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A Phylogeny of the Tropical Genus *Piper* Using ITS and the Chloroplast Intron *psbJ–petA*

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Abstract—*Piper* is one of the largest genera of flowering plants. The uniformity of its small flowers and the vast number of species in the genus has hindered the development of a stable infrageneric classification. We sampled 575 accessions corresponding to 332 species of *Piper* for the ITS region and 181 accessions for the *psbJ–petA* chloroplast intron to further test previous hypotheses about the major clades within *Piper*. Phylogenetic analyses were performed for each marker separately and in combination. The ITS region alone resolves eleven major clades within *Piper*, whereas the *psbJ–petA* intron fails to recover four of these major groupings and provides no resolution at the base of the phylogeny. The combined analysis provides support for ten monophyletic groups and offers the best hypothesis for relationships in *Piper*. Our massive ITS dataset allows us to assign confidently a large number of species in this "giant" genus to a major clade. *Piper* is here divided into ten major clades for which we provide a morphological description. Various clades and subclades are newly identified here: *Peltobryon, Schilleria, Isophyllon, P. cinereum/P. sanctum*. The clades described here provide a solid framework for future, and more focused, evolutionary studies. New names and combinations proposed herein include ***Piper bullulatum***, ***P. hooglandii***, and ***P. melchior***.

Keywords—black-pepper, giant genus phylogeny, Piperaceae.

Piper, with ~2,000 species (Quijano-Abril et al. 2006), is one of the 20 most species rich genera of flowering plants (Frodin 2004). The monophyly of this large genus has been confirmed by molecular phylogenetic analyses of the Piperales (Jaramillo et al. 2004; Wanke et al. 2007; Smith et al. 2008). Monophyly has also been confirmed for other such large plant genera, for example *Astragalus* (Wojciechowski et al. 1999), *Solanum* (Weese and Bohs 2007), and *Croton* (Berry et al. 2005). Because of their large number of species, these "giant" genera present a great challenge, but also a wonderful opportunity to learn about the evolution of morphological characters and geographic distribution. In particular, *Piper* offers a unique opportunity to study the process of diversification in tropical forests. However, to make such investigations tractable, it is crucial to identify and describe smaller monophyletic assemblages within these large genera.

Piper species are shrubs, herbs, climbers, or treelets common in the understory of tropical forests around the world. *Piper* species are economically and ecologically important. *Piper* is the source of black-pepper (*Piper nigrum*) and various species of the genus are of ethnobotanical interest (Colvard et al. 2006). Plants of the genus *Piper* are easy to recognize in the field by their nodose shoots and perianthless flowers arranged in condensed terminal spikes. The apparent uniformity of *Piper* floral morphology and the vast number of species in the genus have hindered the development of a stable infrageneric classification (Table 1). The early classifications of Piperaceae, by Kunth (1839) and Miquel (1843–1844), recognized several distinct genera in what we accept as *Piper* today. Casimir de Candolle continued the study of Piperaceae and lumped many of the early genera into the large genus *Piper*, but he preserved some of Miquel's groupings at the level of section or subgenus (de Candolle 1869, 1923). de Candolle's classification would be followed in the Asian floristic treatments of the early 1900s (Ridley 1924; Quisumbing 1930). The next monographer of Piperaceae, William Trelease, would abandon the infrageneric classification of de Candolle. Trelease recognized a large and unstructured *Piper* along with several small segregates, some described by Miquel and others by himself. Trelease's generic concepts were followed by Yuncker and were largely accepted in the remainder of the 1900s. Callejas (1986), who conducted the first cladistic analysis of the genus using morphological characters, reconsidered the infrageneric groupings within *Piper*. Additionally, five sections/subgenera of Neotropical *Piper* have been revised recently (Bornstein 1989; Callejas 1986; Tebbs 1989, 1990, 1993a).

Molecular phylogenetics have been useful in identifying monophyletic groups within *Piper* (Jaramillo and Manos 2001; Jaramillo and Callejas 2004a, b; Tepe et al. 2004). These studies, based on exemplar sampling of *Piper*, confirmed the monophyly of some traditionally recognized infrageneric groups (i.e. *Macrostachys* Miquel, *Ottonia* Sprengel, *Enckea* Kunth, Miquel 1843–1844; de Candolle 1869, 1923), while suggesting the polyphyletic nature of other assemblages (i.e. *Steffensia* Miquel, *Trianaeopiper* Trelease). For the current study we increased the dataset in two ways: a) by a six-fold increase in sampling, providing a more thorough coverage of the overall distribution of *Piper*, and b) by adding sequence data for a second marker, the chloroplast marker *psbJ–petA*. This much larger dataset allows us to address the following specific objectives: 1) test the monophyly of the major clades identified in previous studies using a much smaller sampling; 2) determine the relationships of African species. This study provides strong support for ten major clades within *Piper*, new clades and subclades of Neotropical *Piper* are recognized, i.e. *Peltobryon* Klotzsch, *Schilleria* Kunth, *Isophyllon* Miquel, *P. cinereum/P. sanctum*. We provide a description of each clade and discuss the discrepancies with previous classifications.

Materials and Methods

Taxon Sampling—We sampled 575 accessions of 332 species of *Piper* for this study. This represents a six-fold increase sampling over previous studies of the genus. Taxa included here represent a broad geographical

TABLE 1. Summary of the taxonomic history of *Piper*. Genera are italized, subgenera and sections are underlined. Names across correspond to group equivalences among treatments. Horizontal lines correspond to clades examined here.

Kunth 1839	Miquel 1843–44, 1845	C. de Candolle 1869	C. de Candolle 1923	Trelease 1928-1950	Trealease and Yuncker 1950; Yuncker 1972, 1973	Callejas 1986	Tebbs 1993a, b
	Muldera	Schizonephos	Muldera			Muldera	
Piper	*Piper*	Eupiper	Eupiper	*Piper*	*Piper*	Piper	*Piper*
	Cubeba					Cubeba	
		Apopiper					
	Chavica					Chavica	
	Peltandron					Peltandron	
	Euchavica						
	Sphaerostachyon						
			Sarcostemon				
				Macropiper			
	Macropiper		Macropiper	*Anderssoniopiper*		Macropiper	*Macropiper*
	Coccobryon	Coccobryon	Coccobryon			Coccobryon	
Enckea	*Enckea*	Enckea	Enckea	*Discipiper*, *Lindeniopiper*		Enckea	
				Arctottonia	*Arctottonia*	Arctottonia	
	Callianira						
				Pleiostachyopiper			
Schilleria	*Sphaerostachys*					Schilleria	
Ottonia	*Ottonia*		Ottonia	*Ottonia*	*Ottonia*	Ottonia	Ottonia
						P. politii-complex	
Heckeria	*Pothomorphe*	Potomorphe	Heckeria	*Pothomorphe*	*Pothomorphe*	Pothomorphe	Lepianthes
						P. marginatum-complex	
	Peltobryon					Peltobryon	
						P. nudifolium-complex	
				Trianaeopiper	*Trianaeopiper*	Trianaeopiper	
Steffensia	*Artanthe*	Steffensia	Steffensia			Steffensia	
	Isophyllon					Isophyllon	
	Churumayu					Churumayu	Churumayu
	Radula					Radula	Radula
	Leiophyllon						
	Ottonioides						
	Nhandi						
	Saliuncae						
	Hymenophyllon						
	Nematanthera	Nematanthera	Nematanthera			Nematanthera	
	Rhyncholepis						
		Carpunya	Carpunya				
	Macrostachys					Macrostachys	Macrostachys
	Hemipodion					Hemipodion	
				Sarcorhachis (= *Manekia*)	*Sarcorhachis*	Sarcorhachis	*Sarcorhachis*
	Zippelia					Zippelia	*Zippelia*

sampling from the Neotropics and the Paleotropics, including Africa and the South Pacific. We have sampled most relevant taxonomic divisions using the major family treatments as a guide (Table 1). We sampled all generic segregates of Miquel's tribe Pipereae (Miquel 1843–1844), and the recent generic segregates of Trelease (Trelease 1928, 1929, 1930, 1934; Stehlé 1946), as well as de Candolle's subgenera (de Candolle 1923), de Candolle's sections (de Candolle 1869; with exception of *Nematanthera*) and Callejas' subgenera (Callejas 1986). The genera *Manekia* (=*Sarcorhachis*), and *Zippelia,* were traditionally recognized within the tribe Pipereae (Miquel 1843–1844) or the genus *Piper* (de Candolle 1923; Callejas 1986). However, molecular phylogenetics confirmed that these are distinct genera in the Piperaceae (Jaramillo et al. 2004; Wanke et al. 2007), thus they have been excluded from this study. We sequenced the ITS region for all accessions and the *psbJ–petA* intron for a representative subsample (181 accessions).

DNA Extraction, PCR, and Sequencing—DNA was extracted from fresh, silica-gel dried, or herbarium specimens using either a modified CTAB method (Doyle and Doyle 1987) or the DNAeasy Plant Mini kit (Qiagen, Valencia, California). The ITS region (including ITS1, 5.8S and ITS2) was amplified by polymerase-chain reaction (PCR) using one of three pairs of primers ITS5-ITS4, LEU1-ITS4 (Baldwin 1992; Baldwin 1993) or ITSA-ITSB (Blattner 1999). The *psbJ–petA* intron was amplified using primers petA-IGSF and psbJ-IGSF (designed by Linda Prince, Rancho Santa Ana Botanic Garden). PCR products were cleaned using the AccuPrep PCR purification kit (Bioneer Inc., Daejeon, South Korea), the QIAquick PCR purification kit (Qiagen Inc.), or the Promega Wizard SV Gel and PCR Clean-up kit (Promega Corp., Madison, Wisconsin). Sequencing was performed on AB1 377 or 3730xl automated sequencers (Applied Biosystems, Foster City, California) or a Li-Cor 4200 LongreadIR (Li-Cor Biosystems, Lincoln, Nebraska). Sequencing was done in several facilities: the Universidade Federal do Rio de Janeiro (Rio de Janeiro, Brazil), MACROGEN, Inc. (Seoul, Korea), Boise State University (Boise, Idaho), and the Center for Bioinformatics and Functional Genomics at Miami University (Oxford, Ohio).

Sequences were assembled in Sequencher (Gene Codes Corporation, Ann Arbor, Michigan) or Seqman (DNASTAR, Inc., Madison, Wisconsin) and deposited in GenBank (see Appendix 1). The ITS sequences were aligned manually using previous alignments as a reference (Jaramillo 2001). The *psbJ–petA* sequences were aligned using ClustalW (Thompson et al. 1994) and corrected manually. In the *psbJ–petA* alignment, we identified two randomly inverted stretches in positions 453–467 and 853–875. DNA folding predictions performed on the KineFold Server (http://

kinefold.curie.fr/) confirmed that these inverted regions correspond to DNA loops, explaining their random directions. Moreover, these inverted regions had identical sequences between distantly related species; therefore these regions were excluded prior to phylogenetic analyses. A combined dataset was assembled for all accessions for which both ITS and *psbJ–petA* were available. In the large ITS dataset we also incorporated previously published sequences obtained from GenBank.

Phylogenetic Analysis—Maximum parsimony analyses were carried out using TNT (Tree analysis using New Technology; Goloboff et al. 2004) using the full suite of "New Technology" analysis options available (i.e. sectorial search, ratchet, drift, and tree fusion) with 100 random addition sequences. TNT produces trees until the consensus tree reaches stability (Goloboff and Farris 2001). Bootstrap values for nodes were estimated using TNT from 5000 replicates using the default settings of sectorial search and the ratchet options of the New Technology analysis. Limitations of computer memory precluded implementation of all of the New Technology search options.

The best substitution model, for the likelihood based analyses, was selected using the Akaike information criterion (AIC) as implemented in MrModeltest 1.1b (Nylander 2003). Maximum likelihood analyses were carried out using Garli (Genetic Algorithm for Rapid Likelihood Inference; Zwickl 2006), default parameters were used for the Garli searches. Bootstrap values for nodes were estimated using Garli from 100 replicates using the default settings. Bayesian phylogenetic analyses were conducted using MrBayes v.3.1.2p (Huelsenbeck and Ronquist 2001). Both data sets were analyzed separately, and subsequently a combined analysis was conducted. For each dataset analyzed, we performed two runs of four chains of the Markov Chain Monte Carlo, sampling one tree every 1,000 generations, for 10 million generations. We discarded the results of the first 5 million generations. We pulled together the results from two independent runs, and a total of 10,002 trees were used to obtain 80% consensus topologies for each analysis. Trees are available at TreeBASE (study number S2188). Prior to combining ITS and cpDNA sequences an ILD test (Farris et al. 1994) was run, implemented as the partition homogeneity test (PHT) of PAUP*. As this test is often sensitive to low signal in some of the partitions (Reeves et al. 2001; Yoder et al. 2001), separate maximum parsimony bootstrap analyses were run for each of the partitions (cpDNA and ITS) to search for areas of hard incongruence (Seelanen et al. 1997).

RESULTS

ITS Data—The alignment of ITS sequences included 575 terminals and 844 aligned nucleotide sites, 556 sites were parsimoniously informative. ITS sequence divergence among *Piper* species ranged between 2.3–15.2%. The HKY + G model of DNA substitution was selected for the Bayesian and maximum likelihood analyses. This substitution model assumes a time-reversible process, a nonuniform distribution of nucleotides and different rates for transitions and transversions (HKY) and a discrete gamma approximation of the rate variation among sites (G). Maximum parsimony analysis recovered five most parsimonious trees. The topologies obtained using the three different methods were very similar (Fig. 1; Supplementary Fig. 1A–F). The analyses recovered three main lineages of distinct geographic distributions: Neotropics, Asian Tropics and the South Pacific. These main lineages comprise eleven major clades, the Neotropical lineage comprises nine of these major clades, the other two clades, *Piper* s.s. and *Macropiper* are each distributed in distinct geographical regions, Asian Tropics and the South Pacific Islands, respectively.

psbJ–petA Data—The alignment of the chloroplast *psbJ–petA* intron included 181 terminals and 930 nucleotide sites, of which 260 were parsimoniously informative. Sequence divergence for *psbJ–petA* ranged from 0.6–13.7%. The GTR + I + G model of nucleotide substitution was selected for the Bayesian analysis, which assumes general time reversibility (GTR), a proportion of invariable sites (I), and a discrete gamma approximation of the rate variation among sites (G). This analysis recovered seven major clades of *Piper* and a clear differentiation between New World and Old World taxa (not shown). Nevertheless, the *psbJ–petA* intron did not provide resolution at the base of the tree and failed to recover all of the major clades identified in the combined analysis (see below).

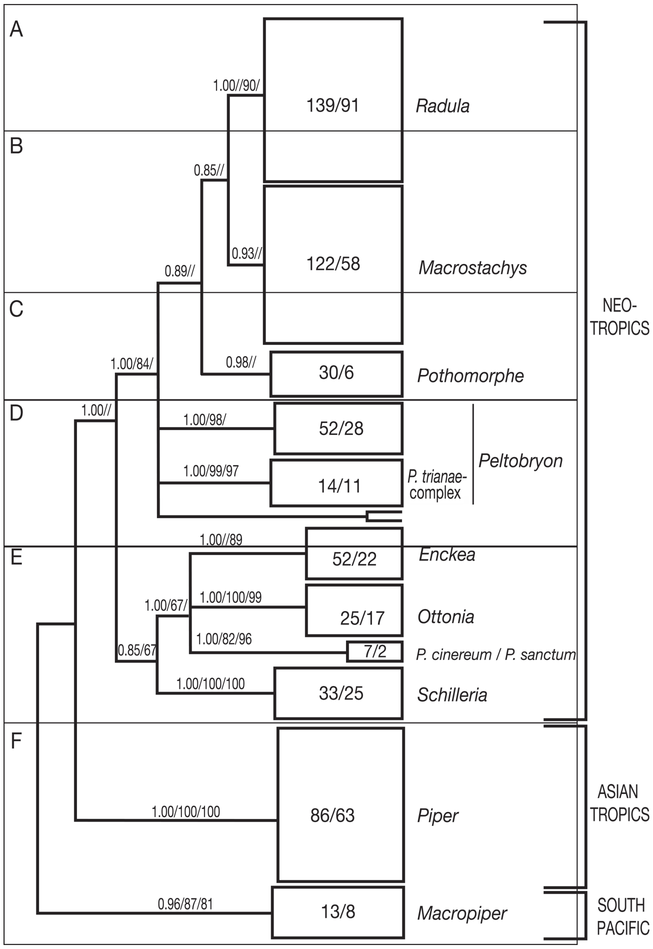

FIG. 1. Schematic diagram summarizing results of the ITS large dataset analysis. Numbers above branches are Bayesian posterior probabilities (B-PP), bootstrap values (>50% are shown) for maximum likelihood (BS-ML) and maximum parsimony (BS-MP) analyses (B-PP/BS-ML/BS-MP). Boxes are proportional to sampling for each clade; numbers within each box are accessions/species. Details for each portion of this phylogeny are found in Supplementary Fig. 1A —F.

Combined Analyses—The PHT indicated significant differences between the two partitions ($p = 0.01$). However, this is likely due to suboptimal trees being found in some of the data partitions where low signal did not result in strongly supported topologies. When examined separately, each partition did not exhibit any area of incongruence that had BS > 75. In fact, only two clades with BS > 50 showed any incongruence between trees and these were all between BS = 54 and 60. Since hard incongruence was not detected (Seelanen et al. 1997), we combined data.

The alignment for the combined dataset included 181 terminals and 1,715 nucleotide sites, 717 sites were parsimoniously informative. For this dataset the model of nucleotide substitution selected was HKY+G. Maximum parsimony analysis recovered eight most parsimonious trees. The topologies obtained using the three different methods were very similar. The Bayesian combined analysis provides strong support for the three main lineages: Neotropical, Asian Tropics, and South Pacific (Fig. 2). These main lineages comprise ten major clades. The Neotropical lineage can be subdivided into eight clades.

DISCUSSION

The results presented here provide strong support for three geographically distinct clades: Neotropical, Tropical Asian, and South Pacific (Figs. 1, 2). Species from Africa are nested within the *Piper* s.s clade (i.e. *P. guineense*, *P. borbonense*) and the *Macropiper* clade (i.e. *P. capense*). The major clades identified here largely correspond to traditional groupings described by Miquel (1843–1844) and recognized in earlier phylogenetic analyses (Jaramillo 2001; Jaramillo and Callejas 2004a, b). We use traditional names, when avail-

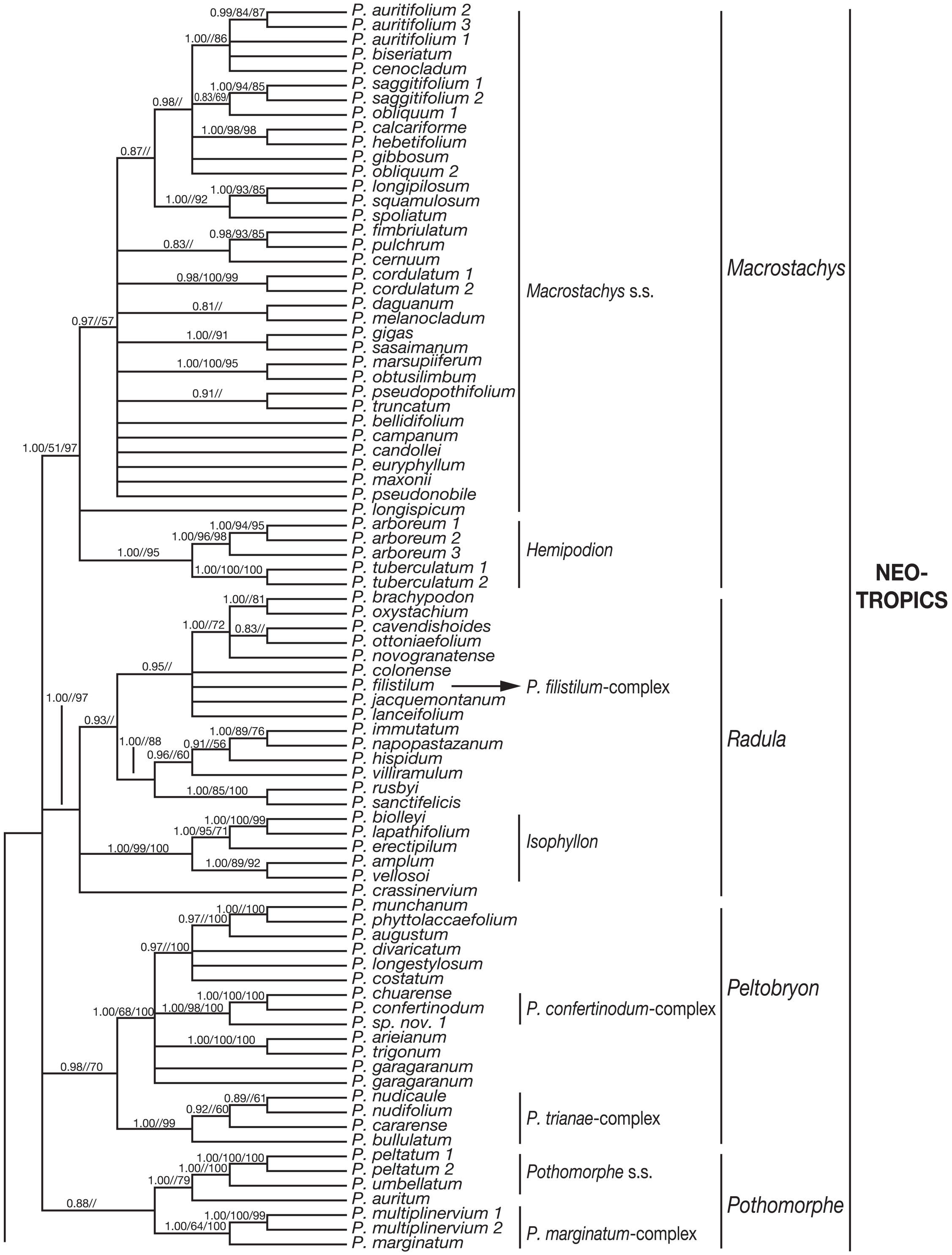

FIG. 2a. Eighty percent majority rule consensus of the Bayesian analysis of the concatenated data set of ITS and *psbJ —petA* intron. Numbers above branches are Bayesian posterior probabilities (B-PP), bootstrap values (>50% are shown) for maximum likelihood (BS-ML) and maximum parsimony (BS-MP) analyses (B-PP/BS-ML/BS-MP). Clade and subclade names correspond to those described in the Discussion. Members of *Arctottonia* are indicated with an asterisk. African species are indicated with an arrow.

able, for the clades obtained in the combined analysis. The current data support several of the clades and subclades identified previously (Jaramillo 2001), and provide evidence for recognition of new monophyletic groups that were previously unresolved (i.e. *Peltobryon, Schilleria, Isophyllon, P. cinereum/P. sanctum*).

Neotropical Piper—In the Neotropics, we can distinguish eight clades that correspond to the classification of Miquel

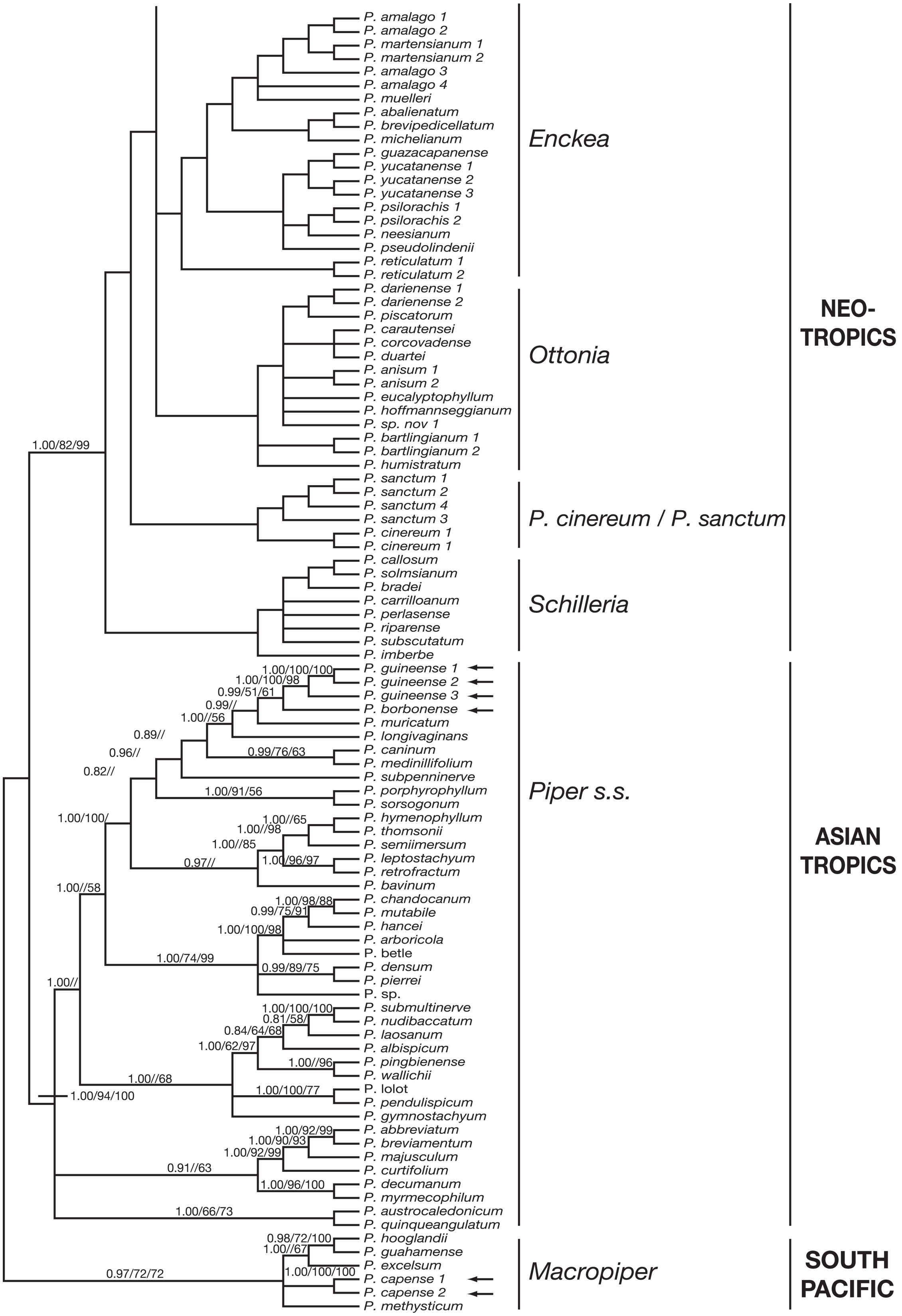

FIG. 2b. (Continued)

(1843–1844) and de Candolle (1869, 1923). Species of *Piper* from the Neotropics are mostly shrubs to small trees, but also climbers and small herbs; the flowers are always bisexual.

MACROSTACHYS MIQUEL—The *Macrostachys* clade, is a species rich lineage of Neotropical *Piper* with ~200–250 species. It is distributed throughout the Neotropics, but most species occur in Central America and the Northern Andes, a few species in the Amazon and a handful in the Atlantic Forest of Brazil. Species of this clade are medium-sized shrubs to small trees. Leaves are pinnately nerved and basally lobulate. The leaf base is symmetric on the monopodial trunk and asymmetric on sympodial branches, and the petioles exhibit a prominent stipular margin which often reaches into the base of the lamina. Inflorescences are compact with four-staminate flowers usually forming banding patterns. Inflorescences are often very long and pendulous. Fruits are free, and typically rectangular. This lineage is divided in the *Macrostachys* s.s. and the *Hemipodium* subclades (Fig. 2; Supplementary Fig. 1B, C). *Hemipodium* includes nearly 20 species, for the most part sun loving plants, much smaller in heigh than those in *Macrostachys*, with erect inflorescences and three staminate flowers, forming banding patterns, and the fruits are free and rectangular. Species of *Hemipodium* have strongly asymmetric leaf bases and petiolar margins extending to the base of the lamina at all nodes. *Hemipodium* includes several species of restricted distribution, i.e. also *Piper holtonii* C.DC., *P. savanense* C.DC, *P. corozolanum* Trelease, *Piper obumbratifolium* Trel, *P. obumbratum* (Miq.) C.DC., *P. olens* Trel. Large number os species have been lumped under *P. arboreum*, a species otherwise restricted to Eastern Amazonia.

Some members of *Macrostachys* exhibit a strong mutualism with ants of the genus *Pheidole* (Tepe et al. 2004, 2007a, b). *Macrostachys* and *Hemipodium* were first described as sections of Miquel's genus *Artanthe* (Miquel 1843–1844), but later lumped into de Candolle's section (de Candolle 1869) and subgenus (de Candolle 1923) *Steffensia*, and considered as part of the large genus *Piper* by Trelease and Yuncker. Miquel's classification was scrutinized again by Callejas, who acknowledged distinct groupings (subgenera) within *Piper*. Burger was the first to suggest a close relationship between *Macrostachys* and *Hemipodium* (Burger, 1971). Following Burger, Tebbs revised section *Macrostachys* including *P. arboreum* and *P. tuberculatum*, the core members of *Hemipodium* (Tebbs 1989). Similarly, Tepe and collaborators provided molecular evidence for the inclusion of *P. arboreum* as part of *Macrostachys* (Tepe et al. 2004). Data presented here suggest that members of *Hemipodium* form a sister clade to *Macrostachys* s.s., supporting Burger's hypothesis regarding the close relationships of these lineages.

RADULA MIQUEL—The *Radula* clade, perhaps the most species rich lineage of Neotropical *Piper* with ~450 species, is broadly distributed in the Neotropics. Many species of this clade occur in open sites and thus are common along roads and forest edges, but some occur in the understory. Species of *Radula* are medium-size shrubs, mostly self-supporting, but some species are herbaceous or lianescent shrubs. Leaves are membranaceous, commonly plinerved but can also be pinnately nerved, basally unequal, with different levels of pubescence, and rarely glabrous. Flowers are tightly arranged in the inflorescences, forming banding patterns. Inflorescences can be erect, and in some species distally curved at anthesis curved as in *P. aduncum* L. *Radula* was first described as a section of Miquel's genus *Artanthe* (Miquel 1843–1844). Most subsequent classifications of *Piper* did not recognize this group (de Candolle 1869,1923; Trelease and Yuncker 1950); neither did Callejas (1986) who included *Radula* within a much larger circumscribed *Steffensia*. Conversely, Tebbs recognized *Radula* as a distinct section of *Piper* (Tebbs 1989), providing a revision for the section (Tebbs 1993a, b). Molecular sequence data presented here provide strong support for the monophyly of *Radula*. In light of our findings, however, Tebbs' revision of *Radula* is misleading in several respects. Tebbs included, within *Radula*, several species that belong to other clades, i.e. *P. marginatum, P. cinereum, P. holdridgeanum, P. pseudolindenii,* and *P. sanctum*. Furthermore, Tebbs lumped into synonymy several distinct species that need to be re-evaluated using a larger sampling.

A number of subclades can be distinguished within *Radula*, but further in-depth analyses are needed before we can describe these species complexes properly. Nonetheless, we would like to remark on two subclades: *Isophyllon* and the *Piper filistilum* complex (Supplementary Fig. 1A, B).

Species of the *Isophyllon* Miquel subclade are medium-sized shrubs, self-supporting or sarmentose. Leaves are oblong or lanceolate, more or less coriaceous, pinnately nerved throughout, and basally obtuse or acute. Flowers are tightly arranged in the inflorescences, forming banding patterns. Inflorescences are erect and apiculate. Fruits are concrescent with the rachis. The *Isophyllon* clade has ~120 species and it is most diverse in the Atlantic Forest and also in Central America. Molecular sequence data provide support for the monophyly of this group (1.00 BPP/91 BS-ML/50 BS-MP, Fig. 2; Supplementary Fig. 1B). The combined data analysis provides support for the inclusion of *Isophyllon* either within *Radula* (Fig. 2) or, alternatively, as its sister taxon. This second finding is supported in the large analysis of ITS sequences (Supplementary Fig. 1A). *Isophyllon* was first described as a section of Miquel's genus *Artanthe* (Miquel 1843–1844). Most subsequent classifications of *Piper* did not distinguish this group (de Candolle 1869,1923; Trelease and Yuncker 1950; Tebbs 1989). Callejas recognized *Isophyllon* at the subgenus level, however his cladistic analysis of morphological data did not provide evidence for suggesting which would be the closest relative to *Isophyllon*. Molecular sequence data presented here confirms *Isophyllon* as a distinct clade, as recognized by Miquel and Callejas. Furthermore, our date suggest that *Isophyllon* is part of *Radula*.

Species of the *Piper filistilum* complex were previously included in the genus *Trianaeopiper*, one of Trelease's segregates that was distinguished by its "axillary inflorescences" (Trelease 1928). Members of the *Piper filistilum* complex share the leaf morphological characteristics of other *Radula* species, but their architecture is largely modified with reduced axillary, sympodial branches that appear to be axillary inflorescences, and inflorescences that do not exhibit the typical banded pattern of *Radula* (Jaramillo and Callejas 2004b). Molecular sequence data provide strong support for the close relationship of this species complex with the *Radula* clade, shedding light on the evolution of an interesting group whose species were hypothesized by de Candolle to be related to his subgenera *Carpunya, Steffensia,* and *Nematanthera* (de Candolle 1923). The *Piper filistilum* complex is restricted to the Chocó Region in northwestern South America.

PELTOBRYON KLOTZSCH—The *Peltobryon* clade with ~80–100 species, is widespread in South America. Most species are restricted to the western Amazon and the eastern Andean slopes in Bolivia, Ecuador, and Perú. A significant portion of this clade occurs in the lowland forests of Costa Rica and Panamá. Few species are known north of Guatemala and apparently none is known from the Caribbean Islands. Species of this clade are shrubs or treelets that thrive in the forest understory. They occur from sea level to 2000 m in elevation. Leaves are pinnately nerved with secondary veins arising throughout the entire lamina, which is marginally ciliate, and often strongly glandular dotted. Leaves can be glabrous or pubescent and then with branched hairs. Inflorescences are for most species erect, thick, and greenish in fruit, the anthers often exhibit prominent connectives protruding above the thecae and are glandular dotted. Floral bracts are marginally fimbriated with a central portion strongly glandular dotted. A banded pattern is apparent in some species. Fruits are oblong, exerted, sessile, fleshy and glandularly dotted, seeds are obovoid and apically depressed. Many species display large stylar projections and prominente stigmatic lobes. *Peltobryon* was first described as a genus by Miquel (1843–1844). However, most subsequent classifications of *Piper* did not acknowledge this group (de Candolle 1869,1923; Trelease and Yuncker 1950; Tebbs 1989). Similarly, previous molecular phylogenetic analyses using an exemplar sampling were not able to recover this lineage (Jaramillo and Manos 2001; Jaramillo and Callejas 2004a, b). On the contrary, Callejas recognized *Peltobryon* as distinct group at the subgenus level based on morphological evidence (Callejas 1986). Molecular sequence data and the much larger sampling used in this study provide evidence for the monophyly and distinctiveness of *Peltobryon*.

The *Peltobryon* clade includes the *Piper confertinodum* complex and the *Piper trianae complex* (Fig. 2; Supplementary Fig. 1D). These two species complexes were included within Trealease's genus *Trianaeopiper* based on the axillary position of the inflorescences (Jaramillo and Callejas 2004a). However, they have all of the characteristics of the *Peltobryon* clade, but with a modified architecture with short axillary branches terminating in inflorescences. Species of the *Piper confertinodum* complex are short shrubs with obovate leaves that are pinnately nerved throughout and basally acute. The flowers are loosely arranged on the inflorescences. Species of the *Piper trianae complex* are short shrubs, with ovate leaves that are plinerved and basally cordate to acute. The flowers are loosely arranged in the inflorescences. Species of these two complexes are restricted to the Chocó Region in northwestern South America and southern Central America.

POTHOMORPHE C. DC—The *Pothomorphe* clade comprises ~10 species, and is distributed throughout the Neotropics. Species in this clade are herbs or shrubs, and the latter can be either self-supporting or climbers. Leaves are palmately or pinnately (only *P. auritum*) nerved, basally obtuse or cordate (peltate in *P. peltatum*), and have sheathing petioles. Inflorescences are dense with the flowers forming banding patterns. In *P. umbellatum* and *P. peltatum*, the inflorescences are congested in leafless axillary branches appearing as umbels. Fruits are free and obovoid. Within this lineage we can recognize two well-supported subclades. The first comprises *Pothomorphe* s.s., which includes the more traditional *Pothomorphe* species (in which the inflorescences appear umbellate) plus *P. auritum*. The second subclade comprises the *Piper marginatum* complex (Callejas 1986). Species of this subclade are shrubs, erect or sarmentose, with leaves that are palmately nerved and basally obtuse or cordate. Flowers are tightly arranged in the inflorescences forming banding patterns. The fruits are free and obovoid. *Pothomorphe*, in its traditional circumscription, has long been considered a distinct genus of the Piperaceae and at least two other names are attributed to the group at the genus level *Lepianthes* Raf. and *Heckeria* Kunth. Molecular sequence data presented here and in previous studies (Jaramillo and Manos 2001; Jaramillo and Callejas 2004a, b) provide strong evidence for the inclusion of *Pothomorphe* within the broader *Piper*. We use the name *Pothomorphe* as it was the first name used at the infrageneric level (de Candolle 1869). Additionally, our data suggests that *Pothomorphe* s.s. clade is sister to *P. marginatum*-complex. The *P. marginatum* complex was first described by Callejas (1986), although it had not been recognized in any other classification of *Piper* (Miquel 1843–1844; de Candolle 1869,1923; Trelease and Yuncker 1950; Tebbs 1989). Molecular sequence data presented here and in previous studies, suggest that *P. marginatum* complex is a distinct clade within *Piper*, sister to the *Pothomorphe* s.s. clade.

ENCKEA KUNTH—The *Enckea* clade has ~120 species, that occur from the humid forests of the Amazon, to the much drier forest west of the Sierra Madre Occidental in México, and the calcareous outcrops of the Greater Antilles. Species of *Enckea* are shrubs or small trees with very characteristic palmately nerved leaves. The leaves are mostly ovate in shape, with acute to cordate bases, and sometimes possess two callosities at the base. Leaves can be symmetrical at all nodes (i.e. *P. tenuipes* C.DC) or asymmetric in sympodial branches and symmetric in monopodial axis (i.e. *P. reticulatum*). *Enckea* is distinctive due to its lax inflorescences with pedicellate or sessile flowers. Inflorescences are mostly erect, but sometimes pendulous. The rachis is often glabrous or else papillate puberulent or sometimes pubescent. Floral bracts are conchaeform to cuccullate or even at fruit stages appearing spatulate, mostly glabrous and if pubescent the hairs are restricted to the margins or the abaxial side. Flowers have 4–6 stamens, and 3–4 lobed stigmas. Stylar projectiosn are lacking, but a stylopodium is apparent in some taxa. Fruits are free and globose.

Our data provide evidence for the inclusion of two generic segregates within the *Enckea* clade: *Callianira* Miquel and *Arctottonia* Trelease. The monotypic *Callianira* was segregated because of its unique combination of characters: palmately nerved leaves and peltate floral bracts. de Candolle included *P. melastomoides*, the sole species of *Callianira*, within section *Enckea* (de Candolle 1869) or later, in subgenus *Steffensia* (de Candolle 1923), and Callejas had included this taxon with the *P. marginatum complex* (Callejas 1986). This study provides evidence for the inclusion of *P. melastomoides* within *Enckea* (Supplementary Fig. 1E). The name *Arctottonia* has been used for the *Piper* species with pedicellate flowers (otherwise recognized as *Ottonia*) with palmately nerved leaves and a North American distribution (Trelease 1930). In the original description, Trelease observed that this group was probably an offshoot of *Enckea*. Bornstein (1989) had also highlighted the close relationship of *Arctottonia* with *Enckea* in his revision of *Arctottonia*, as did Callejas (1986) in his cladistic analysis of *Piper* using morphology. Our results do not support the monophyly of the pedicellate *Enckea* species (Fig. 2; Supplementary Fig. 1E), thus we propose to eliminate the use of *Arctottonia* as it does not form an exclusive monophyletic group.

OTTONIA SPRENG—The *Ottonia* clade has ~50 species and is distributed primarily in the Atlantic Forest of Brazil and the Amazon, but has one species, *P. darienense*, that occurs west of the Andes. Species of *Ottonia* are small shrubs that thrive in the understory of lowland tropical forests. Leaves are pinnately nerved, ovate or lanceolate in shape, and with two basal callosities. *Ottonia* species have lax inflorescences and a flower structure reminiscent of the members of *Enckea* with pedicellate or sessile flowers, a characteristic they share with members of the *Enckea* clade. Inflorescences are mostly erect, but sometimes pendulous. Fruits are globose to ellipsoid. In the taxonomic history of *Ottonia*, this name has been applied to those species in *Piper* with pedicellate flowers (subgenus *Ottonia*, sensu de Candolle 1923), including species with both pinnately and palmately veined leaves. Trelease's concept of *Ottonia* included only species with pedicellate flowers and pinnately nerved leaves (Trelease 1935). Using a representative sampling of species, we provide further phylogenetic evidence for the inclusion of species with pedicellate and sessile flowers in the *Ottonia* clade. Confirming the proposal of Callejas (1986), and suggested by our previous molecular phylogenetic analysis with a much smaller sampling (Jaramillo 2001).

P. CINEREUM/P. SANCTUM—The relationships of this clade to the other groups of Neotropical *Piper* remains enigmatic. *Piper cinereum* was hypothesized to belong to the "subgenus" *Radula* (Tebbs 1993b) or to the *P. marginatum* complex (Callejas 1986). Morphologically, *P. cinereum* is very similar to members of the *P. marginatum* complex as it shares the palmately veined leaves, sheathing petioles, and flowers tightly congested on the rachis and forming banding patterns. *Piper sanctum*, on the other hand, is morphologically similar to members of the *Enckea* clade (Callejas pers. obs.), sharing with this clade the palmately nerved leaves with two callosities in the leaf base. Furthermore, the leaf morphology of these two species is very different, even if the venation is palmate in both cases. Thus, the sister-group relationship of these two species is somewhat surprising. To understand better the relationships of these two taxa, we must study their morphology, anatomy and embryology in greater detail.

SCHILLERIA KUNTH—The *Schilleria* clade includes ~200 species found in Central America and in the Atlantic Forest of Brazil, where they are more diverse. Species in this clade are shrubs, and sometimes sarmentose. Leaves are plinerved or pinnately nerved throughout. The leaf bases are acute and may be decurrent with the petiole, and each leaf has a pair of callosities at the base. Inflorescences are lax, with flowers loosely arranged. Fruits are free and trigonous or obovoid. This lineage includes *Piper piluliferum*, a species with globose inflorescences that was once segregated as the genus *Sphaerostachys* Miq. *Schilleria* was first described as a genus by Kunth (1839), subsequent classifications did not recognize this group. Miquel lumped *Schilleria* into *Artanthe* (Miquel 1843–1844), and later treatments did not recognize *Schilleria* as a group. Callejas was the first to reconsider *Schilleria* at the subgenus level (Callejas 1986). Previous molecular phylogenetic analyses using an exemplar sampling were unable to recover a monophyletic *Schilleria*, and we had provisionally used the name *Schilleria* for a much larger circumscribed group (Jaramillo and Manos 2001, Jaramillo and Callejas 2004b). Molecular sequence data and a much larger sampling presented here provide evidence for the distinctiveness and monophyly of this clade.

Tropical Asian Piper—The phylogeny presented here includes a much larger sampling from both continental (Vietnam and China) and insular (Philippines and Indonesia) tropical Asia than previous phylogenetic studies of *Piper*. In tropical Asia there are ~300 species of *Piper* distributed throughout southeast Asia, extending from the north to southern China, westward to the Indian Subcontinent, and eastward to New Guinea and Australia. *Piper* s.s. is the only major clade occurring in Tropical Asia. Early monographers divided *Piper* s.s. into several genera (Miquel 1843–1844), sections, or subgenera (de Candolle 1869, 1923). The characters used for these divisions included the presence of pedicellate fruits (i.e. *Cubeba*), floral bracts pedicellate (i.e. *Chavica*) vs. sessile (i.e. *Piper* = *Eupiper*). These characters are homoplasious and have evolved in parallel several times (Jaramillo and Manos 2001; Asmarayani and Pancoro 2005). Subdivisions within *Piper* s.s. require more in-depth study to identify diagnostic synapomorphies that characterize the subclades.

Species in the *Piper* s. s. clade are herbs, shrubs or climbers. Leaves are palmately or pinnately nerved. Climbers exhibit strong leaf dimorphism between the monopodial, orthotropic shoots and the sympodial, plagiotropic branches. Leaves on monopodial shoots are cordate or ovate, basally cordate or round, and possess sheathing petioles, whereas leaves on fertile, sympodial branches are ovate, lanceolate or elliptic, and have nonsheathing petioles. The inflorescences are lax, erect or pendulous. Flowers can be bisexual or, if unisexual, then the plants are dioecious. Male inflorescences are filiform or cylindrical. Female inflorescences are filiform, cylindrical or globose. Fruits are free or sunk into the rachis and are often brightly colored. Floral bracts are particularly diverse in the *Piper* s. s. clade, including pedicellate, sessile and cupullate bracts. Cupullate bracts are a diagnostic character for the group known as *Muldera* (= *Schizonephos*). The two species of *Muldera* included here, *P. recurvum* and *P. baccatum*, are nested within the *Piper* s. s. clade. However, a larger sampling of species with cupullate floral bracts is necessary to evaluate how many times this character has evolved.

South Pacific Piper—Our new phylogeny includes a larger sampling of species from the South Pacific Islands. Most species of *Piper* occurring in the South Pacific belong to the *Macropiper* Miq. clade, plus a few members of the *Piper* s.s. clade that are also distributed in this region. The *Macropiper* clade includes ~10 species restricted to the South Pacific (Smith 1975), but with one notable exception, *P. capense* from Africa. Species of *Macropiper* are shrubs or small trees, mostly dioecious (sometimes monoecious). Leaves are mostly ovate, palmately nerved, basally obtuse to deeply cordate, and petioles are sheathing. Inflorescences are often crowded in short axillary branches that appear as umbels, similar to those of the *Pothomorphe* clade. Flowers are loosely arranged in the inflorescences, and associated with peltate floral bracts. Fruits are generally free, but in *P. excelsum* they are concrescent with the rachis. The *Macropiper* clade includes *P. methysticum*, the source of the herbal medicine and mildly narcotic kava-kava (Lebot and Lèvesque 1989). *Macropiper* was first described as a genus by Miquel (1843–1844). Most subsequent classifications recognized *Macropiper* at the generic (Smith 1975; Tebbs 1993a, b) or subgeneric (de Candolle 1923; Callejas 1986) level. Molecular sequence data presented here and in previous analyses (Jaramillo and Manos 2001; Jaramillo and Callejas 2004a) suggest that *Macropiper* is a distinctive clade within a broader *Piper*. *Piper capense* has been traditionally regarded as the core member of *Coccobryon*, a taxon recognized alternatively at the generic (Miquel 1843–1844), subgeneric (de Candolle 1923; Callejas 1986) or sectional (de Candolle 1869) level. Our results suggest that *P. capense* is part of the *Macropiper* clade.

Tropical African Piper—There are very few *Piper* species native to tropical Africa, which is remarkable since other pantropical plant lineages tend to be similarly diverse in these three major tropical regions. The occurrence of *Piper* in Africa is the result of at least two separate dispersal events (Fig. 2; Supplementary Fig. 1F). *Piper capense* is a member of the otherwise South Pacific *Macropiper* clade, and both *P. borbonense* and *P. guineense* are members of the *Piper* s. s. clade, which is broadly distributed in tropical Asia. These results are in full agreement with those of Smith et al. (2008) based on a low copy nuclear gene and cpDNA regions other than the *psbJ–petA* marker used here. Many *Piper* species occurring in Africa are either native to the Neotropics: *P. umbellatum*, *P. arboreum*, or to Asia, *P. nigrum*.

Molecular sequence data provide evidence for the recognition of ten distinct clades within *Piper*. The ITS region has sufficient variation to assign species to the major clades to which they belong. We found much less resolution in the phylogenetic reconstructions based on the chloroplast intron *psbJ–petA*, similar to the low resolution provided by the *matK* gene and *trnK* intron in *Piper* (Wanke et al. 2007). This result suggests that new nuclear markers must be developed to increase our understanding of the relationships within *Piper*. This study provides the most comprehensive reconstruction of phylogenetic relationships to date for the large genus *Piper*. We confirm several clades that have been previously recognized (Jaramillo and Manos 2001; Jaramillo and Callejas 2004a, b; Tepe et al. 2004), in addition to identifying new clades: *Peltobryon, Schilleria, Isophyllon,* and *P. cinereum*/*P. sanctum*. We also determined the relationships of the African species of *Piper* that have been obscure until now. However, we have been unable to resolve relationships among the major clades of *Piper* and, to some extent, within each clade. This phylogeny will serve as a framework for future taxonomic and evolutionary studies in *Piper*. A formal subgeneric classification will be postponed until we have greater resolution at the backbone of the tree.

NOMENCLATURAL CHANGES

Piper bullulatum M. A. Jaram., **nom. nov.** = *Piper parvulum* M.A. Jaram. & Callejas, Taxon 53(2): 277. 2004, **Non** *Piper parvulum* M. Martens & Galeotti. Bulletin de l'Academie Royale des Sciences et Belles-lettres de Bruxelles 10(1): 130. 1843. = *Trianaeopiper bullatum* Cuatrecasas, Revista Acad. Col. Cienc. Exact. 7: 51. 1946. Revista Acad. Col. Cienc. Exact. 7: 51. 1946. – Type: COLOMBIA: Valle: Pacific Coast, Rio Cajambre, Barco, 5–80 m, 26 Apr 1944, *J. Cuatrecasas 17167* (Holotype: COL, Isotype: F, US). = *Trianaeopiper bullatum* var. *archeri* Trel. & Yunck., Piperaceae N. South America 1: 425. 1950. – Type: COLOMBIA: Chocó: headwaters of Rio Tutunendo, E. of Quibdo, 20–21 May 1931, *W. A. Archer 2171* (Holotype: US).

Piper hooglandii (I. Hutton & P.S. Green) M. A. Jaram., **comb. nov**. = *Macropiper hooglandii* I. Hutton & P.S. Green, Kew Bulletin 48(2): 316. 1993.

Piper melchior (Sykes) M. A. Jaram., **comb. nov.** = *Macropiper melchior* Sykes in New Zealand J. Bot 30(3): 231. 1992.

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APPENDIX 1. ***Taxon;*** Genbank accession numbers (ITS, *psbJ–petA*, — = sequence not obtained); country where material was collected, voucher (HERB). A list of collector's abbreviations is provided at the end of the appendix.

P. abalienatum Trel.; EU581075, EU581453; México, *MAJ 552* (DUKE). ***P. abbreviatum*** Opiz; EU581076, EU581454; Philipines, *MAJ 203* (DUKE). ***P. adenandrum*** C. DC.; EU581077, —; French Guiana, *EJT 557* (MU). ***P. aduncum*** L. (1); EU581078, —; New Guinea, *GW 2424* (MIN); ***P. aduncum*** L. (2); AF275159, —; Brazil, *AFO 1253* (DUKE); ***P. aduncum*** L. (3); AF275157, —; Colombia, *MAJ 76* (DUKE); ***P. aduncum*** L. (4); EU581079, —; Brazil, *MCS 266* (RB); ***P. aduncum*** L. (5); EF060061, —; Indonesia, *RA 04* (BO). ***P. aequale*** Vahl. (1); EU581080, —; Panamá, *ET 1018* (MU); ***P. aequale*** Vahl. (2); EU581081, —; Panamá, *EL s/n*, no voucher; *P. aequale* Vahl. (3); EU581082, —; Panamá, *ET 1027* (MU). ***P. aereum*** Trel.; EF056220, —; Costa Rica, *IAC 2213* (MU). **P. aff *anonifolium*** (Kunth) Steud. (1); EU581083, —; Brazil, *MAJ 798* (RB); **P. aff *anonifolium*** (Kunth) Steud. (2); EU581084, —; Brazil, *AL 1242* (MG); **P. aff *anonifolium*** (Kunth) Steud. (3); EU581085, —; Brazil, *MJK 757* (MG). *P. albispicum* C. DC.; AY572317, EU581456; Vietnam, *MAJ 388* (DUKE). ***P. albozonatum*** C. DC.; AY326195, —; Ecuador, *MAJ 697* (DUKE). ***P. amalago*** L. (1); EU581086, EU581457; Guatemala, *AB 964* (SEMO); ***P. amalago*** L. (2); EU581087, EU581458; Guatemala, *AB 972* (SEMO); ***P. amalago*** L. (3); EU581088, EU581459; Dominican Republic, *LAH 426* (SRP); ***P. amalago*** L. (4); EU581089, EU581460; Brazil, *MCS 267* (RB); ***P. amalago*** L. (5); EU581090, —; Brazil, *MAJ 844* (RB); ***P. amalago*** L. (6); EU581091, —; México, *MA 2924* (HEM); ***P. amalago*** L. (7); EU581092, —; Honduras, *AB 712* (SEMO); ***P. amalago*** L. (8); EU581093, —; Honduras, *AB 719* (SEMO); ***P. amalago*** L. (9), EU581094, —; Honduras, *AB 730* (SEMO); ***P. amalago*** L. (10); AF275186, —; México, *MAJ 561* (DUKE). ***P. amoenum*** Yunck.; AF275160, —; Colombia, *MAJ 116* (DUKE). ***P. amplum*** (Kunth) Steud. (1); EU581095, EU581461; Brazil, *MAJ 785* (RB); ***P. amplum*** (Kunth) Steud. (2); EU581096, —; Brazil, *MAJ 804* (RB). ***P. anisum*** (Sprengel) Angely (1); EU581097, EU581462; Brazil, *MAJ 920* (RB); ***P. anisum*** (Sprengel) Angely (2); EU581098, EU581463; Brazil, *MCS 269* (RB); ***P. anisum*** (Sprengel) Angely (3); EU581099,–; Brazil, *RC 1637* (HUA). ***P. anonifolium*** (Kunth) Steud. (1); EU581100, —; French Guiana, *EJT 523* (MU); ***P. anonifolium*** (Kunth) Steud. (2); EU581101, —; French Guiana, *EJT 527* (MU). ***P. appendiculatum*** C. DC.; AY326196, —; Colombia, *MAJ 740* (DUKE). ***P. arboreum*** Aubl. (1); EF056223, EU581464; Panamá, *EJT 1039* (MU); ***P. arboreum*** Aubl. (2),; EF056222, EU581465; French Guiana, *EJT 620* (MU); ***P. arboreum*** Aubl. (3); AF275180, EU581466; Colombia, *MAJ 112* (DUKE); ***P. arboreum*** Aubl. (4); EU581102, —; Panamá, *EL s/n*, no voucher; ***P. arboreum*** Aubl. (5); EF056224, —; Panamá, *EJT 1040* (MU); ***P. arboreum*** Aubl. (6); EU581103, —; Brazil, *MAJ 783* (RB); ***P. arboreum*** Aubl. (7); EU581104, —; Brazil, *MAJ 863* (RB); ***P. arboreum*** Aubl. (8); EU581105, —; Brazil, *MCS 268* (RB); ***P. arboreum*** Aubl. (9); EU581106, —; Brazil, *MaN 1565* (RB); ***P. arboreum*** Aubl. (10); EF056221, —; Costa Rica, *EJT 377*

(MU). **P. arboricola** C. DC.; AY572319, EU581467; Vietnam, *MAJ 467* (DUKE). **P. argyrophyllum** Miq.; EU581107, —; Sri Lanka, *RS s/n*. **P. arieianum** C. DC. (1); AF275163, EU581468; Colombia, *MAJ 69* (DUKE); **P. arieianum** C. DC. (2); EU581108, —; Colombia, *MAJ 638* (DUKE). **P. artanthe** C. DC.; EU581109, —; Colombia, *MAJ 83* (DUKE). **P. atrospicum** C. DC.; AY572318, —; Philipines, *MAJ 168* (DUKE). **P. attenuatum** Buch.-Ham. ex Wall.; EU581110, —; China, *LJM 061416* (PE). **P. augustum** Rudge (1); AF275165, EU581469; Colombia, *MAJ 122* (DUKE); **P. augustum** Rudge (2); EU581111, —; Panamá, *EJT 993* (MU). **P. aulacospermum** Callejas; EU581112, —; French Guiana, *SM 18087* (HUA). **P. auritifolium** Trel. (1); EU581113, EU581470; Costa Rica, *CD 10877* (SRP); **P. auritifolium** Trel. (2); EF056225, EU581471; Costa Rica, *EJT 94* (MU); **P. auritifolium** Trel. (3); EU581114, EU581472; Costa Rica, *CD 10872* (SRP). **P. auritum** Kunth (1); AF275175, EU581473; Colombia, *MAJ 63* (DUKE); **P. auritum** Kunth (2); EU581115, —; Costa Rica, *CD 10892* (SRP); **P. auritum** Kunth (3); EU581116, —; Panamá, *EJT 987* (MU); **P. auritum** Kunth (4); EU581117, —; México, *AR 2409* (XAL); **P. auritum** Kunth (5); EU581118, —; México, *MAJ 1014* (UMO); **P. auritum** Kunth (6); EU581119, —; Colombia, *MAJ 756* (DUKE). **P. austrocaledonicum** C. DC. (1); EU581120, EU581474, New Caledonia, *SaM 530* (GH); **P. austrocaledonicum** C. DC. (2); EU581121, —; New Caledonia, *GMcP 19190* (MO). **P. avellanum** C. DC. (1); EU581122, —; French Guiana, *EJT 616* (MU); **P. avellanum** C. DC. (2); EU581123, —; Colombia, *MAJ 109* (DUKE). **P. baccatum** Blume; EU581124, —; Thailand, *KW 1594* (GH). **P. bartlingianum** C. DC. (1); AF275183, EU581475; Guyana, *RE 1267B* (U); **P. bartlingianum** C. DC. (2); EU581125, EU581499, Brazil, *AL 1157* (MG). **P. basilobatum** Trel. & Yunck.; AY326197, —; Colombia, *MAJ 596* (DUKE). **P. bavinum** C. DC.; AF275199, EU581476; Vietnam, *MAJ 392* (DUKE). **P. begoniicolor** Trel. & Yunck.; EF056226, —; Colombia, *TC 69629* (MO). **P. bellidifolium** Yunck.; EF056227, EU581477; Ecuador, *EJT 1430* (MU). **P. betle** L. (1); AF275201, EU581478; Cultivated, Duke Accesison # 82-29-8, no voucher; **P. betle** L. (2); EU581126, —; Cultivated, *JFS 5808*, (SRP); **P. betle** L. (3); EF060062, —; Indonesia, *RA* 09 (BO); **P. betle** L. (4); EF060063, —; Indonesia, *RA 14* (BO); **P. betle** L. (5); EF060064, —; Indonesia, *RA 30* (BO); **P. betle** L. (6); EF060065, —; Indonesia, *RA 36* (BO). **P. biolleyi** C. DC. (1); EU581127, EU581479; Costa Rica, *EJT 429* (MU); **P. biolleyi** C. DC. (2); EU581128, —; Costa Rica, *CD 10896* (SRP). *P. bisasperatum* Trel.; EU581129, —; Panamá, *EJT 1054* (MU). **P. biseriatum** C. DC. (1); EF056229, EU581480; Costa Rica, *EJT 141* (MU); **P. biseriatum** C. DC. (2); EF056228, —; Costa Rica, *EJT 77* (MU); **P. biseriatum** C. DC. (3); EF056230, —; Costa Rica, *EJT 438* (MU). **P. blattarum** Spreng.; EU581130, —; Puerto Rico, *CMT 11645* (MO). **P. boehmeriaefolium** Wall.; AF275204, —; Vietnam, *MAJ 235* (DUKE). **P. borbonense** C. DC.; EU581131, EU581481; Reunion, *CJB 87.3.616*, no voucher. **P. brachypodon** C. DC.; AY326198, EU581482; Colombia, *MAJ 757* (DUKE). **P. brachypus** Trel.; EU581132, —; México, *MAJ 550* (DUKE). **P. bradei** Yunck.; EU581133, EU581483; Brazil, *MAJ 903* (RB). **P. breviamentum** C. DC.; EU581134, EU581484; Philipines, *MAJ 221* (DUKE). **P. brevicuspe** Merr.; AY572321, —; Philipines, *MAJ 211* (DUKE). **P. brevipedicellatum** Bornstein; AF275189, EU581485; México, *MAJ 544* (DUKE). **P. brownsbergense** Yunck. (1); EU581135, —; French Guiana, *EJT 619* (MU); **P. brownsbergense** Yunck. (2); EU581136, —; French Guiana, *EJT 530* (MU). **P. bullosum** C. DC.; EU581137, —; Ecuador, *EJT 1405* (MU). **P. bullulatum** M. A. Jaram.; AF275167, EU581585; Colombia, *MAJ 55* (DUKE). **P. cabellense** C. DC. (1); EF056231, —; Colombia, *RaF 2697* (NY); **P. cabellense** C. DC. (2); AF275178, —; Colombia, *MAJ 87* (DUKE). **P. cajambrense** Trel. & Yunck. (1); EF056232, —; Ecuador, *HL 210* (MO); **P. cajambrense** Trel. & Yunck. (2); AY326199, —; Colombia, *MAJ 768* (DUKE). **P. calcariforme** Tebbs (1); EF056234, EU581486;Costa Rica, *AE 2397* (CR); **P. calcariforme** Tebbs (2); EF056233, —; Panama, *EJT 1009* (MU); **P. calcariforme** Tebbs (3); EU581138, —; Panamá, *EJT 1001* (MU); **P. caldense** C. DC. (1); EU581139, —; Brazil, *MAJ 797* (RB); **P. caldense** C. DC. (2); EU581140, —; Brazil, *MAJ 805* (RB); **P. caldense** C. DC. (3); EU581141, —; Brazil, *MCS 305* (RB). **P. callosum** Ruiz & Pav.; EU581142, EU581487; Brazil, *MJK 161* (SPF). **P. campanum** Yunck. (1); EF056236, EU581488; Panamá, *EJT 1048* (MU); **P. campanum** Yunck. (2); EF056235, —; Panama, *EJT 1033* (MU). **P. candollei** Sodiro; EF056237, EU581489; Ecuador, *EJT 1449* (MU). **P. caninum** Blume (1); AY326195, EU581490; Philipines, *MAJ 218* (DUKE); **P. caninum** Blume (2); EF060066, —; Indonesia, *RA 21* (BO); **P. caninum** Blume (3); EF060067, —; Indonesia, *RA 29* (BO); **P. caninum** Blume (4); EF060068, —; Indonesia, *RA 35* (BO). **P. capense** L.f. (1); EU581143, EU581491; Uganda, *CD 11004* (SRP); **P. capense** L.f. (2); EU581144, EU581492; Kenya, *CD 11009* (SRP); **P. capense** L.f. (3); AY326200, —; Tanzania, *RF 96-75* (US). **P. caracasanum** Bredem. ex Link; EF056238, —; Venezuela, *WM 1180* (MO). **P. cararense** Trel. & Yunck; (1), AY326201, EU581493; Colombia, *MAJ 601* (DUKE); **P. cararense** Trel. & Yunck. (2); EU581145, —; Colombia, *MAJ 46* (DUKE). **P. carautensei** E.F. Guim & M.Carvalho-Silva; EU581146, EU581494; Brazil, *MAJ 933* (RB). **P. carrilloanum** C. DC.; EU581147, EU581495; Costa Rica, *EJT 415* (MU). **P. cavendishioides** Trel. & Yunck.; AF275153, EU581496; Colombia, *MAJ 70* (DUKE). **P. celtidiforme** Opiz (1); AF275205, —; Philipines, *MAJ 171* (DUKE); **P. celtidiforme** Opiz (2); EU581148, —; New Guinea, *WT 14496* (GH). **P. cenocladum** C. DC. (1); EF056239, EU581497; Costa Rica, *EJT 185* (MU); **P. cenocladum** C. DC. (2); EF056240, —; Costa Rica, *EJT 393* (MU); **P. cenocladum** C. DC. (3); EU581149, —; Costa Rica, *EJT 90* (MU). **P. cernuum** Vell. (1); EU581150, EU581498; Brazil, *MAJ 907* (RB); **P. cernuum** Vell. (2); EF056242, —; Brazil, *GH 46665* (MU); **P. cernuum** Vell. (3); EU581151, —; Brazil, *MAJ 814* (RB). **P. chandocanum** C. DC.; EU581152, EU581500; China, *LJM 06182* (PE). **P. chimonanthifolium** Kunth; EU581153, —; Brazil, *MCFS 400* (RB). **P. chuarense** M. A. Jaram. & Callejas; AY326202, EU581501; Colombia, *MAJ 721* (DUKE). **P. cihuatlanense** Bornstein; AF275187, —; México, *MAJ 543* (DUKE). **P. cinereum** C. DC. (1); AF275190, EU581502; Colombia, *MAJ 66* (DUKE); **P. cinereum** C. DC. (2); EU581154, EU581503; Ecuador, *MAJ 653* (DUKE); **P. cinereum** C. DC. (3); EU581155, —; Colombia, *MAJ 673* (DUKE). **P. coccoloboides** Kunth; EF056243, —; Brazil, *HSI 22879* (US). **P. cocornanum** Trel. & Yunck.; AY326203, —; Colombia, *RC 12493* (HUA). **P. colligatispicum** Trel. & Yunck.; AY326204, —; Colombia, *MAJ 780* (DUKE). **P. colonense** C. DC. (1); EU581156, EU581504; Nicaragaua, *AB 753* (SEMO). **P. colonense** C. DC. (2); EU581157, —; Nicaragua, *AB 751* (SEMO). **P. colonense** C. DC. (3); EU581158, —; Panamá, *EJT 982* (MU); **P. colonense** C. DC. (4); EU581159, —; Costa Rica, *CD 10894* (SRP). **P. concepcionis** Trel. (1); EU581160, —; Colombia, *MAJ 627* (DUKE); **P. concepcionis** Trel. (2); EU581161, —; Costa Rica, *CD 10880* (SRP). **P. confertinodum** (Trel. & Yunck) M. A. Jaram. & Callejas; AF275166, EU581505; Colombia, *MAJ 54* (DUKE). **P. confusum** C. DC. EU581162, —; Cuba, *AHL 14556* (NY). **P. consanguineum** (Kunth) Steud. (1); EU581163, —; French Guiana, *EJT 546* (MU); **P. consanguineum** (Kunth) Steud. (2); EU581164, —; Brazil, *MJK 768* (MG). **P. corcovadense** C. DC. (1); EU581165, EU581506; Brazil, *MAJ 838* (RB); **P. corcovadense** C. DC. (2); EU581166, —; Brazil, *MAJ 843* (RB). **P. cordatilimbum** Quisumb.; AY572323, —; Philipines, *MAJ 178* (DUKE). **P. cordulatum** C. DC. (1); EF056245, EU581507; Panama, *EJT 975* (MU); **P. cordulatum** C. DC. (2); EU581167, EU581508 Panamá, *EL s/n*, no voucher; **P. cordulatum** C. DC. (3); EF056246, —; Panamá, *EJT 1011* (MU); **P. cordulatum** C. DC. (4); EU581168, —; Panamá, *EJT 1016* (MU). **P. corintoananum** Yunck.(cf); EU581169, EU581558; Brazil, *MAJ 944* (RB). **P. costatum** C. DC. (1); EU581170, —; Cultivated, Yale Univ. Plant Collection, no voucher; **P. costatum** C. DC. (2); EU581171, —; Cultivated, *TF 4261* (PTBG). **P. crassinervium** Kunth; EU581172, EU581509; Bolivia, *AM 1183* (MO). **P. cubataonum** C.DC.; EU581173, —; Brazil, *MJK 493* (SPF). **P. cubeba** L.f.; EF060070, —; Indonesia, *RA 02* (BO). **P. curtifolium** C. DC.; EU581174, EU581510; Philipines, *MAJ 194*, (DUKE). **P. curtirachis** W.C.Burger (cf); EU581175, —; Panamá, *EJT 995* (MU). **P. curtispicum** C. DC.; EU581176, —; Panamá, *EJT 1028* (MU). **P. daguanum** C. DC.; EF056247, EU581511; Panamá, *EJT 1044* (MU). **P. darienense** C. DC. (2); EU581177, EU581512; Panamá, *EL s/n*, no voucher; **P. darienense** C. DC. (1); AF275181, EU581513; Colombia, *MAJ 103* (DUKE). **P. decumanum** L.; AF275203, EU581514; Philipines, *MAJ 210* (DUKE). **P. densum** Blume; AY615963, EU581515; Vietnam, *MAJ 508* (DUKE). **P. dilatatum** Rich. (1); EU581178, —; México, *AR 2817* (XAL); **P. dilatatum** Rich. (2); EU581179, —; Brazil, *MAJ 858* (RB). **P. dilatatum** Rich. (3); EU581180, —; Panamá, *EL s/n*, no voucher. **P. diospyrifolium** Kunth; EU581181, —; Brazil, *MJK 431* (SPF). **P. divaricatum** G. Mey. (1); EU581182, EU581516; Ecuador, *EJT 1424* (MU); **P. divaricatum** G. Mey. (2); EU581183, —; Brazil, *MJK 743* (MG). **P. dolichotrichum** Yunck. (1); EU581184, —; Costa Rica, *CD 10878* (SRP); **P. dolichotrichum** Yunck. (2); EU581185, —; Colombia, *MAJ 129* (DUKE). **P. dryadum** C. DC.; EU581186, —; Panamá, *EJT 1047* (MU). **P. duartei** E.F. Guim & M.Carvalho-Silva; EU581187, EU581517; Brazil, *MAJ 928* (RB). **P. dumosum** Rudge (1); EU581188, —; French Guiana, *EJT 532* (MU); **P. dumosum** Rudge (2); EU581189, —; French Guiana, *EJT 560* (MU). **P. entradense** Trel. & Yunck.; EU581190, —; Ecuador, *EJT 1394* (MU). **P. erectipilum** Yunck.; EU581191, EU581518; Brazil, *MJK 762* (MG). **P. eucalyptifolium** Rudge; EU581192, —; French Guiana, *EJT 526* (MU). **P. eucalyptiphyllum** C.DC.; EU581193, EU581519; Brazil, *MAJ 972* (RB). **P. euryphyllum** C. DC. (1); EF056250, EU581520; Costa Rica, *EJT 410* (MU); **P. euryphyllum** C. DC. (2); EF056249, —; Costa Rica, *EJT 173* (MU). **P. eustylum** Diels; EU581194, —; Ecuador, *EJT 1400* (MU). **P. excelsum** G. Forst. (1); AF275193, EU581521; New Zealand, *ROG 8494* (AK); **P. excelsum** G. Forst. (2); EF635476, —; New Zealand, no voucher. **P. fallens** Trel. (cf); EU581195, —; México, *NM 573* (HEM). **P. filistilum** C. DC. (1); AF275155, EU581522; Colombia, *MAJ 157* (DUKE); **P. filistilum** C. DC. (2); EU581196, —; Colombia, *MAJ s/n*, no voucher; **P. filistilum** C. DC. (3); EU581197, —; Ecuador, *MAJ 680* (DUKE); **P. filistilum** C. DC. (4);

EU581198, —; Ecuador, *MAJ 690* (DUKE); ***P. filistilum*** C. DC. (5); EU581199, —; Ecuador, *MAJ 698* (DUKE). ***P. filistilum*** C. DC. (6); EU581200, —; Ecuador, *MAJ 695* (DUKE); ***P. filistilum*** C. DC. (7); EU581201, —; Colombia, *MAJ 592* (DUKE). ***P. fimbriulatum*** C. DC. (1); EF056251, EU581523; Costa Rica, *EJT 115* (MU); ***P. fimbriulatum*** C. DC. (2); EF056252, —; Costa Rica, *EJT 326* (MU); ***P. fimbriulatum*** C. DC. (3); EF056253, —; Panamá, *EJT 971* (MU); ***P. fimbriulatum*** C. DC. (4); EF056254, —; Panamá, *EJT 1037* (MU). ***P. flagellicuspe*** Trel. & Yunck.; AF275154, —; Colombia, *MAJ 65* (DUKE). ***P. flavicans*** C. DC.; EU581202, —; Brazil, *HSI 21202* (MO). ***P. flavidum*** C. DC.; EU581203, —; México, *MA 2826* (HEM). ***P. flaviflorum*** C. DC.; EU581204, —; China, *LJM 06171* (PE). ***P. flavoviride*** C. DC.; EU581205, —; Brazil, *MJK 98* (SPF). ***P. fonteboanum*** Yunck.; EF056255, —; Colombia, *ILA 106885* (US). ***P. friedrichsthalii*** C. DC. (1); EU581206, —; Panamá, *EJT 1010* (MU); ***P. friedrichsthalii*** C. DC. (2); EU581207, —; Costa Rica, *EJT 131* (MU); ***P. friedrichsthalii*** C. DC. (3); AY326205, —; Colombia, *MAJ 584* (DUKE). ***P. frutescens*** C. DC.; EU581208, —; Brazil, *MAJ 878* (RB). ***P. fuligineum*** (Kunth) Steud. (cf); EU581209, —; Brazil, *MAJ 979* (RB). ***P. garagaranum*** C. DC. (1); AF275162, EU581524; Colombia, *MAJ* 73 (DUKE); ***P. garagaranum*** C. DC. (2); EU581210, EU581525; Costa Rica, *CD 10904* (SRP); ***P. garagaranum*** C. DC. (3); EU581211, —; Costa Rica, *CD 10869* (SRP); ***P. garagaranum*** C. DC. (4); EU581212, —; Panamá, *EJT 1025* (MU); ***P. garagaranum*** C. DC. (5); EU581213, —; Panamá, *EJT 1029* (MU). ***P. gaudichaudianum*** Kunth; EU581214, —; Brazil, *MAJ 895* (RB). *P. gibbosum* C. DC. (1); EF056256, EU581526; Costa Rica, *EJT 170* (MU); *P. gibbosum* C. DC. (2); EF056257, —; Costa Rica, *EJT 411* (MU). ***P. gigantifolium*** C. DC. (1); EF056259, —; Brazil, *SM 12866* (NY); ***P. gigantifolium*** C. DC. (2); EF056258, —; Brazil, *JMP 2084* (US). ***P. gigas*** Trel.; EF056260, EU581527; Panamá, *EJT 1000* (MU). ***P. glabratum*** Kunth (1); EU581215, —; Costa Rica, *CD 10888* (SRP); ***P. glabrescens*** C. DC. (1); EU581216, —; México, *RMC 747* (SRP); ***P. glabrescens*** C. DC. (2); EU581217, —; Nicaragua, *AB 749* (SEMO); ***P. glabrescens*** C. DC. (3); EU581218, —; Honduras, *AB 714* (SEMO). ***P. glanduligerum*** C. DC.; EU581219, —; Colombia, *MAJ 588* (DUKE). ***P. goesii*** Yunck.; EU581220, —; Brazil, *MAJ 912* (RB). ***P. grande*** Vahl.(1); EU581221, —; Honduras, *AB* 725 (SEMO); ***P. grande*** Vahl.(2); EU581222, —; Nicaragua, *AB 754* (SEMO); ***P. grande*** Vahl.(3); EU581223, —; Panamá, *EL s/n*, no voucher; ***P. grande*** Vahl.(4); EU581224, —; Panamá, *EJT 1013* (MU). ***P. griffithii*** C. DC.; EU581225, —; Vietnam, *MAJ 511* (DUKE). ***P. guahamense*** C. DC.; EU581226, EU581529; Cultivated, *TF 6748* (PTBG). ***P. guayranum*** C. DC.; EU581227, —; Colombia, *MAJ 78* (DUKE). ***P. guazacapanense*** Trel. & Standl.; EU581228, EU581530; México, *MA 2923* (HEM). ***P. guineense*** Schumach. & Thonn. (1); EU581229, EU581532; Uganda, *CD 11006* (SRP); ***P. guineense*** Schumach. & Thonn. (2); EU581230, EU581533; Cameroon, *JFS 4924* (SCA); ***P. guineense*** Schumach. & Thonn. (3); EU581231, EU581534; Cameroon, *JFS 4923* (SCA). ***P. gymnostachyum*** C. DC.; AY572325, EU581535; Vietnam, *MAJ 389* (DUKE). ***P. hancei*** Maxim.; EU581232, EU581536; China, *LJM 06211* (PE). ***P. hartwegianum*** (Bentham) C. DC.; AY326207, —; Colombia, *MAJ 781* (DUKE). *P. haughtii* Trel. & Yunck.; EU581233, —; Colombia, *MAJ 98* (DUKE). ***P. hebetifolium*** W. C. Burger (1); EF056261, EU581537; Costa Rica, *EJT 448* (MU); ***P. hebetifolium*** W. C. Burger (2); EF056262, —; Costa Rica, *EJT 454* (MU). ***P. hernandiaefolium*** Vahl; AY572324, —; Vietnam, *MAJ 475* (DUKE). ***P. hirtellipetiolum*** C. DC.; EU581234, —; Panamá, *EJT 983* (MU). ***P. hispidum*** Sw. (1); AF275156, EU581538; Colombia, *MAJ 53* (DUKE); ***P. hispidum*** Sw. (2); EU581235, —; French Guiana, *EJT 529* (MU); ***P. hispidum*** Sw. (3); EU581236, —; French Guiana, *EJT 612* (MU); ***P. hispidum*** Sw. (4); EU581237, —; Honduras, *AB 701* (SEMO); ***P. hispidum*** Sw. (5); EU581238, —; Costa Rica, *CD 10891* (SRP); ***P. hispidum*** Sw. (6); EU581239, —; Panamá, *EJT 1021* (MU); ***P. hispidum*** Sw. (7); EU581240, —; México, *RMC 745* (HEM); ***P. hispidum*** Sw. (8); EU581241, —; Brazil, *MCS 304* (RB); ***P. hispidum*** Sw. (9); EU581242, —; México, *RMC 746* (SRP); ***P. hispidum*** Sw. (10); EU581243, —; Panamá, *EJT 978* (MU); ***P. hispidum*** Sw. (11); EU581244, —; Brazil, *MAJ 847* (RB); ***P. hispidum*** Sw. (12); EU581245, —; Brazil, *MAJ 869* (RB). ***P. hoffmannseggianum*** Schult.; EU581246, EU581539; Brazil, *MAJ 891* (RB). ***P. holdridgeianum*** W. C. Burger; EU581247, —; Costa Rica, *CD 10865* (SRP); ***P. holdridgeianum*** W. C. Burger; EU581248, —; Costa Rica, *JF 9128* (MO). ***P. hooglandii*** (I.Hutton & P.S.Green) M. A. Jaram.; AF275192, EU581540; New Zealand, *ROG 8496* (AK). ***P. hostmannianum*** C. DC. (1); EU581249, —; French Guiana, *EJT 573* (MU); ***P. hostmannianum*** C. DC. (2); EU581250, —; French Guiana, *EJT 599* (MU); ***P. hostmannianum*** C. DC. (3); EU581251, —; French Guiana, *SM 25228* (NY). ***P. humistratum*** Görts & Kramer (1); EU581252, —; French Guiana, *EJT 542* (MU); ***P. humistratum*** Görts & Kramer (2); EU581253, EU581541; French Guiana, *SM 25227* (NY). ***P. hymenophyllum*** (Miq.) Wight; AY572327, EU581542; Vietnam, *MAJ 505* (DUKE). ***P. ilheusense*** Yunck.; EU581254, —; Brazil, *MAJ 786* (RB). ***P. imberbe*** Trel. & Standl.; EU581255, EU581543; Honduras, *AB 983* (SEMO). ***P. immutatum*** Trel.; EU581256, EU581544; Ecuador, *EJT 1590* (MU). ***P. imperiale*** C. DC. (1); EF056263, —; Costa Rica, *EJT 402* (MU); ***P. imperiale*** C. DC. (2); EF056264, —; Costa Rica, *EJT 473* (MU); ***P. imperiale*** C. DC. (3); EF056265, —; Costa Rica, *EJT 989* (MU); ***P. imperiale*** C. DC. (4); AF275176, —; Colombia, *MAJ 61* (DUKE). ***P. inaequale*** C. DC. (1); EU581257, —; Colombia, *MAJ 127* (DUKE); ***P. inaequale*** C. DC. (2); EU581258, —; Colombia, *MAJ 134* (DUKE); ***P. inaequale*** C. DC. (3); EU581259, —; Colombia, *MAJ 118* (DUKE). ***P. insipiens*** Trel. & Yunck. (1); EU581260, —; French Guiana, *EJT 536*; (MU); ***P. insipiens*** Trel. & Yunck. (2); EU581261, —; French Guiana, *EJT 545* (MU); ***P. insipiens*** Trel. & Yunck. (3); EU581262, —; French Guiana, *EJT 533* (MU); ***P. insipiens*** Trel. & Yunck. (4); EU581263, —; French Guiana, *EJT 535* (MU). ***P. jacquemontianum*** Kunth; EU581264, EU581545; Honduras, *AB 700* (SEMO). ***P. juliflorum*** Nees & Mart.; EU581265, —; Brazil, *MJK 257* (SPF). ***P. klotzschianum*** C. DC.; EU581266, —; Brazil, *MAJ* 976 (RB). ***P. lacunosum*** Kunth (1); EU581267, —; Costa Rica, *EJT 443* (MU); ***P. lacunosum*** Kunth (2); EU581268, —; Panamá, *EJT 1057* (MU). ***P. laevigatum*** Kunth (1); EU581269, —; Peru, *JS 7167*, (UMO); ***P. laevigatum*** Kunth (2); EU581270, —; Peru, *JZ 626* (HUA); ***P. laevigatum*** Kunth (3); EU581271, —; Bolivia, *AM 1463* (MO). ***P. lanceifolium*** Kunth (1); EU581272, EU581547; Colombia, *EJT 184* (MU); ***P. lanceifolium*** Kunth (2); EU581273, —; Costa Rica, *EJT 1051* (MU). ***P. laosanum*** C. DC.; AY572326, EU581548; Vietnam, *MAJ 468* (DUKE). ***P. lapathifolium*** Steud.; EU581274, EU581549; México, *AR 2296* (XAL). ***P. latifolium*** G. Forst.; EF635465, —; Cook Islands, no voucher; ***P. leptostachyum*** Wall. ex Miq.; EU581275, EU581550; Vietnam, *MAJ 510* (DUKE). ***P. lepturum*** Kunth (1); EU581276, —; Brazil, *MAJ 909* (RB); ***P. lepturum*** Kunth (2); EU581277, —; Brazil, *MAJ 967* (RB). ***P. littorale*** C. DC.; EU581278, —; Colombia, *MAJ 130* (DUKE). ***P. lolot*** C. DC., AY326208, EU581553; Vietnam, *MAJ 234* (DUKE). ***P. longepilosum*** C. DC.; EF056266, EU581555; Ecuador, *EJT 1387* (MU). ***P. longestylosum*** C. DC. (1); EU581279, EU581554; Bolivia, *AM 1228* (MO). ***P. longestylosum*** C. DC. (2); EU581280, —; Bolivia, *AM 1172* (MO). ***P. longicaudatum*** Trel. & Yunck. (cf); EU581281, —; Ecuador, *EJT 1578* (MU). ***P. longispicum*** C. DC. (1); AY326209, EU581556; Colombia, *MAJ 739* (DUKE); ***P. longispicum*** C. DC. (2); EF056267, —; French Guiana, *EJT 410* (MU). ***P. longivaginans*** C. DC.; EU581282, EU581557; Philippines, *MAJ 207* (DUKE). ***P. longivillosum*** Trel. & Yunck. (1); AY326221, —; Colombia, *MAJ 605*, (DUKE); ***P. longivillosum*** Trel. & Yunck. (2); EU581283, —; Colombia, *MAJ 64* (DUKE). ***P. lunulibracteatum*** C. DC.; EU581284, —; Ecuador, *VZ 2854* (MO). *P. macropiper* Pennant (1); AF275202, —; Philippines, *MAJ 192* (DUKE); ***P. macropiper*** Pennant (2); EF060073, —; Indonesia, *RA 10* (BO); ***P. macropiper*** Pennant (3); EF060074, —; Indonesia, *RA 22* (BO). ***P. macrotrichum*** C. DC.; EU581285, —; Ecuador, *EJT 1437* (MU). ***P. majusculum*** Blume; EU581286, EU581559; Philippines, *MAJ 202* (DUKE). ***P. maranyonense*** Trel.; EU581287, —; Colombia, *MAJ 58* (DUKE). ***P. marequitense*** C. DC.; AY326210, —; Colombia, *MAJ 772* (DUKE). ***P. marginatum*** Jacq. (1); AY326211, EU581560; Ecuador, *MAJ 713* (DUKE); ***P. marginatum*** Jacq. (2); EU581288, —; French Guiana, *EJT 588* (MU); ***P. marginatum*** Jacq. (3); EU581289, —; Brazil, *MJK 571* (SPF); ***P. marginatum*** Jacq. (4); EU581290, —; Panamá, *EL s/n*, no voucher; ***P. marginatum*** Jacq. (5); EU581291, —; Brazil, *MJK 759* (MG). ***P. marsupiiferum*** Trel. (1); EF056268, EU581561; Cultivated, *EJT 511* (MU); ***P. marsupiiferum*** Trel. (2); EF056269, —; Ecuador, *EJT 1431* (MU). ***P. martensianum*** C. DC. (1); EU581292, EU581562; Honduras, *AB 951* (SEMO); ***P. martensianum*** C. DC. (2); EU581293, EU581563; Honduras, *AB 958* (SEMO); ***P. martensianum*** C. DC. (3); EU581294, —; Nicaragua, *AB 746* (SEMO). ***P. massiei*** C. DC.; EU581295, —; Vietnam, *MAJ 478* (DUKE). ***P. maxonii*** C. DC.; EF056270, EU581564; Costa Rica, *EJT 370* (MU). ***P. medinillifolium*** Quisumb.; EU581296, EU581565; Philippines, *MAJ 196* (DUKE). ***P. melanocladum*** C. DC.; EF056271, EU581566; Costa Rica, *EJT 134* (MU). ***P. melastomoides*** Schltdl. & Cham.; EU581297, —; México, *MN 26814* (XAL). ***P. melchior*** (Sykes) M. A. Jaram. (1); EF635477, —; New Zealand, no voucher; ***P. melchior*** (Sykes) M. A. Jaram. (2); AF275191, —; New Zealand, *ROG 8495* (AK). ***P. methysticum*** G.Forst. (1); EU581298, EU581567; Hawaii, *WCM 2957* (HAW); ***P. methysticum*** G.Forst. (2); AF275194, —; Cultivated, Accession # 950585 (NTBG); ***P. mexiae*** Trel. & Yunck.; EU581299, —; Ecuador, *EJT 1398* (MU). ***P. michelianum*** C. DC.; AF275188, EU581568; México, *MAJ 537* (DUKE). ***P. mollicomum*** Kunth (1), EU581300, —; Brazil, *MCS 271* (RB); ***P. mollicomum*** Kunth (2); EU581301, —; Brazil, *MAJ 795* (RB). ***P. mollissimum*** Blume; EF060075, —; Indonesia, *RA 15* (BO). ***P. mosenii*** C. DC.; EU581302, —; Brazil, *MAJ 876* (RB). ***P. mourai*** Yunck., EU581303, —; Brazil, *MAJ 914* (RB). ***P. muelleri*** C. DC.; EU581304, EU581569; México, *MAJ 541* (DUKE). ***P. mullesua*** Buch.-Ham.; AF203634, —; China, no voucher. ***P. multiplinervium*** C. DC. (1), AF275168, EU581570; Colombia, *MAJ 139* (DUKE). ***P. multiplinervium*** C.

DC. (2), EU581305, EU581571; Costa Rica, *CD 10899* (SRP). *P. munchanum* C. DC., AF275164, EU581572, Colombia, *MAJ 120* (DUKE). ***P. muricatum*** Blume (1); EF060076, —; Indonesia, *RA 20* (BO); ***P. muricatum*** Blume (2); EU581306, EU581573; Malaysia, *WSW 2* (SRP). ***P. mutabile*** C. DC. (2); EU581307, EU581574; China, *LJM 06183* (PE). ***P. myrmecophilum*** C. DC.; AY572328, EU581575; Philippines, *MAJ 205* (DUKE). ***P. napopastazanum*** Trel. & Yunck.; EU581308, EU581576; Ecuador, *EJT 1589* (MU). ***P. neesianum*** C. DC. (1); EU581309, EU581577; Guatemala, *AB 966* (SEMO); ***P. neesianum*** C. DC. (2); EU581310, —; Guatemala, *AB 973* (SEMO); ***P. neesianum*** C. DC. (3); EU581311, —; México, *MAJ 1007* (UMO). ***P. nicoyanum*** C. DC.; EU581312, —; Costa Rica, *UC 1634* (HUA). ***P. nigrum*** L. (1); AF275198, —; Philippines, *MAJ 181* (DUKE); ***P. nigrum*** L. (2); EF060077, —; Indonesia, *RA 13* (BO); ***P. nigrum*** L. (3); AF275197, —; Cultivated, Duke Accession # 94-006, no voucher; ***P. nigrum*** L. (4); EU581313, —; Cultivated, *JFS 5807* (SRP). ***P. nitidum*** Sw.; EU581314, —; México, *AR 2312* (XAL). ***P. nobile*** C. DC.; EU581315, —; Venezuela, *TC 60527* (MO). ***P. novogalicianum*** Bornstein; EU581316, —; México, *MAJ 549* (DUKE). ***P. novogranatense*** C. DC.; EU581317, EU581528; Colombia, *MAJ 71* (DUKE). ***P. nudibaccatum*** Y.C.Tseng; EU581318, EU581552; China, *LJM 06147* (PE). ***P. nudicaule*** C. DC.; EU581319, EU581578; Costa Rica, *CD 10897* (SRP). ***P. nudifolium*** C. DC.; EU581320, EU581579; Costa Rica, *EJT 469* (MU); ***P. nudifolium*** C. DC. (cf); EU581321, —; Panamá, *EJT 973* (MU). ***P. obliquum*** Ruiz & Pav. (1) (cf); EU581322, —; México, *HGD 254* (HEM); ***P. obliquum*** Ruiz & Pav. (2) (cf); EU581323, —; Panamá, *EJT 1022* (MU); ***P. obliquum*** Ruiz & Pav. (1); EF056275, EU581580; Panama, *EJT 1022* (MU); ***P. obliquum*** Ruiz & Pav. (2); EF056273, EU581581; Costa Rica, *EJT 351* (MU); ***P. obliquum*** Ruiz & Pav. (3); EF056272, —; Costa Rica, *EJT 114* (MU); ***P. obliquum*** Ruiz & Pav. (4); EU581324, —; Costa Rica, *EJT 345* (MU); ***P. obliquum*** Ruiz & Pav. (5); EF056274, —; Panamá, *EJT 974*, (MU); ***P. obliquum*** Ruiz & Pav. (6); EU581325, —; Brazil, *MAJ 830* (RB); ***P. obliquum*** Ruiz & Pav. (7); EU581326, —; Nicaragua, *AB 738* (SEMO). ***P. obovatum*** Ruiz & Pav.; AY326213, —; Colombia, *MAJ 759* (DUKE); ***P. obtusilimbum*** C. DC. (1); EU581327, EU581582; Ecuador, *EJT 1432* (MU); ***P. obtusilimbum*** C. DC. (2); EU581328, —; Cultivated, *EJT 512* (MU). ***P. otophorum*** C. DC.; EU581329, —; Panamá, *ETJ 981* (MU). ***P. ottoniaefolium*** C. DC.; AY326213, EU581583; Colombia, *MAJ 759* (DUKE). ***P. ovatum*** Vahl.; EU581330, —; Trinidad & Tobago, *NJ s/n*, no voucher. ***P. oviedoi*** Urb.; EU581331, —; Haiti, *WSJ 6850* (FLAS). ***P. oxystachyum*** C. DC.; AF275142, EU581584; Colombia, *MAJ 140* (DUKE). ***P. paramaribense*** C. DC.; EU581332, —; French Guiana, *EJT 544* (MU). ***P. pedunculatum*** C. DC.; EU581333, —; Colombia, *MAJ 597* (DUKE). ***P. peltatum*** L. (1); AF275171, EU581586; Colombia, *JB s/n*, no voucher; ***P. peltatum*** L. (2); AF275170, EU581587; Colombia, *MAJ 45* (DUKE); ***P. peltatum*** L. (3); EU581334, —; Panamá, *EL* s/n, no voucher; ***P. peltatum*** L. (4); EU581335, —; México, *MAJ 564* (DUKE); ***P. peltatum*** L. (5); AF275169, —; Colombia, *MAJ 142* (DUKE); ***P. peltatum*** L. (6); EU581336, —; French Guiana, *EJT 589* (MU). ***P. pendulispicum*** C. DC.; EU581337, EU581588; Vietnam, *MAJ 396* (DUKE). ***P. penninerve*** C. DC.; AF275206, —; Philippines, *MAJ 213* (DUKE); ***P. perareolatum*** C. DC.; EF056279, —; Perú, *AlG 74657* (MO). ***P. perlasense*** Yunck.; EU581338, EU581589; Panamá, *EL s/n*, no voucher. ***P. perpusillum*** Callejas; AY326215, —; Ecuador, *MAJ 699* (DUKE). ***P. phytolaccifolium*** Opiz (1); AY326216, EU581590; Colombia, *MAJ* 599 (DUKE); ***P. phytolaccifolium*** Opiz (2); EU581339, —; Honduras, *AB 982* (SEMO). ***P. pierrei*** C. DC.; AF275200, EU581591; Vietnam, *MAJ 394* (DUKE). ***P. pilibracteum*** Trel. & Yunck.; AY768829, —; Colombia, *MAJ* 746 (DUKE). ***P. piluliferum*** Kunth; EU581340, —; Ecuador, *EJT 1411* (MU). ***P. pingbienense*** Y.C.Tseng; EU581341, EU581592; China, *LJM 06151* (PE). ***P. piscatorum*** Trel. & Yunck. (1); EU581342, EU581455; Brazil, *MJK 758* (MG); ***P. piscatorum*** Trel. & Yunck. (2); EU581343, —; Brazil, *MJK 730* (MG); ***P. piscatorum*** Trel. & Yunck. (3); EU581344, —; Brazil, *SSB 667* (HUA). ***P. pittieri*** C. DC.; EU581345, —; Costa Rica, *EJT 444* (MU). ***P. porphyrophyllum*** N.E.Br.; EU581346, EU581593; Malaysia, *WSW 3* (SRP). ***P. praesagium*** Trel. & Yunck. (1); EU581347, —; Colombia, *MAJ 68*, (DUKE); ***P. praesagium*** Trel. & Yunck. (2); EU581348, —; Colombia, *MAJ 82* (DUKE). ***P. premnospicum*** Tebbs; EU581349, —; Panamá, *EJT 1030* (MU). ***P. pseudofuligineum*** C. DC.; EU581350, —; Honduras, *AB 710* (SEMO). ***P. pseudolanceifolium*** Trel.; EU581351, —; Costa Rica, *K 1297* (MO). ***P. pseudolindenii*** C. DC. (1); EU581352, EU581594; Honduras, *AB 952* (SEMO); ***P. pseudolindenii*** C. DC. (2); EU581353, —; Honduras, *AB 711* (SEMO); ***P. pseudolindenii*** C. DC. (3); EU581354, —; Honduras, *AB 718* (SEMO); ***P. pseudolindenii*** C. DC. (4); EU581355, —; Guatemala, *AB 974* (SEMO). ***P. pseudonobile*** C. DC. (1); EF056281, EU581595; Ecuador, *BB 3521* (MO); ***P. pseudonobile*** C. DC. (2); EF056280, —; Ecuador, *EJT 1417* (MU). ***P. pseudopothifolium*** C. DC. (1); EU581356, EU581596; Brazil, *MAJ 943* (RB); ***P. pseudopothifolium*** C. DC. (2); EF056282, —; Brazil, *MAJ 935* (RB). ***P. psilorhachis*** C. DC. (1); EU581357, EU581597; Guatemala, *AB 979* (SEMO); ***P. psilorhachis*** C. DC. (2); EU581358, EU581598; Guatemala, *AB 963* (SEMO). ***P. pterocladum*** C. DC.; EU581359, —; Bolivia, *AM 1079*, (MO). ***P. puberulum*** Benth.; EU581360, —; Cultivated, *TF 6749* (PTBG). ***P. pubistipulum*** C. DC.; EU581361, —; Panamá, *EJT 976* (MU). ***P. pulchrum*** C. DC. (1); AF275177, EU581599; Colombia, *MAJ 100* (DUKE); ***P. pulchrum*** C. DC. (2); EU581362, —; Perú, *AlG 74657* (MO). ***P. quinqueangulatum*** Miq.; AF275208, EU581546; Philippines, *MAJ 184* (DUKE). ***P. recurvum*** Blume (1); EF060078, —; Indonesia, *RA 07* (BO); ***P. recurvum*** Blume (2); EF060079, —; Indonesia, *RA* 18 (BO). ***P. reticulatum*** L. (1); EU581363, EU581600; Bolivia, *AM 1603* (MO); ***P. reticulatum*** L. (2); EU581364, EU581601; Ecuador, *EJT 1395* (MU); ***P. reticulatum*** L. (3); EU581365, —; Panamá, *EJT 1015* (MU); ***P. reticulatum*** L. (4); EU581366, —; Panamá, *EJT 979* (MU); ***P. reticulatum*** L. (5); EU581367, —; Panamá, *EL s/n*, no voucher; ***P. reticulatum*** L. (6); AF275184, —; Colombia, *MAJ 128* (DUKE); ***P. reticulatum*** L. (7); AF275185, —; Colombia, *MAJ 62* (DUKE). ***P. retrofractum*** Vahl. (1); AF275196, EU581602; Vietnam, *MAJ 395* (DUKE); ***P. retrofractum*** Vahl. (2); EF060081, —; Indonesia, *RA 32* (BO); ***P. retrofractum*** Vahl. (3); EF060080, —; Indonesia, *RA 28* (BO); ***P. retrofractum*** Vahl. (4); EF060069, —; Indonesia, *RA 08* (BO). ***P. richardiaefolium*** Kunth (1); EU581368, —; Brazil, *MAJ 925* (RB); ***P. richardiaefolium*** Kunth (2); EU581369, —; Brazil, *MCS 307* (RB); ***P. richardiaefolium*** Kunth (3); EU581370, —; Brazil, *MAJ 852*, (RB). ***P. riparense*** C. DC. (1); EU581371, EU581603; Costa Rica, *EJT 339* (MU); ***P. riparense*** C. DC. (2); EU581372, —; Panamá, *EJT 972* (MU). ***P. robustipedunculum*** Yunck.; EU581373, —; Brazil, *MAJ 871* (RB). ***P. rugosum*** Lam.; EU581374, —; Haiti, *WSJ 6851* (FLAS). ***P. rusbyi*** C. DC.; EU581375, EU581604; Bolivia, *AM 1216* (MO). ***P. sabaletasanum*** Trel. & Yunck.; AY326217, —; Colombia, *MAJ 623* (DUKE). ***P. sagittifolium*** C. DC. (1); EF056284, EU581605; Costa Rica, *EJT 116* (MU); ***P. sagittifolium*** C. DC. (2); EF056285, —; Costa Rica, *EJT 320* (MU); ***P. sagittifolium*** C. DC. (3); EU581376, EU581606; Cultivated, *MAJ s/n*, no voucher. ***P. samanense*** Urb., EU581377, —; Dominican Republic, *PAR 8548* (MO). ***P. sampaioi*** Yunck.; EU581378, —; Brazil, *MAJ 916* (RB). ***P. sanctifelicis*** Trel. (1); EU581379, EU581607; México, *AR 2429* (XAL); ***P. sanctifelicis*** Trel. (2); EU581380, —; Costa Rica, *CD 10887* (SRP). ***P. sanctum*** (Miq.) Schltdl. ex C. DC. (1); EU581381, EU581608; Mexico, *AR 2352* (XAL); ***P. sanctum*** (Miq.) Schltdl. ex C. DC. (2); EU581382, EU581609; Nicaragua, *AB 744* (SEMO); ***P. sanctum*** (Miq.) Schltdl. ex C. DC. (3); EU581383, EU581610; Mexico, *HGD 251* (HEM); ***P. sanctum*** (Miq.) Schltdl. ex C. DC. (4); EU581384, EU581611; Mexico, *MA 2820* (HEM). ***P. sarmentosum*** Roxb. (1); EF060082, —; Indonesia, *RA 17* (BO); ***P. sarmentosum*** Roxb. (2); EU581385, —; Cultivated, *JFS 5806* (SRP). ***P. sasaimanum*** Yunck.; EF056286, EU581612; Panamá, *EJT 1055* (MU). ***P. schiedeanum*** Steud.; EU581386, —; Panamá, *EL s/n*, no voucher. ***P. schuppii*** A. H. Gentry; AY326218, —; Ecuador, *MAJ 687* (DUKE). ***P. schwackei*** C. DC. (1); EU581387, —; Brazil, *MJK 732* (MG); ***P. schwackei*** C. DC. (2); EU581388, —; Brazil, *MJK 767* (MG). **P. *scutifolium*** Yunck.; EU581389, —; Brazil, *MJK 281* (SPF). ***P. scutilimbum*** C. DC.; EU581390, —; Ecuador, *EJT 1438* (MU). ***P. semi-immersum*** C. DC.; EU581391, EU581613; China, *LJM 06161* (PE). ***P. solmsianum*** C. DC. (1); EU581392, EU581614; Brazil, *MAJ 881* (RB); ***P. solmsianum*** C. DC. (2); EU581393, —; Brazil, *MJK 176*; (SPF). ***P. sorsogonum*** C. DC.; AY572320, EU581615; Philippines, *MAJ 185* (DUKE). ***P.* sp.;** EU581394, EU581531; Ghana, *ABG 36 1* (Aburii Botanical Garden Herbarium). ***P. sp. nov.*** 1; AY326227, EU581627; Colombia, *RC 11854* (HUA). ***P. sp. nov.* 2**, AF275182, EU581625; Brazil, *CC 2* (DUKE). ***P. sp. nov.* 3** (1); EU581395, —; Ecuador, *MAJ 674* (DUKE); ***P. sp. nov.* 3** (2); EU581396, —; Ecuador, *MAJ 646* (DUKE). ***P. sp. nov.* 4**; EF056244, —; Colombia, *RC 6431* (MO). ***P. sp. nov.* 5**; AY326230, —; Ecuador, *MAJ 689* (DUKE); ***P. sp. nov.* 6**; AY326206, —; Colombia, *MAJ 694* (DUKE). ***P. sp. nov.* 7**; EU594345, —; Brazil, *GV 430* (RB). ***P. sphaerocarpum*** (Griseb.) C.Wright; EU581397, —; Cuba, *JRA 18913* (FLAS). ***P. spoliatum*** Trel. & Yunck.; AF275179, EU581616; Colombia, *MAJ 60* (DUKE). ***P. sprengelianum*** C. DC.; EU581398, —; Brazil, *MAJ 837* (RB). ***P. squamulosum*** C. DC. (1); EF056287, EU581617; Ecuador, *EJT 1375* (MU); ***P. squamulosum*** C. DC. (2); EF056288, —; Ecuador, *WHC 3747* (US). ***P. sternii*** Yunck.; EU581399, —; Ecuador, *EJT 1393* (MU). ***P. stileferum*** Yunck.; EU581400, —; Ecuador, *EJT 1631* (MU). ***P. stipulaceum*** Opiz; EU581401, —; México, *MAJ 551* (DUKE). ***P. subflavum*** C. DC.; EU581402, —; Colombia, *BRR 1736* (HUA). ***P. subglabribracteatum*** C. DC. (1); EU581403, —; Colombia, *AC 7784* (MO); ***P. subglabribracteatum*** C. DC. (2); EF056289, —; Ecuador, *BMB 2608* (US); ***P. subglabribracteatum*** C. DC. (3); AY326220, —; Colombia, *MAJ 747* (DUKE). ***P. submultinerve*** C. DC. var. nandanicum Y.C.Tseng; EU581404, EU581551; China, *LJM 061410* (PE). ***P. subpedale*** Trel. & Yunck.; AF275161, —; Colombia, *MAJ 57* (DUKE). ***P. subpenninerve*** Ridl.; EU581405, EU581618; Malaysia, *WSW 1* (SRP). ***P. subscutatum*** C. DC.; EU581406, EU581619; Ecuador, *EJT 1604* (MU). ***P. subsessilifolium*** C. DC.; EU581407, —; Panamá, *EJT 1003* (MU).

P. tardans Trel.; EF056290, —; Panamá, *EJT 1056* (MU). (Kunth) Steud.; EU581408, —; French Guiana, *EJT 547* (MU). ***P. terryae*** Standley; AY326221, —; Colombia, *MAJ 605* (DUKE). ***P. thomasii*** Tebbs; EU581409, —; Panamá, *EJT 1038* (MU). ***P. thomsonii*** Hook.f.; EU581410, EU581620; China, *LJM* 061511 (PE). ***P. tomas-albertoi*** Trel. & Yunck. AY326222, —; Colombia, *RC s/n*, no voucher. ***P. tonduzii*** C. DC.; EU581411, —; Costa Rica, *GD 37274* (HUA). ***P. toppingii*** C. DC.; AY572322, —; Philippines, *MAJ 186* (DUKE). ***P. trianae*** C. DC. (1); EU581412, —; Ecuador, *EJT 1392* (MU); ***P. trianae*** C. DC. (2); EU581413, —; Ecuador, *MAJ 662* (DUKE). ***P. trichoneuron*** (Miq.) C. DC.; EU581414, —; French Guiana, *EJT 549* (MU). ***P. tricuspe*** C. DC.; AY326224, —; Colombia, *AG 41* (CUCV). ***P. trigonum*** C. DC. (1); EU581415, EU581621; Costa Rica, *CD 10881* (SRP). ***P. trigonum*** C. DC. (2); EU581416, —; Colombia, *MAJ 52* (DUKE); ***P. trigonum*** C. DC. (3); EU581417, —; Panamá, *EJT 1007* (MU); ***P. trigonum*** C. DC. (4); EU581418, —; Panamá, *EJT 1026* (MU); ***P. trigonum*** C. DC. (5); EU581419, —; Costa Rica, *CD 10874* (SRP); ***P. trigonum*** C. DC. (6); EU581420, —; Panamá, *EJT 1019* (MU); ***P. trigonum*** C. DC. (7); EU581421, —; Panamá, *EJT 980* (MU). ***P. truncatibaccum*** C. DC.; EU581422, —; New Guinea, *WT 14507* (GH). ***P. truncatum*** Vell. (1); EF056291, EU581622; Brazil, *MAJ 937* (RB); ***P. truncatum*** Vell. (2); EU581423, —; Brazil, *MAJ 971* (RB). ***P. tuberculatum*** Jacq. (1); EF056292, EU581623; Panamá, *EJT 1061* (MU); ***P. tuberculatum*** Jacq. (2); EU581424, EU581624; Brazil, *MJK 741* (SPF); ***P. tuberculatum*** Jacq. (3); EF056293, —; Belize, *MAV 5989* (MU); ***P. tuberculatum*** Jacq. (4); EU581425, —; Brazil, *MJK 573* (SPF); ***P. tuberculatum*** Jacq. (5); AY326225, —; Ecuador, *MAJ 710* (DUKE); ***P. tuberculatum*** Jacq. (6); EU581426, —; Honduras, *AB 699* (SEMO). ***P. tuerckheimii*** C. DC.; EU581427, —; Honduras, *AB 941* (SEMO). ***P. umbellatum*** L. (1); AF275172, EU581626; Brazil, *AFO 1251* (DUKE); ***P. umbellatum*** L. (2); EU581428, —; Honduras, *AB 709* (SEMO); ***P. umbellatum*** L. (3); EU581429, —; Panamá, *EJT 998* (MU); ***P. umbellatum*** L. (4); AF275174, —; Cultivated, FBG Accession # 78-211B, no voucher; ***P. umbellatum*** L. (5); EU581430, —; New Guinea, *GW 2435* (MIN); ***P. umbellatum*** L. (6); EU581431, —; Dominican Republic, *LAH 446* (SRP); ***P. umbellatum*** L. (7); EU581432, —; México, *MA 2904* (HEM); ***P. umbellatum*** L. (8); AF275173, —; Philippines, *MAJ 224* (DUKE); ***P. umbellatum*** L. (9); EU581433, —; Colombia, *MAJ 35* (DUKE). ***P. umbricola*** C. DC.; EU581434, —; Honduras, *AB 721* (SEMO); ***P. umbricola*** C. DC. (cf); EU581435, —; Panamá, *EJT 1014* (MU). ***P. umbriculum*** (Cuatrec.) M.A. Jaram. & Callejas; AY326226, —; Colombia, *MAJ 602* (DUKE). ***P. urdanetanum*** C. DC.; AF275207, —; Philippines, *MAJ 232* (DUKE). ***P. urophyllum*** C. DC.; EU581436, —; Costa Rica, *EJT 421* (MU). ***P. urostachyum*** Hemsl. (1); EU581437, —; Nicaragua, *AB 757* (SEMO); ***P. urostachyum*** Hemsl. (2); EU581438, —; Costa Rica, *CD 10870* (SRP). ***P. vellosoi*** Yunck.; EU581439, EU581628; Brazil, *MAJ 872* (RB). ***P. vicosanum*** Yunck.; EU581440, —; Brazil, *MAJ 809* (RB). ***P. villiramulum*** C. DC.; EU581441, EU581629; Honduras, *AB 947* (SEMO). ***P. villosum*** C. DC.; AY326228, —; Ecuador, *MAJ 667* (DUKE). ***P. vitaceum*** Yunck.; EU581442, —; Perú, *RV 1405* (MO). ***P. wachenheimii*** Trel.; EU581443, —; French Guiana, *EJT 574* (MU). ***P. wallichii*** Hand.-Mazz.; EU581444, EU581630; China, *LJM 06212* (PE). ***P. xanthostachyum*** C. DC. (1); EU581445, —; Nicaragua, *AB 732* (SEMO); ***P. xanthostachyum*** C. DC. (2); EU581446, —; Panamá, *EJT 1058* (MU). ***P. xylosteoides*** Steud.; EU581447, —; Brazil, *MJK 262* (SPF). ***P. yanaconasense*** Trel. & Yunck.; AY326229, —; Colombia, *MAJ 774* (DUKE). ***P. yucatanense*** C. DC. (1); EU581448, EU581631; Honduras, *AB 724* (SEMO); ***P. yucatanense*** C. DC. (2); EU581449, EU581632; Honduras, *AB 956* (SEMO); ***P. yucatanense*** C. DC. (3); EU581450, EU581633; México, *MA 2898* (SRP); ***P. yucatanense*** C. DC. (4); EU581451, —; Guatemala, *AB 969* (SEMO); ***P. yucatanense*** C. DC. (5); EU581452, —; Honduras, *AB 984* (SEMO).

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