - central, Col. - Colombia, Mex. - Mexico, n. - northern, N.Am. - North America, s. - southern, se. - southeastern, sw. – southwestern, S.Am. - South America, Ven. - Venezuela.

Genus	Total Species	Included Species	Geographic Range	Literature Source
'Autana'	1	1	sw. Ven.	Philbrick et al. (unpublished results)
Apinagia	51	11	n. S.Am. to n. Arg.	van Royen (1951)
Castelnavia	5	5	c. Brz.	Philbrick et al. (2009)
Ceratolacis	2	-	se. Brz.	Philbrick et al. (2004b)
Cipoia	2	-	se. Brz.	Philbrick et al. (2004a); Bove et al. (2006)
Diamantina	1	-	se. Brz.	Philbrick et al. (2004a)
Jenmaniella	7	2	n. S.Am.	van Royen (1951)
Lonchostephus	1	1	n./c. Brz.	van Royen (1953); Philbrick et al. (2010)
Lophogyne	1	1	se. Brz.	Bove et al. (in press)
Macarenia	1	-	Col.	van Royen (1951)
Marathrum	9	4	Mex. to Arg.	van Royen (1951); Novelo et al. (2009); Tur (2003)
Monostylis	1	1	c. Brz.	Philbrick et al. (2010)
Mourera	6	3	n. S.Am. to n. Arg.	van Royen (1953)
Oserya	7	3	Mex. to n. Brz.	van Royen (1953); Philbrick et al. (2010)
Podostemum	11	1	N.Am. to se. S.Am.	Philbrick and Novelo (2004)
Rhyncholacis	22	2	n./c. S.Am.	van Royen (1951)
Tristicha	1	1	Mex. to c. S.Am.	van Royen (1953)
Tulasneantha	1	-	c. Brz.	van Royen (1953)
Vanroyenella	1	1	Mex.	Novelo and Philbrick (1997)
Weddellina	1	1	n./c. S.Am.	Philbrick et al. (2010)
Wettsteiniola	3	-	s. S.Am.	van Royen (1951)
Total	135	38		

and *Devillea* Tul. & Wedd. (van Royen 1954) are appropriately subsumed in *Podostemum* (Philbrick and Novelo 2004). Conversely, species from the Indian subcontinent that historically were considered part of *Podostemum* are now recognized as members of other genera (i.e. *Polypleurum* (Tul.) Warm. and *Zeylanidium* Engl.; Kita and Kato 2001; Philbrick and Novelo 2004). Genera of Neotropical Podostemoideae range in size from a single species (e.g. *Lonchostephus*, *Lophogyne*, *Monostylis*, *Vanroyenella*) to about 50 species (*Apinagia*; Table 1). Fourteen (78%) of the genera have fewer than 10 species.

Classification of Neotropical Podostemaceae has been limited by several factors. The developmental morphology of vegetative structures can be difficult to interpret (e.g. Rutishauser 1997; Jäger-Zürn 2005), with even basic distinctions among roots, stems, and leaves often being unclear. Demarcation of species can be hindered by extensive variability in vegetative form, much of which apparently is induced by local environmental factors (Philbrick, pers. obs.). Indeed, the understanding of how the environment influences vegetative form remains rudimentary. Revisionary studies of genera conducted over the last decade consistently have recognized far fewer species than previous treatments (e.g. *Podostemum*, Philbrick and Novelo 2004; *Castelnavia*, Philbrick et al. 2009; *Marathrum*, Novelo et al. 2009; Philbrick et al. 2010). The high incidence of monotypic genera existing historically in the family evidently reflects systematic approaches that focused more on characteristics that distinguish taxa rather than those shared among them. Lastly, circumscription of some of the larger genera (e.g. *Apinagia*, *Marathrum*) has been difficult, owing to weakly-defined genus concepts, whereby a species might just as easily belong to one genus as another (van Royen 1951).

Our main objective was to reevaluate the taxonomy and classification of Neotropical Podostemaceae using contemporary analytical methods. By conducting phylogenetic analyses of morphological and molecular data, we endeavored to evaluate the monophyly of Podostemoideae genera, ascertain the relationships among taxa, and then apply any taxonomic changes necessary to accommodate our results.

Materials and Methods

***Taxon Sampling*—**We analyzed 140 accessions, including 13 nucleotide sequences that were retrieved from GenBank, representing 38 taxa (from 14 recognized genera and a novel genus provisionally identified as 'Autana'; Appendix 1). Specimens (including voucher specimens for GenBank sequences where available) were identified to species using relevant literature sources (van Royen 1951, 1953, 1954; Novelo and Philbrick 1997; Philbrick and Novelo 2004; Bove et al. 2006; Novelo et al. 2009; Philbrick et al. 2009). We followed Bove et al. (in press) in interpreting *Lophogyne* as monotypic. *Apinagia nana* was retained as a distinct species, although van Royen (1951) placed it in synonymy with *A. pilgeri* Mildbr. The outgroup comprised two accessions of *Podostemum ceratophyllum*, which molecular phylogenetic analyses have resolved within the sister clade to the Neotropical genera (Kita and Kato 2001; Moline et al. 2007), as well as Neotropical representatives of subfamilies Tristichoideae (*Tristicha trifaria*) and Weddellinoideae (*Weddellina squamulosa*).

***Morphological Data*—**Specimen accessions were scored for 45 morphological characters (Appendix 2), representing vegetative and reproductive features commonly used to distinguish species (cf. Philbrick and Novelo 2004; Philbrick et al. 2004a, 2004b, 2009; Bove et al. in press). Morphological data were scored individually from specimens that were included in the phylogenetic analysis of combined data (see below) and encoded as consensus data for all accessions of a given taxon. We scored morphology data for *Apinagia yguazuensis*, for which sequences were published previously (Les et al. 1997; Moline et al. 2006). However, other taxa that were represented only by GenBank sequences were omitted from morphological and combined molecular data analyses because their voucher specimens were incomplete or were not examined. We also obtained morphological data for *Tulasneantha monadelpha* (Bongard) P. Royen, for which no molecular data were available.

***Molecular Data*—**Molecular data were obtained from specimens that were collected by the authors and preserved in the field using liquid CTAB (Rogstad 1992). Genomic DNA was extracted and amplified for select gene regions following Les et al. (2008). Primers used for amplification and sequencing were as follows: ITS - ITS2, ITS3, ITS4, and ITS5 (Baldwin

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1992); *trnL* intron - c and d (Taberlet et al. 1991); *rbcL* - rbcLz-1 and rbcLz-1204R (designed by G. Zurawski; Andreasen and Bremer 2000). Amplified DNA fragments were purified using 0.1 µL ExoSAP-IT® enzyme mixture (Affymetrix, Inc., Santa Clara, California), 0.4 µL water, and 1.0 µL amplification product in a 1.5 µL reaction. Sequencing reactions were conducted using 1.5 µL of cleaned amplicon, 1.0 µL of Big Dye®, 2.0 µL of 5 × ABI buffer (Applied Biosystems, Foster City, California), and 3.2 pmol of sequencing primer in a 10 µL reaction. Cycle sequencing and cleanup followed Les et al. (2008); sequencing was performed on an ABI PRISM® 3100 genetic analyzer (Applied Biosystems).

Chromatograms were edited using the program 4Peaks ver. 1.7 (Griekspoor and Groothuis 2005) and were assembled into contigs using CodonCode Aligner ver. 3.0.3 (CodonCode Corporation, Dedham, Massachusetts). Nucleotide sequences were aligned against each other manually using MacClade ver. 4.06 (Maddison and Maddison 2000). Insertions and deletions (indels) were scored for the aligned *trnL* matrix using simple indel coding (Simmons and Ochoterena 2000) in the program SeqState ver. 1.4.1 (Müller 2005, 2006). Molecular sequence data generated for this study were deposited in GenBank (accession numbers HM470255-HM470563; Appendix 1), and the morphological and molecular data matrices were submitted to TreeBASE (study number S10676).

Phylogenetic Analyses—Data were analyzed separately (morphology, ITS, *trnL* nucleotide and indel data) and in combination (molecular data only), using both equally-weighted maximum parsimony and maximum likelihood methods. Prior to combining data, partition-homogeneity / incongruence-length difference (ILD) tests were conducted using PAUP* ver. 4.0b10 (heuristic search, 1,000 replicates, maxtrees = 1,000; Farris et al. 1994; Swofford 2002), with constant and uninformative characters excluded (Lee 2001) and a significance threshold of $p < 0.01$, to evaluate the relative congruency of the different data partitions examined (ITS [ITS-1, 5.8S, and ITS-2], *rbcL*, and *trnL* DNA sequences, the coded *trnL* indel matrix, and morphological characters).

Heuristic tree searches were performed under parsimony in PAUP* (Swofford 2002) with 100 replicates of random stepwise addition and branch swapping by tree bisection and reconnection (TBR), using maxtrees = 100,000. Multistate taxa in the morphology data were treated as polymorphisms and ambiguous nucleotide states in the molecular data as uncertainties. Support for internal nodes was evaluated using 1,000 bootstrap replicates in PAUP* with the following options: heuristic search, one random stepwise addition per replicate, swapping by TBR, and maxtrees = 10,000. Trees were depicted as strict-consensus cladograms of all most-parsimonious topologies.

After model selection with Modeltest ver. 3.4 under the AIC (Posada and Crandall 1998; Posada and Buckley 2004; Posada 2006), likelihood analysis was implemented using GARLI ver. 0.97.r737 (Zwickl 2006), with the combined data matrix partitioned among ITS (GTR + I + G), *rbcL* (HKY + I + G), *trnL* indels (Mkv model; Lewis 2001), and *trnL* nucleotide data (TIM + I + G). Likelihood analyses of uncombined molecular data used the same models as the respective partitions in the combined data matrix, and morphology data were analyzed under the Mkv model. Ten separate likelihood runs were performed using different random starting seeds, and the tree with the maximum likelihood score was compared with the parsimony consensus tree. Bootstrap analysis was conducted in GARLI using 1,000 replicates.

Morphological Character Evolution—Morphological character state transitions were mapped onto the morphology and combined data trees under parsimony, using the 'reconstruct' option in PAUP*. We focused on two particular characters of interest, stem form (character 2, Appendix 2) and gynophore (character 32). Stems with a single attachment point, regardless of their orientation relative to the substrate, were scored as "upright," and stems with multiple attachment points along the substratum were coded as "prostrate." Presence of a gynophore (i.e. a stalk between the stamen attachment point and the ovary base) was evaluated strictly during anthesis because several Podostemaceae can have mature capsules that are stalked, yet lack a gynophore at anthesis.

Results

Morphological Data—Forty of the 45 morphological characters included in our analysis were parsimony-informative (Appendix 2), and 11.4% of cells lacked data for the matrix of 38 accessions (Supplemental Appendix 1). Several characters varied for only one taxon in our data matrix. Only *Apinagia riedelii* had a stem that was both upright and thalloid (character 3). Traits unique to *Castelnavia* included a curved pedicel (character 19), flowers retained within the spathella at anthesis (character 20), an asymmetrically inflated pedicel apex (character 23), and a unilocular ovary (character 35). A pedicel apex that is hollow and inflated at maturity (character 39) was specific to 'Autana', and a capsule wing (character 43) characterized both included species of *Rhyncholacis.* Both *Monostylis* and *Rhyncholacis* had laterally compressed capsules (character 40), which were compressed parallel to the septum in the former and perpendicularly in the latter (character 45). Only *Tristicha* and *Weddellina* lacked a spathella (character 16), and dyad pollen (character 31) occurred only in *Podostemum ceratophyllum*.

Molecular Data—Separate data matrices were obtained for ITS (127 accessions, 1,568 characters, 754 parsimony-informative, 2.8% missing data excluding gaps), *rbcL* (84 accessions, 1,178 characters, 110 parsimony-informative, 3.4% missing), and *trnL* (119 accessions, 50 / 552 [indel / nucleotide] characters, 29 / 118 parsimony-informative, 0.5% / 2.9% missing). The matrix of combined molecular data comprised 71 accessions and 3,098 characters (885 parsimony-informative, 5.0% missing). The ILD test indicated no significant incongruence between the gene regions ITS, *rbcL*, and *trnL* (including coded indels; $p = 0.96$); however, the molecular and morphological data were incongruent ($p = 0.004$).

Phylogenetic Analyses—Phylogenetic analysis of morphological data reached the imposed limit of 100,000 most-parsimonious trees (111 steps, CI = 0.49, CI_{exc} = 0.46, RI = 0.72; Fig. 1) and returned a maximum likelihood score (lnL) of -444. The ITS data analysis also obtained 100,000 most-parsimonious trees (3,583 steps, CI = 0.46, CI_{exc} = 0.44, RI = 0.86; Fig. 2A), as did analysis of *trnL* data (430 steps, CI = 0.76, CI_{exc} = 0.66, RI = 0.91; Fig. 2B). Parsimony analysis of combined data yielded 975 trees (3,899 steps, CI = 0.53, CI_{exc} = 0.48, RI = 0.79; Fig. 3). Likelihood analysis resulted in trees with natural log likelihood scores of -17,177 (ITS), -2,870 (*trnL*), and -21,197 (combined data). The maximum likelihood trees (not shown) differed only slightly in topology from the corresponding strict consensus trees that were recovered under parsimony, and incongruent nodes received poor bootstrap support (< 80%) in both parsimony and likelihood analyses.

The combined data (Fig. 3) resolved most of the same relationships that were recovered in the analyses of nuclear (ITS; Fig. 2A) and chloroplast (*trnL*; Fig. 2B) data. *Marathrum* was not monophyletic, although a clade consisting of *M. foeniculaceum*, *M. tenue*, and *M. utile*, and also including *Vanroyenella plumosa* (clade A, Fig. 3) was supported strongly in all separate and combined data analyses. Relationships among the abovementioned species, however, were unresolved or poorly supported on the molecular data trees (Figs. 2–3). The only *Marathrum* species analyzed from South America (*M. aeruginosum*) resolved within a clade that was far removed topologically from other *Marathrum* species (clade J; see below).

Of the ten *Apinagia* species included in the combined molecular data analysis, eight (*A. corymbosa*, *A. fluitans*, *A. longifolia*, *A. richardiana*, *A. riedelii*, *A. staheliana*, *A. yguazuensis*, and one undescribed species) comprised a well-supported clade (clade C, Fig. 3). However, two *Apinagia* species resolved elsewhere on the tree. *Apinagia nana* was sister to *Marathrum*/*Vanroyenella* (clade A), whereas *A. fimbrifolia* belonged to a well-resolved clade along with *Jenmaniella*, *Lophogyne*, *Monostylis*, and *Marathrum aeruginosum* (clade J; see below).

Oserya was not monophyletic, but rather comprised two clades corresponding to the geographic regions of Mexico

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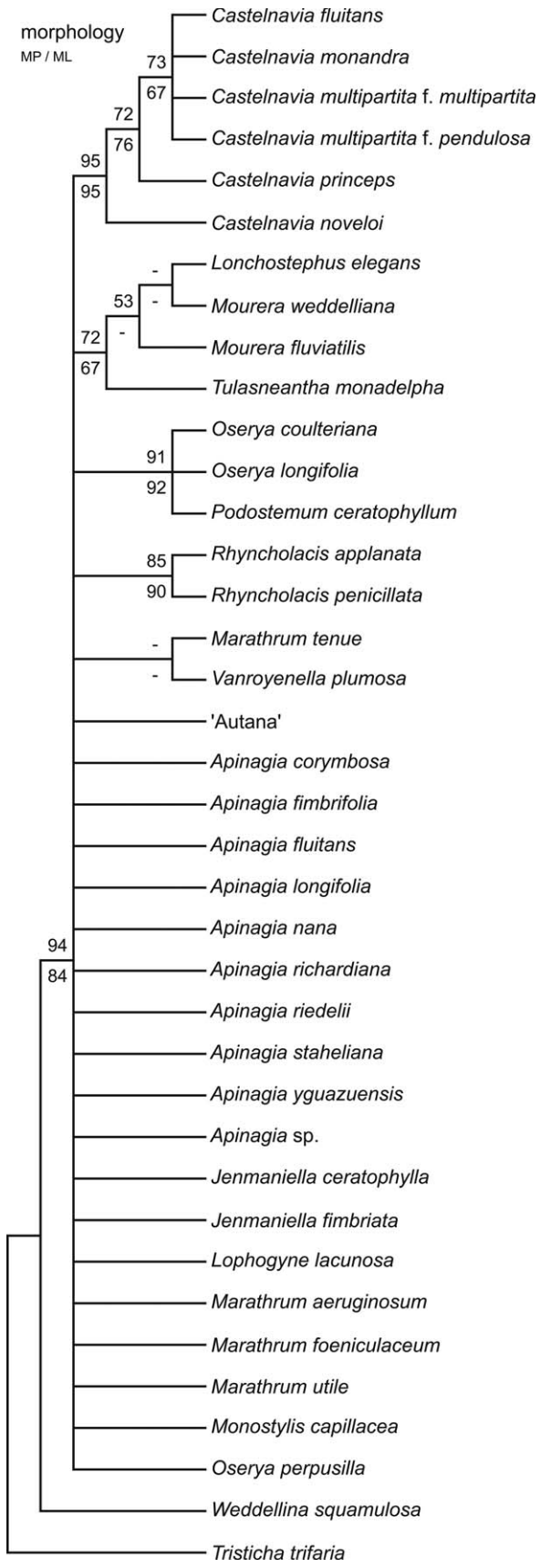


FIG. 1. Strict consensus tree constructed using maximum parsimony analysis of morphological data (Supplemental Appendix 1; Appendix 2). Nodal values above and below branches indicate parsimony and likelihood bootstrap values, respectively. Nodes with less than 50% bootstrap support are labeled with a dash (-).

(*O. coulteriana*, *O. longifolia*; clade E, Fig. 3) and northern South America (*O. perpusilla*; clade D). Each of these clades was monophyletic, and together they were weakly supported by the combined data as paraphyletic relative to clades A-C, with which they associated as a well-supported clade (clade L). *Rhyncholacis* (clade F) and *Castelnavia* (clade G) were both well supported as monophyletic but were unresolved relative to clades A-E. Accessions of 'Autana' resolved in a well-supported clade (clade H) that was moderately resolved by combined data as sister to a clade of the above taxa (Fig. 3), but minimally resolved on the separate ITS and *trnL* trees (Fig. 2).

The genera *Jenmaniella*, *Lophogyne*, and *Monostylis*, along with *Apinagia fimbrifolia* and *Marathrum aeruginosum*, constituted a strongly-supported clade (clade J, Fig. 3) that was moderately supported as sister to the aforementioned taxa (clades A-H). Within this clade, *Jenmaniella* and *Monostylis* together formed a subclade in which the two species of *Jenmaniella* were paraphyletic to *Monostylis capillacea*. The relative positions of the other taxa in clade J, particularly *A. fimbrifolia* and *Lophogyne lacunosa*, received low bootstrap support and varied considerably in analyses of different gene regions (Figs. 2–3). *Lonchostephus* and *Mourera* comprised a clade that was sister to all other ingroup taxa (clade K, Fig. 3). However, these genera were not reciprocally monophyletic, and in both the ITS and combined data analyses *L. elegans* was paraphyletic toward *M. weddelliana*.

Several accessions retrieved from GenBank (Moline et al. 2006) were included in the phylogenetic analysis of ITS data (Fig. 2A). Accessions of *Marathrum foeniculaceum* (DQ397955, DQ397956) and *Oserya longifolia* (DQ397957) resolved with their respective taxa. Accessions of *Apinagia yguazuensis* (DQ397951) and *A. rangiferina* (DQ397958) resolved in a clade with *A. corymbosa*. Several *rbcL* sequences from previous studies (Les et al. 1997; Savolainen et al. 2000; Kita and Kato 2004), which were not included in our phylogenetic analyses, nevertheless showed minimal divergence from sequences that we obtained (by uncorrected p distance, determined in PAUP*; Swofford 2002). Two sequences of *Marathrum*, ascribed to *M. foeniculaceum* (U68085) and *M. oxycarpum* (AJ402971), taxa that Novelo et al. (2009) considered synonymous, were identical to sequences we obtained for *M. foeniculaceum*. A sequence for *Mourera aspera* (U68086) most closely matched our sequence of *M. weddelliana*. The GenBank sequence for *Vanroyenella plumosa* (U68090) was most similar to our sequence for that taxon, and sequences for *Mourera fluviatilis* (AB113759), *Oserya coulteriana* (U68087), and *Podostemum ceratophyllum* (U68088) matched our sequences for those taxa exactly.

Morphological Character Evolution—Several morphological characters (Appendix 2) exhibited high homoplasy (homoplasy index > 0.5, determined in PAUP*; Swofford 2002) on both the morphological (12 characters; Fig. 1) and combined data (17 characters; Fig. 3) trees. Nevertheless, some characters aligned with major clades that were resolved in the combined data tree. Fundamental differences in stem form (character 2) mapped to four ingroup branches (arrows, Fig. 3), which included the large clade of *Apinagia* species (clade C). Species of *Apinagia* with prostrate stems (i.e. *A. fimbrifolia*, *A. nana*) did not resolve within clade C. Localized transitions to upright stem were observed for *Castelnavia multipartita* f. *pendulosa*, *Oserya coulteriana*, and *Monostylis capillacea*. Species with a gynophore (character 32; *Jenmaniella ceratophylla*, *J. fimbriata*, *Monostylis capillacea*) were monophyletic within

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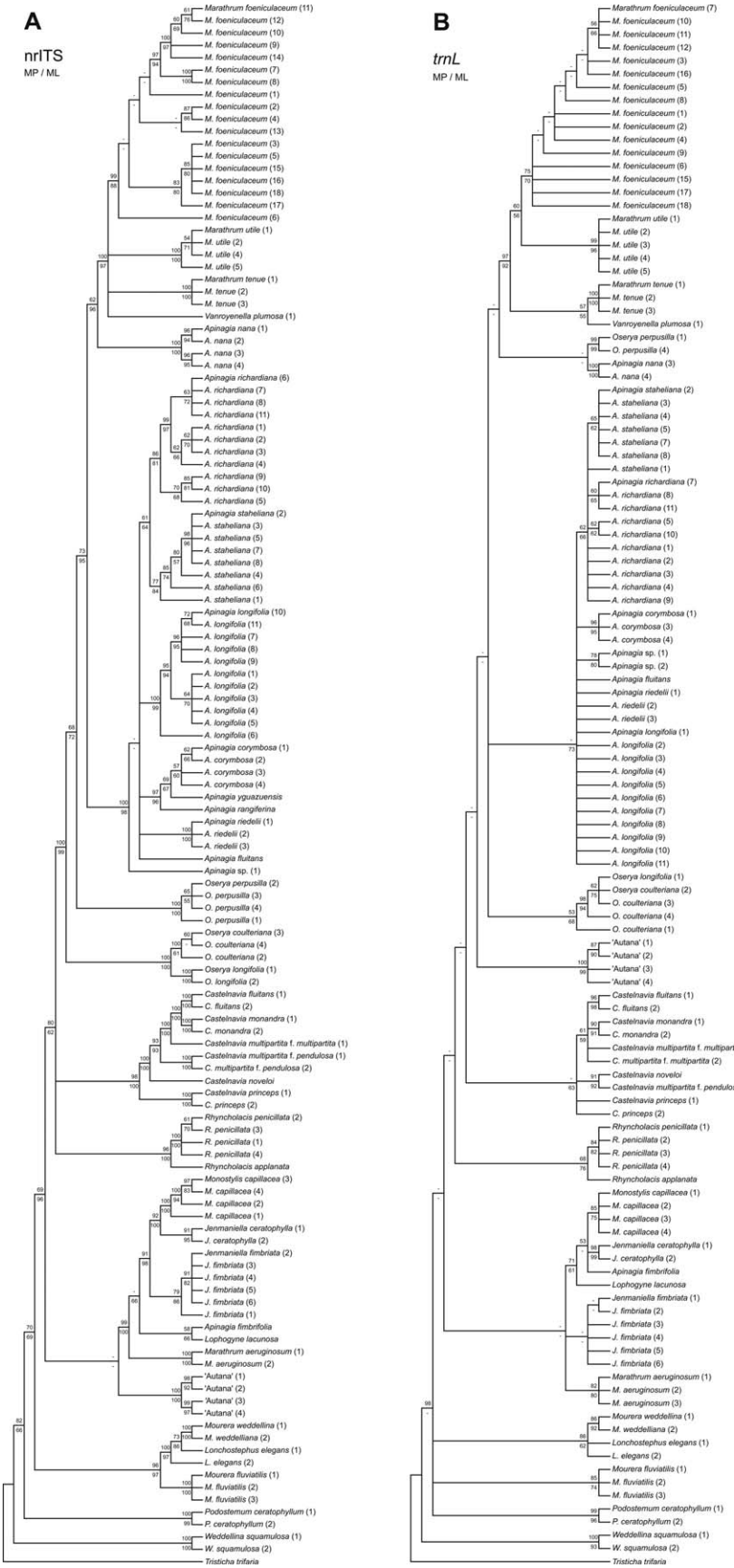


FIG. 2. Strict consensus trees constructed using maximum parsimony analysis of nuclear (ITS) and chloroplast (*trnL*) data. Nodal values above and below branches indicate parsimony and likelihood bootstrap values, respectively. Nodes with less than 50% bootstrap support are labeled with a dash (-). Taxon names are spelled in full and then abbreviated within a clade or unresolved group of the same taxon; numbers in parentheses denote accession numbers (Appendix 1). A. ITS nucleotide data. B. *trnL* nucleotide and indel data.

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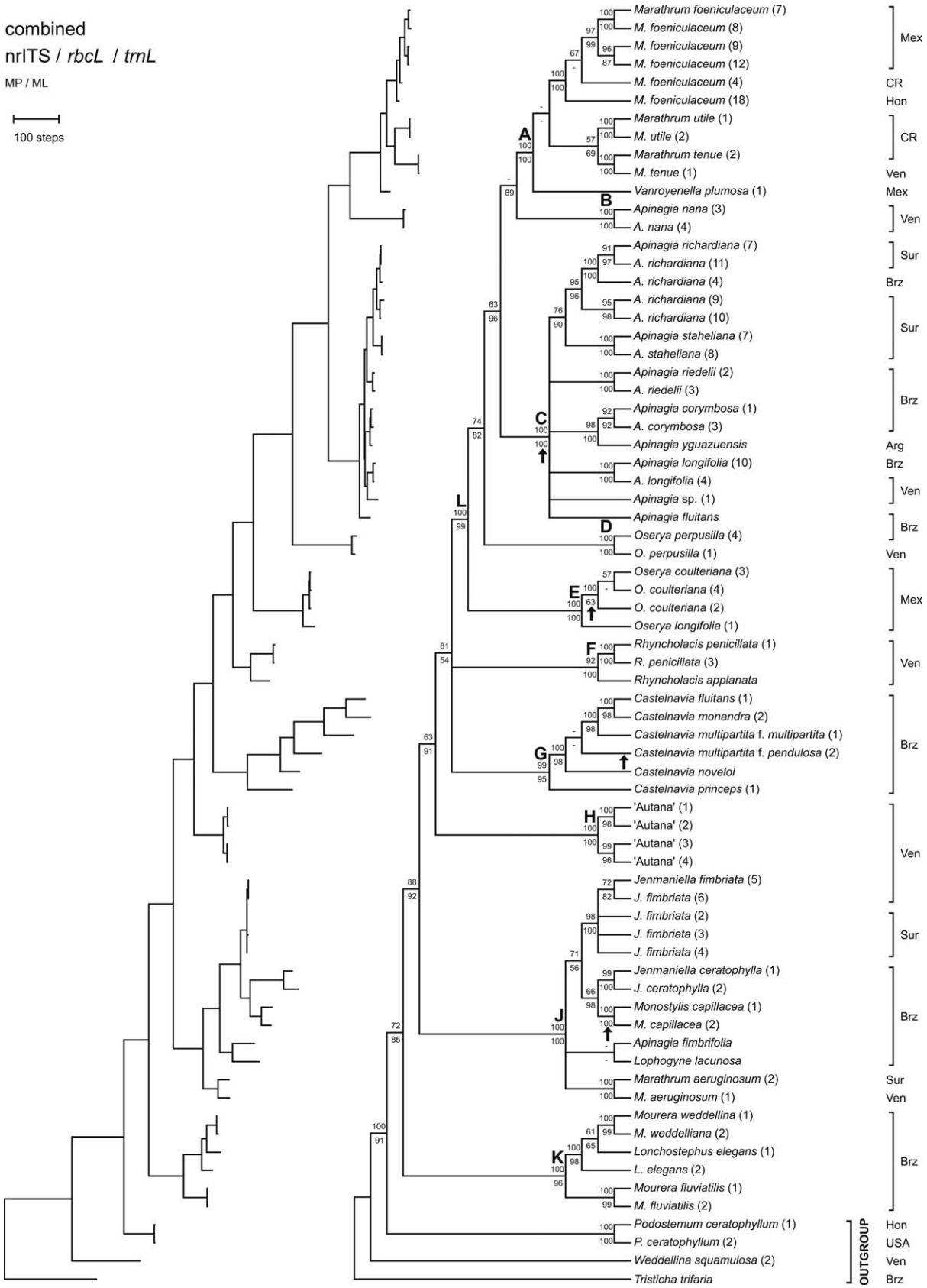


FIG. 3. Strict consensus cladogram (right) and representative most-parsimonious phylogram (left) constructed using maximum parsimony analysis of combined molecular data (ITS, *rbcL*, *trnL*). Nodal values above and below branches indicate parsimony and likelihood bootstrap values, respectively. Nodes with less than 50% bootstrap support are labeled with a dash (-). Taxon names are spelled in full and then abbreviated within a clade of the same taxon; numbers in parentheses denote accession numbers (Appendix 1). Geographic region of specimen collection is given at right (Arg - Argentina; Brz - Brazil; CR - Costa Rica; Hon - Honduras; Mex - Mexico; Sur - Suriname; Ven - Venezuela). Four reconstructed instances of upright stem habit evolution are depicted by arrows.

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clade J, and evolution of the gynophore mapped only to their subtending branch on the tree.

Discussion

Major Clades and Their Resolution—Van Royen (1951, 1953, 1954) developed a comprehensive taxonomic treatment of Neotropical Podostemaceae, in which he established two subfamilies: Tristichoideae, including *Tristicha* and *Weddellina,* and Podostemoideae, with the latter divided into two tribes: Mourereae (*Lonchostephus*, *Mourera*, and *Tulasneantha* P. Royen) and Podostemeae (= Eupodostemeae; all other Neotropical genera). Our results supported the division of Mourereae and Podostemeae, but we also resolved many intra- and intergeneric relationships that had not been suggested previously by van Royen or other authors.

We identified 11 major clades with strong bootstrap support (> 90%; clades A-L, Fig. 3); however, the relationships among them were incompletely resolved. The sister relationship of clade K (*Lonchostephus* and *Mourera*) and all other Neotropical Podostemoideae is consistent with the tribal classification of van Royen (1951), except for the position of *Podostemum*, which previous studies determined to be only distantly related to our ingroup (Kita and Kato 2001; Moline et al. 2007). Clade L (*Vanroyenella*, all species of *Oserya*, and most species of *Apinagia* and *Marathrum*) also was strongly supported as monophyletic, even though it does not correspond to any currently recognized taxonomic group. Whether this clade should be recognized taxonomically as a discrete infrafamilial category will depend upon the outcome of subsequent phylogenetic analyses that include additional species from the larger Neotropical genera (e.g. *Apinagia*, *Marathrum*, *Rhyncholacis*) and additional Neotropical genera not included herein (e.g. *Cipoia* C. T. Philbrick, Novelo & Irgang, *Macarenia* P. Royen, *Wettsteiniola* Suess.). Results obtained by Ruhfel et al. (in press) have placed *Ceratolacis* and *Diamantina* outside of the major Neotropical Podostemoideae clade, but other genera have not been sampled yet in a molecular phylogenetic study.

Some genera of Neotropical Podostemaceae have been circumscribed with difficulty, most notably *Apinagia* and *Marathrum* (van Royen 1951). Moreover, the existence of seven monotypic genera (Table 1) arguably reflects a lack of confidence in the placement of their species (cf. Philbrick and Novelo 1995). The present study provides some insight to assist with the refinement and circumscription of the large genera and also the phylogenetic placement of the many monotypic genera.

Clade A (Marathrum and Vanroyenella)—*Marathrum* was established by Humboldt and Bonpland (1808) with their description of *M. foeniculaceum*. Subsequently, over 30 *Marathrum* species have been recognized (van Royen 1951; Tur 2003). Many of these have been considered synonymous, however, with recent treatments recognizing only nine species (Novelo and Philbrick 1997; Novelo et al. 2009). One species (*M. tenue*) is restricted to Central America and Mexico, whereas two (*M. foeniculaceum* and *M. utile*) span this region into northwestern Venezuela and northern Colombia. *Marathrum cubanum* C. Wright is endemic to Cuba, and five species (*M. aeruginosum*, Suriname and Venezuela; *M. azarensis* Tur, Argentina; *M. pauciflorum* Tul., Guyana; *M. squamosum* Wedd., Brazil, Venezuela; *M. striatifolium* P. Royen, Peru) occur only in South America.

Marathrum was strongly supported as polyphyletic in our analyses, although only four of the nine species were included. Three largely Mesoamerican species and the monotypic *Vanroyenella* (*V. plumosa*), were monophyletic (clade A, Fig. 3), but their interspecific relationships were poorly resolved. In contrast, *M. aeruginosum* resolved to a distant group on the tree (clade J; see below).

Marathrum foeniculaceum is characterized by pinnately compound leaves and stamens that encircle the ovary, and ranges from central Mexico to Colombia. Previous authors (e.g. van Royen 1951; Burger 1983; Novelo and Philbrick 1997) have recognized additional species from the same geographic region, on the basis of minor differences (e.g. the degree of leaf dissection). However, with respect to the characters mentioned above, the additional species do not differ from *M. foeniculaceum*. We included in our analyses 18 accessions of *M. foeniculaceum* (Appendix 1), with varying degrees of leaf dissection, which resolved inconsistently on the ITS and *trnL* trees (Fig. 2). Based on the monophyly of *M. foeniculaceum*, the lack of any clear internal phylogenetic structure, and a broadly-distributed sample of collections, our results support Novelo et al. (2009), who recognized only one species within this taxon.

The monophyly of *Vanroyenella* and three species of *Marathrum* (including *M. foeniculaceum*, the type for the genus) supports the transfer of *V. plumosa* to *Marathrum* (see Taxonomic Treatment). Morphologically, *V. plumosa* grouped with *Marathrum tenue* (Fig. 1), from which it differs by only three characters, the fewest of any pairwise comparison; it was equally distant from *M. utile*. Although the plumose leaves of *V. plumosa* (character 10, Appendix 2) are unique among Neotropical Podostemaceae, that feature alone does not warrant recognition of a separate genus in light of its phylogenetic placement. Thus, we recommend its transfer to *Marathrum* to maintain a phylogenetically meaningful classification.

Marathrum aeruginosum localized to a clade with species of *Apinagia*, *Jenmaniella*, *Lophogyne*, and *Monostylis* (clade J, Fig. 3), not with other species of *Marathrum*. It is notable that van Royen (1951) identified *M. aeruginosum* (also *M. pauciflorum* and *M. striatifolium*) as a species of *Marathrum* that could have been assigned as readily to *Apinagia* as *Marathrum*. At this time, a revised taxonomic designation for *M. aeruginosum* (e.g. transfer to another genus or recognition of a new genus) is deferred, pending the outcome of expanded phylogenetic analyses that include the remaining species of *Marathrum* from South America, along with broader taxonomic sampling from *Apinagia* and *Jenmaniella*.

Clades B and C (Apinagia)—*Apinagia* consists of about 50 Neotropical species (van Royen 1951; Philbrick et al. 2010), many of which were placed originally among three genera that no longer are recognized (i.e. *Ligea* Poit. ex Tul., *Neolacis* Wedd., *Oenone* Tul.; van Royen 1951). Tulasne (1849) initiated *Apinagia* with his description of several new species and the transfer of others from the genus *Lacis* Dulac. Engler (1927, 1930) and van Royen (1951) subsequently transferred many species from the aforementioned genera to *Apinagia* and also described numerous new species.

Our results indicated that *Apinagia* is polyphyletic as currently circumscribed. Although the majority of species analyzed herein resolved in a strongly-supported clade (clade C, Fig. 3), *A. nana* (clade B) resolved weakly as the sister to *Marathrum/Vanroyenella* (clade A), and *A. fimbrifolia* occurred in a distant location in the phylogeny (clade J, see below). All eight species in clade C have upright stems, in contrast to the

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prostrate stems of the phylogenetically anomalous *A. fimbrifolia* and *A. nana*. Moreover, the ITS sequence of *A. rangiferina* placed it in the clade of upright-stemmed species (Fig. 2A), whereas van Royen (1951) described it as having a prostrate stem. Evaluation of the *A. rangiferina* voucher specimen (Appendix 1) revealed it to be polymorphic for stem morphology, with some plants prostrate and others with short (2–3 mm) upright stems (Philbrick, pers. obs.). Although not included in our analyses, the type for *Apinagia, A. fucoides* (Mart. & Zucc.) Tul. (cf. van Royen 1951), also has an upright stem, indicating circumstantially that the type also should belong to this large *Apinagia* clade. Consequently, we refer to clade C provisionally as *Apinagia* s. s. However, taxonomic changes for the anomalous species *A. fimbrifolia* and *A. nana* are deferred, pending further sampling from *Apinagia* and *Marathrum*.

Clades D and E (Oserya)—*Oserya* is a Neotropical genus established by Tulasne (1849), who described four species having extrorsely dehiscent anthers. Two were from Brazil (*O. biceps* Tul. & Wedd., *O. flabellifera* Tul. & Wedd.), one from Guyana (*O. sphaerocarpa* Tul. & Wedd.) and one from Mexico (*O. coulteriana*). Went (1910) questioned the recognition of the genus based simply on anther dehiscence and placed *Oserya* in synonymy with *Apinagia*. Van Royen (1954) followed Tulasne (1849) in accepting *Oserya* as distinct from *Apinagia*, emphasizing other features in addition to anther dehiscence that supported its recognition. Specifically, he contrasted the unistaminate flowers, basifixed anthers, and bulbous style of *Oserya* with the rarely unistaminate flowers, dorsifixed anthers, and linear style found in *Apinagia*. Van Royen (1954) recognized six species in *Oserya*, including the four described by Tulasne (1849) and two additional species from northern South America. *Oserya minima* P. Royen from Suriname was a new species, whereas *O. perpusilla* (see below) originally had been placed in *Apinagia* by Went (1910). Novelo and Philbrick (1995) later described a seventh species in the genus (*O. longifolia*) from western Mexico.

Oserya is disjunct geographically; its northern range includes central and southern Mexico, whereas its southern range is predominantly northern South America (central Venezuela, the Guianas, and northern Brazil). The two *Oserya* clades resolved by our analysis (clades D and E, Fig. 3) precisely reflect the Mexican / South American disjunction. Although the paraphyly of these clades was not supported strongly in our combined data analysis (Fig. 3), none of the analyses resolved them as monophyletic. Novelo and Philbrick (1997) questioned the inclusion of Mexican *Oserya* species (*O. coulteriana* and *O. longifolia*) in the genus because of their considerable morphological divergence from South American species. The Mexican species have introrsely or latrorsely dehiscent anthers, one to three (*O. coulteriana*) or two (*O. longifolia*) stamens per flower, and capsules with six nonsuture ribs. In contrast, South American oseryas have extrorse anther dehiscence, a single stamen, and ten nonsuture ribs.

Oserya perpusilla is common in Suriname and Venezuela (Philbrick et al. 2010), whereas the other South American *Oserya* species are rare. Field studies by C. T. P. in Suriname and Venezuela have failed to locate any species other than *O. perpusilla*, and thus yielded only one South American species for the current study. However, cladistic analyses of morphological data for all *Oserya* species (Philbrick, unpubl. data) resolved *O. flabellifera* (the genus type) within a strictly South American clade (which also included *O. minima*, *O. perpusilla*, and *O. sphaerocarpa*). Based on the monophyly of the four South American oseryas indicated by phylogenetic analysis of morphological data, combined with the molecular evidence for the paraphyly of the genus and the geographical disjunction of subclades, we propose to subdivide the genus to better reflect the phylogenetic affinities of species. Because *Oserya flabellifera* is the type of the genus (cf. van Royen 1954), the name is retained for the South American species. Consequently, the Mexican species are transferred to the new genus *Noveloa* (see Taxonomic Treatment).

Clade F (Rhyncholacis)—*Rhyncholacis* (Tulasne 1849) contains 22 species ranging throughout northern South America (northern Brazil, Colombia, Guyana, French Guiana, Suriname, and Venezuela), with its richest diversity in the Guianas (van Royen 1951). *Rhyncholacis* is distinctive morphologically in having capsules that are "winged", i.e. with flattened midrib extensions on opposite sides of the capsule that are contiguous with the persistent, rigid styles. In addition, the flowers arise in fascicles from between fused leaf bases. Similar fascicles notably also occur in *Marathrum tenue*, *M. utile*, and *Vanroyenella plumosa*, which were closely related to one another but distant from *Rhyncholacis* in our analyses, and in the unsampled genus *Wettsteiniola* (Supplemental Appendix 1; van Royen 1951). Although the two *Rhyncholacis* species included in our study were monophyletic (clade F, Fig. 3), a broader taxonomic sampling of this relatively large genus will be necessary before the monophyly of the entire genus can be evaluated with confidence.

Clade G (Castelnavia)—A monographic study by Philbrick et al. (2009) indicated that *Castelnavia* was monophyletic based on eight synapomorphic morphological characters: absence of roots, ovary surrounded by stem tissue during and after anthesis, ovary horizontal at anthesis, unilocular mature ovary, asymmetrically inflated pedicel apex, anisolobous ovary, ovary longitudinal axis at 45–90° angle relative to pedicel axis, and one deciduous capsule valve. In the present study, morphological and molecular data also strongly supported the monophyly of *Castelnavia* (Fig. 1; clade G, Fig. 3). However, combined molecular data failed to resolve the genus relative to *Rhyncholacis* or clade L (Fig. 3).

Philbrick et al. (2009) recognized two taxonomic forms within *Castelnavia multipartita*, the prostrate *C. m.* f. *multipartita* and the upright-stemmed *C. m.* f. *pendulosa*, and proposed that these two taxa were contrasting, environmentally-induced forms of one highly variable species. The data presented herein, however, indicate that the two taxonomic forms of *C. multipartita* are as distinct genetically as are other species in the genus (Fig. 3). Consequently, we recommend elevating *C. m.* f. *pendulosa* to the species level (see Taxonomic Treatment).

Clade H—Clade H in our analysis (Fig. 3) comprised four accessions of a novel genus (Philbrick et al. unpublished results), to which we provisionally refer as 'Autana'. Two conspicuous morphological characters distinguish 'Autana' from all other Neotropical Podostemaceae. The prostrate, flattened stems of 'Autana' have ridges derived from leaf margins that occur in a distinct and unique anastomosing pattern. Secondly, the pedicel apices are inflated, hollow, and in fruit are provided with obovoid processes where stamen filaments had attached. In contrast, other species do not have pedicel apices that are both inflated and hollow, and the shape of the stamen attachment scar also is unique to 'Autana' (Philbrick et al. unpublished results). The monophyly of clade H received

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strong support, and it was moderately supported as the sister group of clades A-G.

Clade J—Our analyses also resolved a highly heterogeneous but strongly-supported clade that included a single species each of *Apinagia* and *Marathrum*, the monotypic genera *Lophogyne* and *Monostylis*, and two species of *Jenmaniella* (clade J, Fig. 3). This clade was sister to the clades mentioned above. Little additional resolution was evident within this clade, although *Jenmaniella* and *Monostylis* comprised a moderately-supported subclade.

Despite considerable morphological diversity in clade J, there are no apparent morphological synapomorphies to facilitate its taxonomic recognition. The prominent features found among species in this clade also occur elsewhere in Neotropical Podostemaceae. For example, all members of the clade (except *Monostylis capillacea*) have prostrate stems, which help to define such genera as *Castelnavia* (Philbrick et al. 2009), *Ceratolacis* (Philbrick et al. 2004b), and *Rhyncholacis* (van Royen 1951). Several *Jenmaniella* species notably have upright stems, including the genus type *J. varians* Engl. (van Royen 1951). However, these taxa were not available for study, and thus their phylogenetic position is unknown. *Lophogyne lacunosa* and the two *Jenmaniella* species that we sampled have circinate leaf development, whereas the remaining species in clade J do not. Circinate leaves also occur in Mexican species of *Oserya* (Novelo and Philbrick 1997) and *Rhyncholacis* (Philbrick, unpubl. data). Considerable variation in capsule rib number occurs in Neotropical Podostemaceae (van Royen 1951, 1953, 1954), and the number of nonsuture ribs per valve in clade J ranges from three (*Apinagia fimbrifolia*, *Jenmaniella fimbriata, Lophogyne lacunosa*, *Marathum aeruginosum*) to five (*J. ceratophylla*) to seven (*Monostylis capillacea*). Pinnately or dichotomously divided leaves occur in clade J, but both leaf types also are common in other Neotropical Podostemaceae. Pinnate leaves characterize many *Apinagia* species (van Royen 1951), Central American species of *Marathrum* (Novelo et al. 2009), and some *Castelnavia* species (Philbrick et al. 2009). Dichotomously divided leaves are present in some species of *Cipoia* (Philbrick et al. 2004a), *Ceratolacis* (Philbrick et al. 2004b), and *Podostemum* (Philbrick and Novelo 2004). Another feature shared by the six species in clade J is the distribution of stamens on only one side of the ovary. However, many other Neotropical Podostemaceae have a similar stamen arrangement, e.g. *Oserya* (van Royen 1954; Novelo and Philbrick 1997), some species of *Apinagia* (van Royen 1951), *Castelnavia* (Philbrick et al. 2009), and *Cipoia* (Philbrick et al. 2004a).

Three morphological characters occur only in taxa that resolved to clade J in our analyses, but these were not diagnostic for the entire clade. *Jenmaniella* and *Monostylis*, which ITS and combined data grouped together, both have a stalked ovary (gynophore) at anthesis. The gynophore is uncommon in Neotropical Podostemaceae, but it is found in *Cipoia* and *Diamantina* (Philbrick et al. 2004a), which were not included in our study. Phylogenetic analyses that included *Diamantina*, however, resolved it as sister to all other Podostemoideae (Ruhfel et al. in press). Several taxa from Africa notably also have a gynophore, e.g. species of *Angolaea* Wedd., *Dicraeanthus* Engl., *Leiothylax* Warm., and *Zehnderia* C. Cusset (cf. Cook and Rutishauser 2007). Two prominent characters are autapomorphic for single species in clade J. Specifically, the flattened, irregularly dentate stigma of *Lophogyne lacunosa* contrasts markedly with the linear stigmas of the other species, and the capsules of *Monostylis capillacea* are compressed, while those of other species are round to slightly oval in cross-section. Although clade J is well supported by molecular data, the absence of distinctive morphological synapomorphies makes it difficult for us to define or recognize it taxonomically. Moreover, five species of *Jenmaniella* were not included in our analysis, and their phylogenetic placement could affect the taxonomic disposition of clade J. Future studies should be undertaken with additional species (and a renewed morphological scrutiny) to further evaluate relationships within the clade.

Although interspecific relationships within clade J generally received poor support (Fig. 3), our results have at least provided new insights regarding several Neotropical genera. The anomalous placement of *Marathrum aeruginosum* indicates the polyphyletic nature of the genus *Marathrum* (see above). This result indicates that a phylogenetic investigation of the unsampled *Marathrum* species from South America (*M. azarensis*, *M. pauciflorum*, *M. squamosum*, and *M. striatifolium*) could yield further inconsistencies. Additionally, our analyses showed that the monotypic *Monostylis,* which has an upright stem (van Royen 1951; Philbrick and Bove, pers. obs.), is not a member of the *Apinagia* s. s. clade with upright stems (clade C; see above), although recent authors have considered these two genera synonymous (Cook and Rutishauser 2007). At this time we advocate the continued recognition of *Monostylis* as distinct from *Apinagia* and retain the generic name at least until the taxonomy of clade J has been settled more thoroughly.

Clade K (Lonchostephus and Mourera)—Clade K (Fig. 3) contained *Lonchostephus* and *Mourera*, two genera of tribe Mourereae (van Royen 1951), but lacked material of *Tulasneantha*, the third included genus. *Mourera* was established by Aublet (1775) who described *M. fluviatilis*, arguably the most conspicuous species of Podostemaceae, owing to its erect, two-sided, spike-like, monochasial inflorescence of showy, pink-purple flowers. Additional *Mourera* species were added subsequently by Tulasne (1849, 1852), Warming (1899), Bongard (1835), and van Royen (1953). Tulasne (1852) originally distinguished the monotypic *Lonchostephus elegans* on the basis of its broad, almost petal-like stamen filaments and cristate styles. Although van Royen (1953) followed Tulasne (1852) in recognizing *Lonchostephus*, Baillon (1888) transferred it to *Mourera*.

The two *Mourera* species represented in our study were not monophyletic, but resolved in a clade with two accessions of *Lonchostephus elegans*. *Lonchostephus* and *Mourera* are similar and share several morphological features, including a spike-like inflorescence, subtending floral bracts, and warty or prickly leaf projections (cf. Rutishauser 1997). In addition to their morphological similarity, these genera comprise a clade exhibiting substantial molecular divergence from other taxa and lack reciprocal monophyly (Fig. 3). Consequently, we recommend that *Lonchostephus* be merged under the generic name *Mourera*, for which the nomenclatural combination *Mourera elegans* (Tul.) Baillon has been provided previously (Baillon 1888).

The third genus included in tribe Mourereae by van Royen (1951) is the monotypic *Tulasneantha* (*T. monadelpha*). This species shares the two-sided, monochasial, spike-like inflorescence with *Lonchostephus* and *Mourera* (van Royen 1953). Because such an inflorescence is unique to Mourereae (and absent in other neo- and paleotropicical Podostemaceae), it represents a strong, unifying synapomorphy. Although *T. monadelpha* was not available for inclusion in our molecular

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data analyses, analysis of morphological data resolved it in a clade with *Lonchostephus* and *Mourera* (Fig. 1). We thus predict its molecular phylogenetic association with clade K and provide the necessary nomenclatural transfer below (see Taxonomic Treatment).

***Morphological Character Evolution*—**Phylogenetic relationships revealed by our analyses provide insight into the evolution of several morphological characters. Podostemaceae species have either upright or prostrate stems. Upright stems characterize the outgroup taxa *Podostemum*, *Tristicha*, and *Weddellina*, and also are common in several paleotropical taxa (e.g. *Angolea*, *Djinga* C. Cusset, *Endocaulos* C. Cusset, *Ledermanniella* Engl.). Our analyses reconstructed a single evolutionary transition to prostrate stem form at the basal node of the ingroup, from which upright stem morphology evolved independently on four branches (Fig. 3, arrows). About one-third of the species included in our study have an upright stem, including eight species of *Apinagia*, *Castelnavia multipartita* f. *pendulosa*, *Monostylis capillacea*, and *Oserya coulteriana*, whereas the remaining species have prostrate stems. All species of *Marathrum*, *Mourera*, and *Rhyncholacis* have prostrate stems, and stem form varies within the genera *Apinagia* (see below), *Castelnavia*, *Jenmaniella*, and *Oserya*. For *Jenmaniella*, only prostrate-stemmed species were available for inclusion in our study, and it remains to be determined where the upright-stemmed species (e.g. *Jenmaniella varians*) will resolve on the phylogeny.

All eight *Apinagia* s. s. species (clade C, Fig. 3) share upright stems. The remaining two *Apinagia* species included in our analyses (*A. fimbrifolia* and *A. nana*) have prostrate stems, and each occurred in a different location in the phylogeny. The grouping of upright-stemmed species partially supports the infrageneric classification of Tulasne (1849, 1852), who divided *Apinagia* into three sections based, in part, on whether stems were prostrate (thalloid) or upright. Section *Apinagia* Tul. (= *Euapinagia*; van Royen 1951) had species with prominent, upright, branched stems, section *Chamaelacis* Tul. had stems that were short and upright or prostrate, and section *Hymenolacis* Tul. had prostrate stems. Van Royen (1951) also recognized three sections, but he characterized those using markedly different criteria, i.e. rib number per capsule and the nature of anther dehiscence (introrse or extrorse). Under his treatment, sections *Apinagia* (0–8 ribs per capsule) and *Hymenolacis* (1–14 ribs per capsule) were characterized by introrsely dehiscing anthers, and section *Wentia* P. Royen had extrorsely dehiscing anthers. Our analyses failed to support the sectional classification of van Royen (1951), perhaps due to evolutionary lability in anther dehiscence, which in other plants often correlates with the breeding system (i.e. introrse dehiscence with autogamy and extrorse dehiscence with xenogamy; Ornduff 1969). The resolution of *Apinagia* s. s. in our analysis (clade C) supports the monophyly of section *Apinagia* as defined by Tulasne (1849, 1852), but not as modified by van Royen (1951).

The phylogenetic study of Neotropical Podostemaceae is far from complete. Our study accounted for only about one-quarter of the total species, and studies that increase species representation from such complex genera as *Apinagia*, *Marathrum*, and *Rhyncholacis* will no doubt elucidate additional phylogenetic patterns not identified here. Only after such studies are addressed will it be possible to obtain a classification of Neotropical Podostemaceae that truly reflects natural evolutionary groupings.

Taxonomic Treatment

Castelnavia pendulosa (C. T. Philbrick & C. P. Bove) C. T. Philbrick & C. P. Bove, stat. nov. *Castelnavia multipartita* forma *pendulosa* C. T. Philbrick & C. P. Bove, Syst. Bot. 34: 726–727. 2009.—TYPE: BOLIVIA. Santa Cruz: Velasco, Parque Nacional Noel Kempff Mercado, 13°46′S, 60°59′W, 24 Apr 1993, *Killeen et al. 5454* (holotype: MO!).

Marathrum plumosum (Novelo & C. T. Philbrick) C. T. Philbrick & C. P. Bove, comb. nov. *Vanroyenella plumosa* Novelo & C. T. Philbrick, Syst. Bot. 18: 66. 1993.—TYPE: MÉXICO. Jalisco: Puente Los Horcones sobre el río, 6 Feb 1991, *Novelo 981* (holotype: MEXU; isotype: RSA-POM).

Mourera monadelpha (Bong.) C. T. Philbrick & C. P. Bove, comb. nov. *Lacis monadelpha* Bong., Mém. Acad. Imp. Sci. Saint-Pétersbourg, sér. 6, Sci. Math., Seconde Pt. Sci. Nat. iii. II. 78. 1835. *Tulasneantha monadelpha* (Bong.) P. Royen, Acta Bot. Neerl. 2: 17. 1953.—TYPE: BRAZIL. Pará: Rio Madeira, *Riedel 1268* (holotype: LE; isotypes: B, G, P, U).

Noveloa C. T. Philbrick, gen. nov.—TYPE: *Oserya coulteriana* Tul., Ann. Sci. Nat., Bot. sér. 3, 11: 106. 1849. ≡ *Noveloa coulteriana* (Tul.) C. T. Philbrick.

Oseryae simillima, sed foliis dichotomis subdichotomisve divisis, staminibus 1–3, et capsulibus cum costis nonsuturalibus 6 differt.

Annual or perennial, small herbs. Roots elongate, prostrate, flattened. Stems arising laterally along roots, opposite or subopposite, prostrate or upright. Leaves distichous, petiole cylindrical or flattened, winged or wing absent, blade repeatedly dichotomously or subdichotomously divided. Flowers hermaphroditic, zygomorphic, pedicellate, borne singly, axillary, covered by a sac-like spathella. Spathella clavate. Tepals 2–4, scale-like. Stamens 1–3, deciduous, anthers basifixed, dehiscing extrorsely or latrorsely; stamen filaments fused for about half their length. Pollen in monads. Ovary 2-locular, with 2 unequal carpels. Stigmas 2, free or basally fused, conical; ovules numerous, placenta axile. Capsules 2-locular, with 2 unequal valves, one valve sometimes caducous, with 3 nonsuture ribs per valve, suture margins also rib-like. Seeds 0–85 per capsule (mean 32 ± SD 22, n = 55).

Noveloa is differentiated from the related genus *Oserya* by its dichotomous or subdichotomous leaf divisions (pinnate in *Oserya*), three nonsuture ribs per capsule valve (five in *Oserya*), and stamens numbering 1–3 (flowers unistaminate in *Oserya*).

The name of the genus is in honor of Dr. Alejandro Novelo Retana (1951–2006), who played an important role in advancing the understanding of aquatic angiosperms in Mexico and Neotropical Podostemaceae.

Noveloa coulteriana (Tul.) C. T. Philbrick, comb. nov. *Oserya coulteriana* Tul., Ann. Sci. Nat. Bot. sér. 3, 11: 106. 1849.—TYPE: MÉXICO. Jalisco: near San Blas, *Coulter 1394* (holotype: K!; isotype: NY!).

Noveloa longifolia (Novelo & C. T. Philbrick) C. T. Philbrick, comb. nov. *Oserya longifolia* Novelo & C. T. Philbrick, Novon 5: 54. 1995.—TYPE: MÉXICO. Jalisco: la Huerta, rio Purificacion, 26 Mar 1993, *Novelo & Philbrick 1166* (holotype: MEXU!; isotypes: MO!, NY!, WCSU!).

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– Ministério do Meio Ambiente, dos Recursos Hídricos e da Amazônia Legal). Materials were collected in Suriname with a permit from the Suriname Forest Service and the Nature Conservation Division. This work was supported by a National Science Foundation Grant DEB-0444589 and Connecticut State University-AAUP research grants to C. T. P., and by a Produtividade em Pesquisa Grant (2009-2011: proc. 307073/2008-4) from the Conselho Nacional de Desenvolvimento Científico e Tecnológico – Ministério de Ciência e Tecnologia (CNPq-MCT) to C. P. B. The authors thank the following people who provided valuable assistance in planning and conducting field studies: Arturo Mora (Mexico); Sibitrie Jairam-Doerga, Iwan E. Molgo (Suriname); George Pilz (Honduras); Carlos Lasso and Arnaldo Ferrer P., Fundación La Salle de Ciencias Naturales, Caracas (Venezuela); Dana Ramey (Honduras). The following WCSU undergraduate students provided valuable assistance in field studies: Thomas Edson, Christofer Fort, David Gera, and Stephanie Tucci. We also thank Brad Ruhfel and two anonymous reviewers for helpful comments on earlier drafts of the manuscript.

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Appendix 1. Voucher specimens for accessions cited in this study. Accession numbers in parentheses correspond to those depicted on phylogenetic trees (Figs. 2–3). Locality and voucher information is followed by GenBank accession numbers for ITS, *rbcL*, and *trnL*, respectively (— = not sequenced). Asterisks (*) indicate previously published sequences that were retrieved from GenBank.

'Autana'. **Venezuela. Amazonas: Autana River**, 04°48′08″N, 67°29′10″W, 5 Jan 2006, **(1)** *Philbrick et al. 5860* (MEXU, VEN, WCSU), HM470255, HM470377, HM470445; 04°45′57″N, 67°27′23″W, 5 Jan 2006, **(2)** *Philbrick et al. 5862* (MEXU, VEN, WCSU), HM470256, HM470378, HM470446; **Cataniapo River**, 05°36′12″N, 67°35′37″W, 9 Jan 2006, **(3)** *Philbrick et al. 5875* (MEXU, VEN, WCSU), HM470258, HM470380, HM470448; **Cuao River**, 05°02′39″N, 67°33′37″W, 7 Jan 2006, **(4)** *Philbrick et al. 5867* (MEXU, VEN, WCSU), HM470257, HM470379, HM470447.

Apinagia Tul.: ***A. corymbosa*** (Tul.) Engl. **Brazil. Goiás: Almas River**, 15°18′09″S, 49°34′20″W, 5 Jun 2005, **(1)** *Philbrick et al. 5819* (MEXU, R, WCSU), HM470259, HM470381, HM470449; **São Patrício River**, 15°00′11″S, 49°24′51″W, 5 Jun 2005, **(2)** *Philbrick et al. 5821* (MEXU, R, WCSU), HM470260, —, —. **Mato Grosso:** 15°36′10″S, 56°12′14″W, 17 Jul 2006, **(3)** *Philbrick et al. 5960* (R, WCSU), HM470262, HM470382, HM470451. **Tocantins: Lajeado River**, 09°46′09″S, 48°20′57″W, 7 Jun 2005, **(4)** *Philbrick et al. 5823* (MEXU, R, WCSU), HM470261, —, HM470450. ***A. fimbrifolia*** P. Royen. **Brazil. Tocantins: Balsas River**, 11°01′04″S, 47°29′06″W, 27 Jul 2006, *Philbrick et al. 6004* (R, WCSU), HM470263, HM470383, HM470452. ***A. fluitans*** P. Royen. **Brazil. Mato Grosso: Aripuanã River**, 10°09′51″S, 59°27′13″W, 23 Sep 2007, *Bove et al. 1896* (R, WCSU), HM470264, HM470384, HM470453. ***A. longifolia*** (Tul.) P. Royen. **Brazil. Roraima: Amajarí River**, 03°50′05″N, 61°28′15″W, 10 Oct 2008, **(1)** *Bove et al. 1954* (R, WCSU), HM470269, —, HM470458; **Anauã River**, 01°08′19″N, 60°19′28″W, 14 Oct 2008, **(2)** *Bove et al. 1975* (R, WCSU), HM470270, —, HM470459; **Branco River**, 01°55′45″N, 61°00′09″W, 8 Oct 2008, **(3)** *Bove et al. 1950* (R, WCSU), HM470266, —, HM470455; 01°55′19″N, 61°00′33″W, 9 Oct 2008, **(4)** *Bove et al. 1951* (R, WCSU), HM470267, HM470385, HM470456; 01°57′08″N, 60°55′34″W, 9 Oct 2008, **(5)** *Bove et al. 1952* (R, WCSU), HM470268, —, HM470457; **Jauaperí River**, 00°28′55″N, 60°29′55″W, 7 Oct 2008, **(6)** *Bove et al. 1943* (R, WCSU), HM470265, —, HM470454. **Venezuela. Bolivar: Caura River**, 06°53′60″N, 64°50′07″W, 9 Jan 2007, **(7)** *Philbrick et al. 6016A* (VEN, WCSU), HM470271, —, HM470460; 06°53′60″N, 64°50′07″W, 9 Jan 2007, **(8)** *Philbrick et al. 6016B* (VEN, WCSU), HM470272, —, HM470461; 06°28′15″N, 64°45′59″W, 10 Jan 2007, **(9)** *Philbrick et al. 6020* (VEN, WCSU), HM470273, —, HM470462; 06°19′31″N, 64°31′36″W, 10 Jan 2007, **(10)** *Philbrick et al. 6023* (VEN, WCSU), HM470274, HM470386, HM470463; 06°19′31″N, 64°31′36″W, 10 Jan 2007, **(11)** *Philbrick et al. 6024* (VEN, WCSU), HM470275, —, HM470464. ***A. nana*** Went. **Suriname. Sipaliwini: Lucie River**, 03°33′54″N, 57°29′04″W, 20 Oct 2007, **(1)** *Philbrick et al. 6180* (BBS, WCSU), HM470277, HM623456, —; **Suriname River**, 04°13′28″N, 55°26′24″W, 28 Oct 2007, **(2)** *Philbrick et al. 6222* (BBS, WCSU), HM470278, HM623457, —. **Venezuela. Amazonas: Ventuari River**, 05°03′06″N, 65°37′29″W, 9 Mar 2009, **(3)** *Philbrick et al. 6322* (VEN, WCSU), HM470279, HM470388, HM470466; **Bolivar: Caura River**, 06°28′15″N, 64°45′59″W, 10 Jan 2007, **(4)** *Philbrick et al. 6022* (VEN, WCSU), HM470276, HM470387, HM470465. ***A. rangiferina*** P. Royen. **Brazil. Mato Grosso: Araguaia River**, 16°11′33″S, 52°33′02″W, *Philbrick et al. 5579* (WCSU), DQ397958*, —, —. ***A. richardiana*** (Tul.) P. Royen. **Brazil. Roraima: Caroebe River**, 00°52′28″N, 59°39′50″W, 13 Oct 2008, **(1)** *Bove et al. 1971* (R, WCSU), HM470282, —, HM470469; 00°52′28″N, 59°39′50″W, 13 Oct 2008, **(2)** *Bove et al. 1972* (R, WCSU), HM470283, —, HM470470; **Jauaperí River**, 00°28′55″N, 60°29′55″W, 7 Oct 2008, **(3)** *Bove et al. 1945* (R, WCSU), HM470280, —, HM470467; **Jauarí River**, 03°45′28″N, 60°59′50″W, 10 Oct 2008, **(4)** *Bove et al. 1956* (R, WCSU), HM470281, HM470389, HM470468. **Suriname. Sipaliwini: Lawa River**, 04°19′23″N, 54°23′32″W, 3 Nov 2007, **(5)** *Philbrick et al. 6257* (BBS, WCSU), HM470290, —, HM470476; **Lucie River**, 03°33′54″N, 57°29′04″W, 20 Oct 2007, **(6)** *Philbrick et al. 6177* (BBS, WCSU), HM470285, —, —; **Suriname River**, 04°01′28″N, 55°28′04″W, 27 Oct 2007, **(7)** *Philbrick et al. 6208* (BBS, WCSU), HM470286, HM470391, HM470472; 04°22′53″N, 55°23′23″W, 30 Oct 2007, **(8)** *Philbrick et al. 6234* (BBS, WCSU), HM470287, —, HM470473; **Tapanahoni River**, 04°01′52″N, 54°47′58″W, 1 Nov 2007, **(9)** *Philbrick et al. 6242* (BBS, WCSU), HM470288, HM470392, HM470474; 04°07′32″N, 54°38′05″W, 2 Nov 2007, **(10)** *Philbrick et al. 6246* (BBS, WCSU), HM470289, HM470393, HM470475; **Zuid River**, 03°04′07″N, 56°29′01″W, 15 Oct 2007, **(11)** *Philbrick et al. 6144* (BBS, WCSU), HM470284, HM470390, HM470471. ***A. riedelii*** Tul. **Brazil. Pará: unspecified river**, 08°03′50″S, 49°57′56″W, 10 Jun 2005, **(1)** *Philbrick et al. 5841* (MEXU, R, WCSU), HM470292, —, HM470478; **Tocantins: Lontra River**, 06°33′40″S, 48°38′3″W, 24 Jul 2006, **(2)** *Philbrick et al. 5992* (R, WCSU), HM470293, HM470395, HM470479; **Taquassu River**, 10°18′21″S, 48°10′18″W, 8 Jun 2005, **(3)** *Philbrick et al. 5831* (MEXU, R, WCSU), HM470291, HM470394, HM470477. ***A. staheliana*** (Went) P. Royen. **Brazil. Pará: São Benedito River**, 09°03′11″S, 56°35′07″W, 18 Sep 2007, **(1)** *Bove et al. 1868* (R, WCSU), HM470295, —, HM470482. **Suriname. Sipaliwini: Corentyne River**, 03°27′17″N, 57°37′55″W, 22 Oct 2007, **(2)** *Philbrick et al. 6191* (BBS, WCSU), HM470299, —, HM470486; 03°27′17″N, 57°37′55″W, 22 Oct 2007, **(3)** *Philbrick et al. 6192* (BBS, WCSU), HM470300, —, HM470487; 03°32′51″N, 57°38′43″W, 22 Oct 2007, **(4)** *Philbrick et al. 6197* (BBS, WCSU), HM470301, —, HM470488; **Lucie River**, 03°33′54″N, 57°29′04″W, 20 Oct 2007, **(5)** *Philbrick et al. 6176* (BBS, WCSU), HM470298, —, HM470485; **Suriname River**, 04°00′46″N, 55°28′31″W, 26 Oct 2007, **(6)** *Philbrick et al. 6199* (BBS, WCSU), HM470302, —, —; **Zuid River**, 03°11′46″N, 56°38′55″W, 16 Oct 2007, **(7)** *Philbrick et al. 6159* (BBS, WCSU), HM470296, HM470397, HM470483; 03°16′34″N, 56°44′18″W, 18 Oct 2007, **(8)** *Philbrick et al. 6171* (BBS, WCSU), HM470297, HM470398, HM470484. ***A. yguazuensis*** Chodat & Visch. **Argentina. Missiones: Iguazu Rive**r, 25°41′09″S, 54°26′49″W, 9 Jan 1996, *Tur et al. 2122* (LP, MEXU, WCSU), DQ397951*, U68083*, —. ***Apinagia*** **sp. Venezuela. Amazonas: Ventuari River**, 05°03′06″N, 65°37′29″W, 9 Mar 2009, **(1)** *Philbrick et al. 6320* (VEN, WCSU), HM470294, HM470396, HM470480; 05°03′06″N, 65°37′29″W, 9 Mar 2009, **(2)** *Philbrick et al. 6321* (VEN, WCSU), HM623458, —, HM470481.

Castelnavia Tul. & Wedd. ***C. fluitans*** Tul. & Wedd. **Brazil. Pará: Araguaia River**, 08°21′02″S, 49°16′36″ W, 10 Jun 2005, **(1)** *Philbrick et al. 5840* (MEXU, R, WCSU), HM470303, HM470399, HM470489; 06°23′16″S, 48°32′02″W, 24 Jul 2006, **(2)** *Philbrick et al. 5989* (R, WCSU), HM470304, —, HM470490. ***C. monandra*** Tul. & Wedd. **Brazil. Pará: Araguaia River**, 05°18′20″S, 48°55′43″ W, 13 Jun 2005, **(1)** *Philbrick et al. 5849* (MEXU, R, WCSU), HM470305, —, HM470491; 05°18′12″S, 48°56′13″W, 22 Jul 2006, **(2)** *Philbrick et al. 5982* (R, WCSU), HM470306, HM470400, HM470492. ***C. multipartita*** Tul. & Wedd. **f. *multipartita***. **Brazil. Goiás: São Patrício River**, 15°00′11″S, 49°24′51″W, 5 Jun 2005, **(1)** *Philbrick et al. 5820* (MEXU, R, WCSU), HM470307, —, HM470493; **Mato Grosso: Aripuanã River**, 10°9′58″S, 59°26′59″W, 23 Sep 2007, **(2)** *Bove et al. 1892* (R, WCSU), —, —, HM470494. ***C. multipartita*** **f. *pendulosa*** C. T. Philbrick & C. P. Bove. **Brazil. Mato Grosso: Aripuanã River**, 10°09′51″S, 59°27′13″W, 23 Sep 2007, **(1)** *Bove et al. 1894* (R, WCSU), HM470309, HM623461, —; **Teles Pires River**, 09°21′02″S, 56°46′41″W, 19 Sep 2007, **(2)** *Bove et al. 1871* (R, WCSU), HM470308, HM470401, HM470495. ***C. noveloi*** C. T. Philbrick & C. P. Bove. **Brazil. Tocantins: Taquarussu River**, 10°18′21″S, 48°10′18″W, 8 Jun 2005, *Philbrick et al. 5830* (MEXU, R, WCSU), HM470310, —, HM470496. ***C. princeps*** Tul. & Wedd. **Brazil. Mato Grosso: Nobres River**, 14°41′56″S, 56°21′56″W, 17 Jul 2006, **(1)** *Philbrick et al. 5966* (R, WCSU), HM470312, HM470402, HM470498; **Pará: Araguaia River**, 05°18′20″S, 48°55′43″W, 13 Jun 2005, **(2)** *Philbrick et al. 5850* (MEXU, R, WCSU), HM470311, —, HM470497.

Jenmaniella Engl. ***J. ceratophylla*** Engl. **Brazil. Pará: São Benedito River**, 09°03′11″S, 56°35′07″W, 18 Sep 2007, **(1)** *Bove et al. 1864* (R, WCSU), HM470313, HM470403, HM470499; 09°03′11″S, 56°35′07″W, 18 Sep 2007, **(2)** *Bove et al. 1866* (R, WCSU), HM470314, HM470404, HM470500. ***J. fimbriata*** P. Royen. **Brazil. Tocantins: Taquarussu River**, 10°18′18″S, 48°10′31″W, 9 Jun 2005, **(1)** *Philbrick et al. 5833* (MEXU, R, WCSU),

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HM470315, —, HM470501. **Suriname. Sipaliwini: Suriname River**, 04°00′57″N, 55°28′24″W, 26 Oct 2007, **(2)** *Philbrick et al. 6204* (BBS, WCSU), HM470318, HM470407, HM470504; **Zuid River**, 03°04′07″N, 56°29′01″W, 15 Oct 2007, **(3)** *Philbrick et al. 6147* (BBS, WCSU), HM470316, HM470405, HM470502; 03°12′17″N, 56°42′40″W, 16 Oct 2007, **(4)** *Philbrick et al. 6162* (BBS, WCSU), HM470317, HM470406, HM470503. **Venezuela. Amazonas: Ventuari River**, 04°00′13″N, 67°01′18″W, 6 Mar 2009, **(5)** *Philbrick et al. 6313* (VEN, WCSU), HM470319, HM470408, HM470505; 04°00′28″N, 66°58′53″W, 6 Mar 2009, **(6)** *Philbrick et al. 6314* (VEN, WCSU), HM470320, HM470409, HM470506.

Lonchostephus Tul. ***L. elegans*** Tul. **Brazil. Mato Grosso: Roosevelt River**, 09°09′52″S, 60°44′11″W, 25 Sep 2007, **(1)** *Bove et al. 1899* (R, WCSU), HM470322, HM470411, HM470508; **Pará: Araguaia River**, 05°18′28″S, 48°55′23″W, 22 Jul 2006, **(2)** *Philbrick et al. 5976* (R, WCSU), HM470321, HM470410, HM470507.

Lophogyne Tul. ***L. lacunosa*** (Gardner) C. P. Bove & C. T. Philbrick. **Brazil. Rio de Janeiro: Aldeia Velha River**, 11 May 2002, *Bove 1342* (R), HM470323, HM470412, HM470509.

Marathrum Bonpl. ***M. aeruginosum*** P. Royen. **Suriname. Sipaliwini: Suriname River**, 04°01′41″N, 55°27′43″W, 27 Oct 2007, **(1)** *Philbrick et al. 6214* (BBS, WCSU), HM470324, HM470413, HM470510. **Venezuela. Amazonas: Confluence of Orinoco and Ventuari Rivers**, 03°57′35″N, 67°05′54″W, 6 Mar 2009, **(2)** *Philbrick et al. 6309* (VEN, WCSU), HM470325, HM470414, HM470511; 03°57′42″N, 67°05′08″W, 6 Mar 2009, **(3)** *Philbrick et al.* 6312 (VEN, WCSU), —, HM623462, HM470512. ***M. foeniculaceum*** Humb. & Bonpl. **Costa Rica. Alajuela: Barranca River**, 10°07′22″N, 84°28′12″W, 13 Mar 2006, **(1)** *Philbrick et al. 5888* (INB, NHA, WCSU), HM470326, —, HM470513; **Cote River**, 10°38′40″N, 84°50′08″W, 14 Mar 2006, **(2)** *Philbrick et al. 5903* (INB, NHA, WCSU), HM470328, —, HM470515; **Guanacaste: Animas River**, 11°03′00″N, 85°35′11″W, 15 Mar 2006, **(3)** *Philbrick et al. 5911* (INB, NHA, WCSU), HM470329, —, HM470516; **Quequer River**, 10°30′13″N, 84°49′19″W, 14 Mar 2006, **(4)** *Philbrick et al. 5901* (INB, NHA, WCSU), HM470327, HM470415, HM470514; **Tempisquito River**, 10°47′21″N, 85°33′04″W, 15 Mar 2006, **(5)** *Philbrick et al. 5913* (INB, NHA, WCSU), HM470330, —, HM470517; **Heredia: San Ramon River**, 10°23′47″N, 84°07′28″W, 20 Mar 2006, **(6)** *Philbrick et al. 5947* (INB, NHA, WCSU), HM470331, —, HM470518. **Mexico. Jalisco: Horcones River**, 20°27′13″N, 105°17′24″W, 2 Dec 2007, **(7)** *Philbrick et al. 6262* (WCSU), HM470332, HM470416, HM470519; 20°28′52″N, 105°17′46″W, 3 Dec 2007, **(8)** *Philbrick et al. 6268* (WCSU), HM470335, HM470418, HM470522; **Juntas River**, 20°14′45″N, 105°18′42″W, 2 Dec 2007, **(9)** *Philbrick et al. 6265* (WCSU), HM470333, HM470417, HM470520; **Mismaloya River**, 20°31′57″N, 105°17′17″W, 3 Dec 2007, **(10)** *Philbrick et al. 6266* (WCSU), HM470334, —, HM470521; **Veranos River**, 20°29′13″N, 105°16′43″W, 4 Dec 2007, **(11)** *Philbrick et al. 6269B* (WCSU), HM470336, —, HM470523, **(12)** *Philbrick et al. 6271* (WCSU), HM470337, HM470419, HM470524; **Tabasco: Pedregal River**, 17°23′42″N, 93°39′44″W, 26 Apr 2000, **(13)** *Novelo & Philbrick 3978* (MEXU), DQ397955*, —, —; **Veracruz: unspecified river**, 19°21′23″N, 99°39′0″W, 28 Apr 2000, **(14)** *Novelo & Philbrick 3983* (MEXU), DQ397956*, —, —. **Honduras. Atlantida: Jilamito River**, 15°36′45″N, 87°19′54″W, 16 Apr 2008, **(15)** *Philbrick & Ramey 6293* (EAP, WCSU), HM470340, —, HM470527; **Comayagua: Churune River**, 14°36′06″N, 87°37′25″W, 18 Apr 2008, **(16)** *Philbrick & Ramey 6301* (EAP, WCSU), HM470341, —, HM470528; **Lima River**, 14°29′37″N, 87°47′23″W, 13 Apr 2008, **(17)** *Philbrick & Ramey 6282* (EAP, WCSU), HM470339, —, HM470526; **unspecified river**, 14°31′51″N, 87°49′40″W, 13 Apr 2008, **(18)** *Philbrick & Ramey 6280* (EAP, WCSU), HM470338, HM470420, HM470525; **GenBank: (19)** —, U68085*, —. ***M. oxycarpum*** Tul. **GenBank:** —, AJ402971*, —. ***M. tenue*** Liebm. **Costa Rica. San Jose: Chirripó Pacifico River**, 09°26′01″N, 83°37′42″W, 17 Mar 2006, **(1)** *Philbrick et al. 5926* (INB, NHA, WCSU), HM470342, HM470421, HM470529; **unspecified river**, 09°50′16″N, 84°11′13″W, 22 Mar 2006, **(2)** *Philbrick et al. 5957* (INB, NHA, WCSU), HM470343, HM470422, HM470530; **Puntarenas: Guacimal River**, 10°13′01″N, 84°51′03″W, 23 Mar 2006, **(3)** *Philbrick et al. 5958* (INB, NHA, WCSU), HM470344, —, HM470531. ***M. utile*** Tul. **Costa Rica. San Jose: Chirripó Pacifico River**, 09°27′19″N, 83°36′22″W, 17 Mar 2006, **(1)** *Philbrick et al. 5929* (INB, NHA, WCSU), HM470348, HM470424, HM470536. **Venezuela. Merida: Capazon River**, 08°49′18″N 71°27′15″W, 16 Jan 2006, **(2)** *Philbrick et al. 5887* (VEN, WCSU), HM470347, HM470423, HM470535; **Zulia: Negro River**, 10°02′59″N, 72°41′06″W, 12 Jan 2006, **(3)** *Philbrick et al. 5884* (VEN, WCSU), —, —, HM470532; 10°02′59″N, 72°41′06″W, 12 Jan 2006, **(4)** *Philbrick et al. 5885* (VEN, WCSU), HM470345, —, HM470533; **Yaza River**, 10°02′54″N, 72°42′57″W, 13 Jan 2006, **(5)** *Philbrick et al. 5886* (VEN, WCSU), HM470346, —, HM470534.

Monostylis Tul. ***M. capillacea*** Tul. **Brazil. Mato Grosso: Apiacás River**, 09°17′59″S, 57°04′05″W, 21 Sep 2007, **(1)** *Bove et al. 1883* (R, WCSU), HM470351, HM470425, HM470539; **Aripuanã River**, 10°09′51″S, 59°27′13″W, 23 Sep 2007, **(2)** *Bove et al. 1898* (R, WCSU), HM470352, HM470426, HM470540; **Tocantins: Lajeado River**, 09°50′09″S, 48°17′38″W, 7 Jun 2005, **(3)** *Philbrick et al. 5825* (MEXU, R, WCSU), HM470349, —, HM470537; **Taquarussu River**, 10°18′21″S, 48°10′18″W, 8 Jun 2005, **(4)** *Philbrick et al. 5832* (MEXU, R, WCSU), HM470350, —, HM470538.

Mourera Aubl. ***M. aspera*** Tul. **GenBank:** —, U68086*, —. ***M. fluviatilis*** Aubl. **Brazil. Roraima: Amajarí River**, 03°50′05″N, 61°28′15″W, 10 Oct 2008, **(1)** *Bove et al. 1955* (R, WCSU), HM470354, HM470428, HM470542; **Jauaperí River**, 00°28′55″N, 60°29′55″W, 7 Oct 2008, **(2)** *Bove et al. 1944* (R, WCSU), HM470353, HM470427, HM470541. **Suriname. Sipaliwini: Zuid River,** 03°04′07″N, 56°29′01″W, 15 Oct 2007, **(3)** *Philbrick et al. 6146* (BBS, WCSU), HM470355, —, HM470543; **GenBank: (4)** —, AB113759*, —. ***M. weddelliana*** Tul. **Brazil. Pará: São Benedito River**, 09°02′01″S, 56°38′24″W, 18 Sep 2007, **(1)** *Bove et al. 1870* (R, WCSU), HM470357, HM470430, HM470545; **Tocantins: Balsas River**, 11°01′04″S, 47°29′06″W, 27 Jul 2006, **(2)** *Philbrick et al. 6001* (R, WCSU), HM470356, HM470429, HM470544.

Oserya Tul. & Wedd. ***O. coulteriana*** Tul. **Mexico. Colima: Hermenegildo River**, 19°18′12″N, 104°09′04″W, 25 Mar 2009, **(1)** *Philbrick et al. 6345* (UAT, WCSU), —, HM623460, HM470549; **Jalisco: Horcones River**, 20°27′12″N, 105°17′24″W, 2 Dec 2007, **(2)** *Philbrick et al. 6263* (WCSU), HM470358, HM470431, HM470546; **Marabasco River**, 19°24′57″N, 104°18′14″W, 25 Mar 2009, **(3)** *Philbrick et al. 6343* (UAT, WCSU), HM470360, HM470433, HM470548; **Nayarit: Llano River**, 21°25′34″N, 105°11′04″W, 22 Mar 2009, **(4)** *Philbrick et al. 6329* (UAT, WCSU), HM470359, HM470432, HM470547; **GenBank: (5)** —, U68087*, —. ***O. longifolia*** Novelo & C. T. Philbrick. **Mexico. Jalisco: Purification River**, 19°29′46″N, 104°40′23″W, 24 Mar 2009, **(1)** *Philbrick et al. 6340* (UAT, WCSU), HM470361, HM470434, HM470550; 19°30′00″N, 104°40′05″W, **(2)** *Philbrick & Novelo 3235* (MEXU, WCSU), DQ397957*, —, —. ***O. perpusilla*** (Went) P. Royen. **Brazil. Roraima: Jauaperí River**, 00°28′55″N, 60°29′55″W, 7 Oct 2008, **(1)** *Bove et al. 1946* (R, WCSU), HM470362, HM470435, HM470551. **Suriname. Sipaliwini: Lucie River**, 03°34′49″N, 57°35′41″W, 21 Oct 2007, **(2)** *Philbrick et al. 6190* (BBS, WCSU), HM470365, HM623459, —; **Zuid River**, 03°11′32″N, 56°38′31″W, 16 Oct 2007, **(3)** *Philbrick et al. 6157* (BBS, WCSU), HM470364, —, —. **Venezuela. Bolivar: Rio Caura**, 06°28′15″N, 64°45′60″W, 10 Jan 2007, **(4)** *Philbrick et al. 6021* (VEN, WCSU), HM470363, HM470436, HM470552.

Podostemum Michx. ***P. ceratophyllum*** Michx. **Honduras. Comayagua: Calan River**, 14°34′34″N, 87°50′20″W, 13 Apr 2008, **(1)** *Philbrick & Ramey 6285* (EAP, WCSU), HM470367, HM470438, HM470554. **U. S. A. Connecticut: Pootatuck River**, 41°25′14″N, 73°16′58″W, 31 May 2007, **(2)** *Philbrick 6061* (WCSU), HM470366, HM470437, HM470553. **GenBank: (3)** —, U68088*, —.

Rhyncholacis Tul. ***R. applanata*** K. I. Goebel. **Venezuela. Bolivar: Paragua River**, 06°18′07″N, 63°37′22″W, 14 Jan 2007, *Philbrick et al. 6046* (VEN, WCSU), HM470368, HM470439, HM470555. ***R. penicillata*** Matthiesen. **Venezuela. Bolivar: Carrao River**, 06°14′58″N, 62°50′47″W, 15 Jan 2007, **(1)** *Philbrick et al. 6052* (VEN, WCSU), HM470369, HM470440, HM470556; 06°14′58″N, 62°50′47″W, 15 Jan 2007, **(2)** *Philbrick et al. 6052A* (VEN, WCSU), HM470370, —, HM470557; 06°18′08″N, 62°52′16″W, 15 Jan 2007, **(3)** *Philbrick et al. 6053* (VEN, WCSU), HM470371, HM470441, HM470558; 06°14′48″N, 62°50′48″ W, 18 Jan 2007, **(4)** *Philbrick et al. 6060* (VEN, WCSU), HM470372, —, HM470559.

Tristicha Thouars. ***T. trifaria*** (Bory ex Willd.) Spreng. **Brazil. Pará: São Benedito River**, 09°03′11″S, 56°35′07″W, 18 Sep 2007, *Bove & Philbrick 1869* (R, WCSU), HM470373, HM470442, HM470560.

Vanroyenella Novelo & C. T. Philbrick. ***V. plumosa*** Novelo & C. T. Philbrick. **Mexico. Jalisco: Horcones River**, 20°27′12″N, 105°17′24″W, 2 Dec 2007, **(1)** *Philbrick et al. 6264* (WCSU), HM470374, HM470443, HM470561. **GenBank: (2)** —, U68090*, —.

Weddellina Tul. ***W. squamulosa*** Tul. **Brazil. Tocantins: Lajeado River**, 09°45′28″S, 48°21′47″W, 7 Jun 2005, **(1)** *Philbrick et al. 5827* (R, WCSU), HM470375, —, HM470562. **Venezuela. Amazonas: Cuao River**, 05°02′07″S, 67°33′06″W, 7 Jan 2006, **(2)** *Philbrick et al. 5870* (VEN, WCSU), HM470376, HM470444, HM470563.

Appendix 2. Morphological characters and states that were scored for taxa in this study (see Supplemental Appendix 1).

1. Roots: 0 = absent, 1 = present. **2. Stem orientation:** 0 = prostrate (multiple attachment points along length), 1 = upright/pendant (single attachment point). **3. Upright stem form:** 0 = linear (cylindrical), 1 = thalloid (flattened). **4. Prostrate stem form:** 0 = linear thalloid, 1 = flattened. **5. Leaf base relative to stem:** 0 = narrow attachment point, 1= sheathing (amplexicaul). **6. Stipules:** 0 = absent, 1 = present. **7. Leaf type (mature leaves):** 0 = simple (lamina not divided to midrib; entire or lobed), 1 = compound (lamina divided to midrib), 2 = ramulus. **8. Simple leaf type margin:** 0 = entire, 1 = lobed or lobulate, 2 = pinnately lobed, 3 = apically lobed.

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9. Dichotomous filamentous segments located at lobes of simple (lobed) leaves: 0 = absent, 1= present. **10. Type of compound (divided) mature leaf:** 0 = dichotomous or subdichotomous, 1 = pinnate, 2 = plumose. **11. Circinate leaf development:** 0 = absent, 1 = present. **12. Leaf petiole (narrowed, terete):** 0 = absent, 1 = present. **13. Petioles:** 0 = wingless, 1 = winged (oval to rounded with flattened, extended margins). **14. Upper leaf surface:** 0 = smooth, 1 = with projections. **15. Upper leaf surface projections:** 0 = tufts of filaments, 1 = warts, 2 = prickles. **16. Spathella:** 0 = absent, 1 = present. **17. Flower grouping:** 0 = solitary, 1 = clusters (two or more arising together), 2 = spike-like monochasium. **18. Inflorescence:** 0 = sessile, 1 = pedunculate. **19. Pedicel orientation relative to spathella axis:** 0 = straight or nearly so, 1 = pedicel apex curved and fused laterally to ovary base. **20. Flower position at anthesis:** 0 = enclosed within ruptured spathella, 1 = projecting from ruptured spathella. **21. Flower orientation at anthesis:** 0 = vertical, 1 = horizontal. **22. Floral bracts:** 0 = absent, 1 = present. **23. Pedicel apex:** 0 = not inflated, 1 = inflated asymmetrically. **24. Scale tepal shape:** 0 = linear or subulate, 1 = short and triangular. **25. Andropodium:** 0 = absent, 1 = present. **26. Stamen position:** 0 = encircling ovary, 1 = restricted to one side of ovary. **27. Number of stamen whorls per flower:** 0 = 1, 1 = 2. **28. Stamen filament:** 0 = free from tepals, 1 = fused to tepals. **29. Stamen filament texture:** 0 = membranous, 1 = indurate after anthesis. **30. Anther shape:** 0 = parallel sides with thecae apices free, 1 = triangular (thecae divergent at base) with thecae apices fused. **31. Pollen:** 0 = monad, 1 = dyad. **32. Gynophore:** 0 = absent, 1 = present. **33. Carpel number:** 0 = 2, 1 = 3. **34. Carpel symmetry:** 0 = isolobous (symmetrical), 1 = anisolobous (asymmetrical). **35. Locule number:** 0 = 1, 1 = 2, 2 = 3. **36. Papillae near apex of ovary:** 0 = absent, 1 = present. **37. Stigma form:** 0 = linear, 1 = fan-shaped, 2 = capitate. **38. Stigma margin type:** 0 = entire, 1 = irregularly dentate. **39. Fruiting pedicel apex:** 0 = not inflated and hollow, 1 = inflated and hollow. **40. Capsule shape:** 0 = cylindrical, 1 = laterally compressed. **41. Capsule axis orientation relative to pedicel axis:** 0 = parallel to pedicel, 1 = 30-45° angle, 2 = ca. 90° angle. **42. Ribs on mature capsule:** 0 = absent (smooth), 1 = present (ribbed). **43. Capsule wing:** 0 = absent, 1 = present. **44. Capsule valves:** 0 = persistent, 1 = one deciduous. **45. Capsule compression type:** 0 = compressed parallel to septum, 1 = compressed perpendicular to septum.

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