

## A LATE CRETACEOUS *PIPER* (PIPERACEAE) FROM COLOMBIA AND DIVERSIFICATION PATTERNS FOR THE GENUS<sup>1</sup>

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- *Premise of the study:* Documented fossil floras in the neotropics are sparse, yet their records provide evidence on the spatial and temporal occurrence of taxa, allowing for testing of biogeographical and diversification scenarios on individual lineages. A new fossil *Piper* from the Late Cretaceous of Colombia is described here, and its importance for assessing diversification patterns in the genus is addressed.
- *Methods:* Leaf architecture of 32 fossil leaf compressions from the Guaduas Formation was compared with that of 294 extant angiosperm species. The phylogenetic position of the fossil named *Piper margaritae* sp. nov. was established based on leaf traits and a molecular scaffold of *Piper*. The age of the fossil was independently used as a calibration point for divergence time estimations.
- *Key results:* Natural affinities of *P. margaritae* to the Schilleria clade of *Piper* indicate that the genus occurred in tropical America by the Late Cretaceous. Estimates of age divergence and lineage accumulation reveal that most of the extant diversity of the genus accrued during the last ~30 Myr.
- *Conclusions:* The recent radiation of *Piper* is coeval with both the Andean uplift and the emergence of Central America, which have been proposed as important drivers of diversity. This pattern could exemplify a recurrent theme among many neotropical plant lineages.

**Key words:** Colombia; dated phylogeny; fossil leaves; Guaduas Formation; Late Cretaceous; paleobotany; *Piper*; Piperaceae; radiation.

The neotropical region comprises around 37% of the world's flora (in numbers of species; Thomas, 1999), with an estimated total number of flowering plant species that exceeds the floral richness of tropical Africa, tropical Asia, and Oceania combined (Gentry, 1982; Thomas, 1999). Although the origin of this diversity remains elusive, standing hypotheses are not

mutually exclusive and explain extant biodiversity through museum or cradle models of diversification (Antonelli and Sanmartín, 2011). Whereas the museum model depicts the gradual accumulation and/or preservation of lineages over time (Mittelbach et al., 2007), the cradle model describes the recent and rapid accumulation of species. There are numerous examples of clades that have rapidly diversified within the last few million years in the lowland neotropics as well as in the high Andes (Richardson et al., 2001; Madriñán et al., 2013). The plant fossil record shows that extant lowland rainforests have been dominated by the same families at least since the middle Paleocene (Doria et al., 2008; Herrera et al., 2008; Gómez-Navarro et al., 2009; Wing et al., 2009; Carvalho et al., 2011; Ricklefs and Renner, 2012), and tropical plant diversity has not been steadily increasing, but rather has fluctuated during the Cenozoic (Jaramillo et al., 2006, 2010b; Jaramillo and Cárdenas, 2013). If a similar set of families has dominated the tropical forests for such a long time, why is there not a steady increase in diversity over time? The diversification of neotropical floras has been favored by instances of rapid radiations, yet the factors driving diversification do not seem to be constant though time in spite of acting on a similar set of genetic pools. A growing wealth of evidence indicates that the Andean uplift acted as a driver for diversification, not only because it generated new

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landscapes and ecosystems (e.g., páramo), but also because it altered regional climate, nutrient deposition, and riverine systems of lowland habitats throughout the Cenozoic (Hooen et al., 2010). Here, we present a case study of diversification patterns inferred for a highly speciose and ubiquitous genus with a presumed long history in tropical America.

We describe a new fossil *Piper* L. (Piperaceae) from the Late Cretaceous of Colombia, an emblematic and species-rich lineage of tropical rainforests with a scant, unreliable, and poorly studied fossil record. *Piper* is nested within the magnoliid order Piperales (APG, 2009), an early-diverging clade within angiosperms. With ~2000 species distributed pantropically (Fig. 1; Jaramillo and Manos, 2001; Quijano-Abril et al., 2006), *Piper* occurs from sea level up to 2500 m, with few species occurring above 3000 m (Gentry, 1990). Over 70% of all species are restricted to the neotropics, mainly concentrated in the Andean slopes, the Central American lowlands, and Central Amazonia (Jaramillo and Manos, 2001; Quijano-Abril et al., 2006). Within the neotropics, Andean floras have the highest number of *Piper* species per unit area, most of which have a wide distribution and are shared with floras of other biogeographical regions including Amazonia, the Atlantic forests of Brazil, and dry or wet forests of Central America (Marquis, 2004). The relatively young age of the Andean Cordillera, coupled with the diversity and close association of *Piper* species to Andean floras, is at odds with a scenario of a lineage with a long-standing history in tropical America, making this genus an example to test for diversification patterns that follow either a museum or a cradle model of evolution.

Recent molecular phylogenetic studies of Piperaceae have indicated *Piper* as monophyletic and sister to *Peperomia* Ruiz & Pav. (Jaramillo and Manos, 2001; Wanke et al., 2006, 2007; Jaramillo et al., 2008; Smith et al., 2008). Three major clades are recovered within *Piper*, and these have neotropical (1300 spp.), tropical Asian (600 spp.) and South Pacific (10 spp.) distributions (Fig. 1). Within the neotropical group, eight additional clades have been described. These follow the nomenclature of previously proposed genera: *Macrostachys* Miquel, *Radula* Miquel, *Peltobryon* Klotzsch, *Pothomorphe* C. DC., *Enckea* Kunth, *Otonia* Spreng, *Piper cinereum* C. DC./*Piper sanctum*

(Miq.) Schldl. ex C. DC., and *Schilleria* Kunth (Quijano-Abril et al., 2006; Jaramillo et al., 2008). The few endemic species that are present in Africa today are nested within the tropical Asian and South Pacific clades, and their distribution is probably the result of at least two separate dispersal events (Jaramillo et al., 2008).

Despite *Piper* having high species diversity, a wide geographical representation, and recent phylogenetic studies, its origin and evolution have barely been addressed (Jaramillo and Manos, 2001; Quijano-Abril et al., 2006; Jaramillo et al., 2008). Little is known about possible environmental drivers responsible for speciation processes and diversification ages within *Piper*. Piperales is a relatively early-diverging angiosperm lineage (Wikström et al., 2004; Moore et al., 2007; Bell et al., 2010; Naumann et al., 2013). Smith et al. (2008) used the topology of Piperales and the fossil record of *Lactoris* Phil. (Lactoridaceae) to establish a minimum stem age for Piperaceae/Saururaceae of 91.2 million years before present (Ma), and crown ages of *Piper* at 71.7 Ma and *Peperomia* at 88.9 Ma. Other molecular calibration analyses for Piperales using external calibration points have also estimated Cretaceous ages for the divergence of Piperaceae (111 Ma [98–122 Ma]; Naumann et al., 2013), and Paleogene ages for the divergence and diversification of *Piper* (e.g., 57 Ma; Symmank et al., 2011; 31 Ma [40–25 Ma]; Naumann et al., 2013). Even though these estimates suggest a Late Cretaceous origin for Piperaceae, the scant fossil record and lack of internal calibration points within Piperaceae limit cross-validation between estimated ages of divergence and fossil taxa, as well as further inferences on net diversification rates.

Several fossil leaves have been associated with *Piper* and described under *Piperites* Goepfert (Goepfert, 1854; Table 1). Nonetheless, their affinities to *Piper* are not entirely reliable. Most species of *Piperites* were described in the early 20th century, mostly based on single specimens, and have not been recently reevaluated (Table 1). Additionally, type and original materials are poorly preserved, and collection localities are not described in detail, making ages hard to corroborate. One exception is a well-preserved seed from the Pleistocene deposits of the Tequendama Lake (Wijninga, 1996) in the eastern

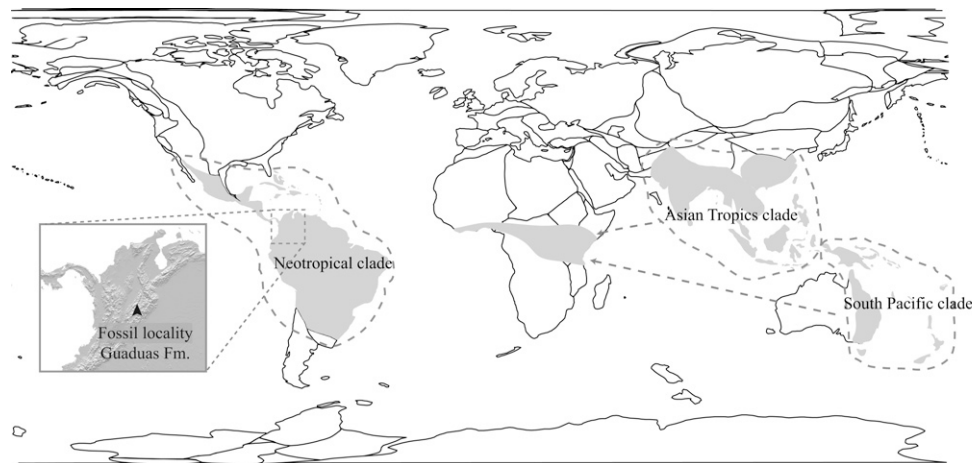


Fig. 1. Extant distribution of the genus *Piper* and location of the fossil locality. Gray color indicates the pantropical distribution of the genus *Piper*. The gray dashed lines demarcate the distribution of the principal clades within *Piper*. The black arrow shows the location of the Guaduas Formation in Colombia. Map modified from Paleogeographic Atlas from Scotese (2001). Distribution of *Piper* taken from Jaramillo and Manos (2001).

TABLE 1. Fossil leaves associated with *Piperites* Goeppert and *Piper* L.

Name	Age	Area	Locality	References
<i>Piper arcuatile</i>	Upper Cretaceous	Alaska	Yukon River, north bank	Hollick, 1936
<i>Piperites tuscaloosensis</i>	Upper Cretaceous	United States	Mississippi, Tuscaloosa Formation	Berry, 1919
<i>Piper chapinii</i>	Cenozoic	Alaska	Eska Creek	Hollick, 1936
<i>Piper concavum</i>	Cenozoic	Alaska	Kupreanof Island	Hollick, 1936
<i>Piper convertabilis</i>	Cenozoic	Alaska	Chignik Lake	Hollick, 1936
<i>Piper disputabilis</i>	Cenozoic	Alaska	Canyon Creek	Hollick, 1936
<i>Piper septentrionalis</i>	Cenozoic	Alaska	Chignik Lake	Hollick, 1936
<i>Piper feistmantelii</i>	Cenozoic	Australia	New South Wales, New England	von Ettingshausen, 1886
<i>Piper</i> sp.	Paleogene	Japan	Shinsaka, Tsushima Islands	Matsuo, 1971
<i>Piper europaeum</i>	Paleogene	Germany	Hesse, Messel near Darmstadt	Engelhardt, 1922
<i>Piperites bullatus</i>	Eocene	Java Island	Jampang District	Goeppert, 1854
<i>Piperites miquelianus</i>	Eocene	Java Island	Jampang District	Goeppert, 1854
<i>Piper heeri</i>	Eocene	United States	Golden, Colorado	Lesquereux, 1888
<i>Piper antiquum</i>	Eocene	Sumatra	Sangkarawang River	Heer, 1883
<i>Piper</i> sp.	Eocene	United States	Whatcom County, Washington	Knowlton, 1919
<i>Piperites quinquecostatus</i>	Miocene	Costa Rica	Northeast Talamanca Valley	Berry, 1921 <sup>a</sup>
<i>Piperites cordatus</i>	Miocene	Costa Rica	Northeast Talamanca Valley	Berry, 1921 <sup>a</sup>
<i>Piperites cordatus</i>	Miocene	Venezuela	Betijoque, Trujillo	Berry, 1936
<i>Piperites cf. cordatus</i>	Miocene	Trinidad and Tobago	Siparia, Trinidad	Berry, 1925
<i>Piperites potosiensis</i>	Pliocene	Bolivia	Potosí	Berry, 1939
<i>Piper erewhonensis</i>	Pliocene	New Zealand	Canterbury: Erewhon Station	McQueen, 1954
<i>Piper</i>	Pleistocene	Costa Rica	Near La Selva Biological Station	Horn et al., 2003

Note: <sup>a</sup> Specimens observed at the Paleobotanical Collection of the Smithsonian Institution.

cordillera of the Andes of Colombia, which seems to be related to the extant species *Piper bartlingianum* (Miq.) C. DC. (R. Callejas, Universidad de Antioquia, personal communication).

The fossils described here are leaf impressions and compressions from the Guaduas Formation, a Maastrichtian (Late Cretaceous) assemblage from the central Andes of Colombia. Given its age, this flora provides unique evidence of the early angiosperm-dominated forests in the neotropics. Preliminary analyses of leaf physiognomy of the Guaduas flora suggest a warm and wet paleoclimate, as is seen in extant tropical rainforests (Gutierrez and Jaramillo, 2007; Jaramillo et al., 2010a). In this paper we describe and assess the phylogenetic relationships of *Piper margaritae* sp. nov., a commonly recovered leaf morphotype from this flora, in an attempt to identify one of the components of this Late Cretaceous tropical forest. The phylogenetic relationships of this taxon within *Piper* allow us to better infer the diversification scenarios of a speciose, early-diverging lineage with a long-standing history in the neotropics, as an example of the complex processes that have led to the exceptional plant diversity of extant neotropical forests.

## MATERIALS AND METHODS

**Fossil locality and description**—Fossil leaves were collected by M. Gutiérrez in 2005 from a single fossil-bearing horizon (locality 0502) in the middle Guaduas Formation, at the Montecristo Ubaté underground coalmine, Cundinamarca, Colombia (5°14'08.5"N, 73°48'15.2"W, 2591 m a.s.l.; Fig. 1). The Guaduas Formation outcrops along the Eastern Cordillera of Colombia and is a sequence of coal seams interbedded with fluvial sandstones and mudstones. This depositional sequence suggests paleoenvironments that ranged from a supratidal zone to coastal floodplains and swamps in lowland settings (Sarmiento-Rojas et al., 2006; Amaya et al., 2010) and occurred before the uplift of the northern Andes. These sediments have been dated to be ca. 68–66 Ma based on palynological biostratigraphy (Correa et al., 2010) that has been calibrated using foraminifera (Muller et al., 1987).

Thirty-two partial to whole leaf specimens were associated with the morphotype informally named GD5. These were described based on leaf terminology

from Ellis et al. (2009) and were studied using a Nikon SMZ1500 stereoscope and photographed with a Nikon D90s camera with varied low-angle lighting. Some specimens were visualized using a scanning electron microscope (JSM-6490LV) to reveal venation details. Type specimens were drawn using a camera lucida attached to the stereoscope and digitized with Adobe Illustrator CS5 (San Jose, California, USA). All the fossil material studied was deposited at the paleontological collection of the Museo de Historia Natural of the Universidad de los Andes, in Bogotá, Colombia (ANDES-Paleo: 001–032).

**Comparison of fossil and extant leaves**—Leaf architecture characters of the fossils were compared with leaves of various extant angiosperm families. Eight families were selected based on the morphological similarities to the fossil morphotype: Aristolochiaceae, Ericaceae, Euphorbiaceae, Fabaceae, Menispermaceae, Piperaceae, Saururaceae, and Smilacaceae. The comparison was done using the National Cleared Leaf Collection at the Smithsonian Natural History Museum (NCLC-W), the botanical collections of the United States National Herbarium (US), the herbaria of the Universidad de Antioquia (HUA) and the Universidad Nacional de Colombia (COL), and the virtual Field Museum Neotropical Herbarium.

Subsequently, a more detailed revision of leaf morphology of all genera within Piperaceae was carried out. A morphological matrix of 33 leaf architecture characters (Appendix S1, see Supplemental Data with the online version of this article) and 230 species was built (Appendix S2, see online Supplemental Data). The morphological matrix included 221 species of *Piper* and nine species of *Peperomia* (Appendix 1). Species were chosen based on the most recent phylogeny of the genus (Jaramillo et al., 2008), aiming to include representative species of all major clades, geographical regions, and leaf morphological diversity of *Piper*. Leaf characters of *Peperomia* were partially scored based on morphological descriptions of Samain et al. (2009) and direct observation of herbarium specimens at US. Species of *Peperomia* were also included in the matrix to include an outgroup in subsequent phylogenetic analyses.

**Natural affinities**—We used a phylogenetic scaffolding approach (Springer et al., 2001; Manos et al., 2007; Herrera et al., 2011) to establish the affinities of the fossil taxon within clades of *Piper*. We first estimated relationships of living species of *Piper* using internal transcribed spacer (ITS) data and then used the resulting topology as a scaffold to ascertain the most parsimonious placement of our fossil using morphological characters.

The tree used as a backbone constraint was retrieved from 221 sequences of the ITS of species of *Piper*, in addition to sequences of nine species of *Peperomia* obtained from the GenBank accessions of Jaramillo et al. (2008) (Appendix 1). The species selected corresponded to those included in our morphological



matrix, which were chosen seeking an equal representation of all major clades, biogeographical areas, and variations in leaf morphology of *Piper*. The sequences were aligned using the program MUSCLE 3.6 (Edgar, 2004) of the European Molecular Biology Laboratory-European Bioinformatics Institute (Hinxton, UK; Goujon et al., 2010), producing an alignment of 987 characters. Maximum parsimony methods were implemented in the program WinClada-Asado (K. Nixon, Cornell University, Ithaca, New York, USA). All characters were unweighted and only parsimony-informative characters (PIC; 491 characters) were included. Fifty parsimony ratchet analyses (Nixon, 1999) were performed using 300 replicates per ratchet, holding one tree per iteration, and sampling 30% of the PIC. The strict consensus tree obtained was used as a phylogenetic scaffold for placing the fossil, using the leaf morphology matrix previously described.

The scaffold analysis was carried in the program PAUP\* (Swofford, 1999) and was based on a heuristic search with 10 replicates of random-sequence addition, tree bisection–reconnection, using the strict consensus tree (above) as a backbone constraint. All morphological characters were coded as unordered and were equally weighted (see online Appendix S1), and the maximum number of saved trees was set to 10000. As a final step, characters from the leaf morphology matrix were optimized onto the consensus tree that includes the fossil taxon, using an unordered parsimony algorithm implemented in the program Mesquite v. 2.75 (Maddison and Maddison, 2011). These characters are used to support the association of our fossil with the Schilleria clade of *Piper*, and the fossil was used to calibrate a minimum age for the divergence of the Schilleria clade.

**Divergence time estimation**—A dated phylogeny of *Piper* was estimated using the ITS sequences and species selection previously described for this genus. Because long-branch attraction and unequal sampling are known to introduce bias and reduce the accuracy of the age estimation (Bergsten, 2005), we excluded all accessions of *Peperomia* from this analysis. This new data set contained 221 species of *Piper* and 823 characters, and the sequences were realigned using the same parameters described above. The alignment is available from the database TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:S16846>). The best-fit substitution model for ITS region under the Akaike information criterion, as implemented in the program MrModelTest 2.2 (Nylander, 2004), was GTR+I+G. A likelihood ratio test was estimated between scores computed with and without enforcing a molecular clock in PAUP\*, indicating that the strict clock model should be rejected.

Two calibration and time divergence analyses were performed to assess divergence age sensitivity to internal node calibration. These compare the effect of placing the fossil calibration (66–68 Ma; Correa et al., 2010) at the divergence of the Schilleria clade, based on the natural affinities of our fossil, vs. an additional estimation using the divergence of the Neotropical clade as the internal calibration. The molecular scaffold approach used to place the fossil within *Piper* consistently recovered *Piper margaritae* as nested within the Schilleria clade (see Results). However, because the backbone constraint was inconclusive in resolving the Schilleria clade as monophyletic (online Appendix S3), and this may have influenced the placement of our fossil in relation to the clade as a whole (see Results), we take a conservative approach and set *P. margaritae* to indicate a minimum divergence age for the Schilleria clade.

The additional calibration analysis placing the internal calibration at the divergence of the Neotropical clade was meant to test the effect of our calibration on divergence age estimates, following a biogeographical scenario. Because all neotropical species form a monophyletic clade (Jaramillo and Manos, 2001; Jaramillo et al., 2008; Smith et al., 2008), *Piper margaritae* could be interpreted as indicative of the earliest evidence for the divergence of this clade. Calibrating at this node is equivalent to assuming a lower taxonomic resolution for *P. margaritae*.

Both analyses were performed using the program BEAST v.1.8.0 (Drummond and Rambaut, 2007) and a maximum diversification age for *Piper* constrained at 110.56 Ma with a standard deviation equal to 5, in accordance with the age estimated by Naumann et al. (2013) for the divergence of Piperaceae. Even though other ages are also available in the literature for the divergence of *Piper*, these are more recent than the age of *Piper margaritae*, and their inclusion in the calibration was not possible (ca. 57 Ma: Symmank et al., 2011; ca. 31 Ma: Naumann et al., 2013). The only exception was the age assigned by Smith et al. (2008, 91.2 Ma); however, this age was not included in our analysis because it is based on the fossil record of *Lactoris*, rather than estimated by their molecular clock.

To account for the rate heterogeneity described for *Piper* by Wanke et al. (2007), we set BEAST to estimate the substitution rates using an uncorrelated

log-normal relaxed-clock model, one internal calibration point and a maximum age constraint. The internal calibration was set as a prior with a log-normal distribution, an offset of 67 Myr and a standard deviation equal to 1. A run of 20 million generations was carried out using a Yule process and a substitution model GTR+I+G as tree priors. The output log files were then evaluated in the program Tracer v. 1.6 (Drummond and Rambaut, 2007), and a maximum-clade credibility tree was computed, and 95% confidence intervals of ages were calculated given mean heights and a burn-in of 15% using the program TreeAnnotator v1.8. (Drummond and Rambaut, 2007).

**Net diversification/lineage accumulation through time**—Diversification patterns for *Piper* were analyzed using lineages through time (LTT) plots based on the two estimated calibrated phylogenies using the program R (R Development Core Team, 2013) and the APE package (Paradis et al., 2004). The obtained LTT plots were compared with hypothetical null expectations of constant species accumulation (museum model) and rapid recent radiations (cradle model). These hypothetical models were simulated using the R package TreeSim (Stadler, 2011), recreating a bifurcating tree of 221 species that originates at 111 Ma (following the calibrations here obtained for *Piper*).

The constant species accumulation scenario represents the museum model of diversification and was simulated assuming constant origination and extinction rates ( $\lambda = 0.02$  and  $\mu = 0.05$ , respectively) in 50 replicates following Stadler (2011). A second scenario of rapid recent radiation was created to simulate the cradle model of diversification, in which lineage accumulation follows a sudden increase in speciation rates. The cradle model aims to represent a scenario in which an increase in speciation rates correlates with the Andean uplift, assuming constant origination and extinction between 111 and 25 Ma (0.02 and 0.05, respectively), followed by an increase in origination rates between 25 Ma and the recent to 0.1. The shift in origination rates at 25 Ma corresponds to an age of rapid exhumation and surface uplift of the northern Andes (Restrepo-Moreno et al., 2009; Farris et al., 2011). This event was chosen for our model based on biogeographical evidence that suggests that the Andean cordillera could have been an ancestral area for neotropical *Piper* species (Marquis, 2004) and a center of diversity (Quijano-Abril et al., 2006). We estimated LTT plots for both models and compared them with those estimated for calibrations of *Piper*.

## RESULTS

**Taxonomic summary—Family**—Piperaceae Giseke.

**Species**—*Piper margaritae* Martínez-A., sp. nov. (Fig. 2)

**Specific diagnosis**—Leaves ovate and entire with a marginal to submarginal abaxial petiole insertion. Petiole striate and wider at its base. Leaf lamina symmetrical, with a straight to slightly acuminate apex and a rounded to cordate base. Primary venation pinnate. Secondary venation brochidodromous and irregularly spaced, with 4–5 basalmost secondary veins alternate and clustered at the leaf base. Secondary veins decurrent. Intersecondary veins present. Tertiary venation mostly opposite sinuous, and quaternary and quinary veins irregular polygonal reticulate. Single-branched freely ending veinlets with tracheoid idioblast terminations.

**Etymology**—The epithet *margaritae* honors Margarita Gómez and Mateo Matamala, two biology students who died in 2011 as victims of the armed conflict while exploring field sites in Colombia.

**Holotype** *hic designatus*—ANDES-Paleo-001 (Fig. 2A, B, STRI 4974).

**Paratypes**—ANDES-Paleo 004 (STRI 4956; Fig. 2C), ANDES-Paleo 003 (STRI 4976; Fig. 2D), ANDES-Paleo 002 (STRI



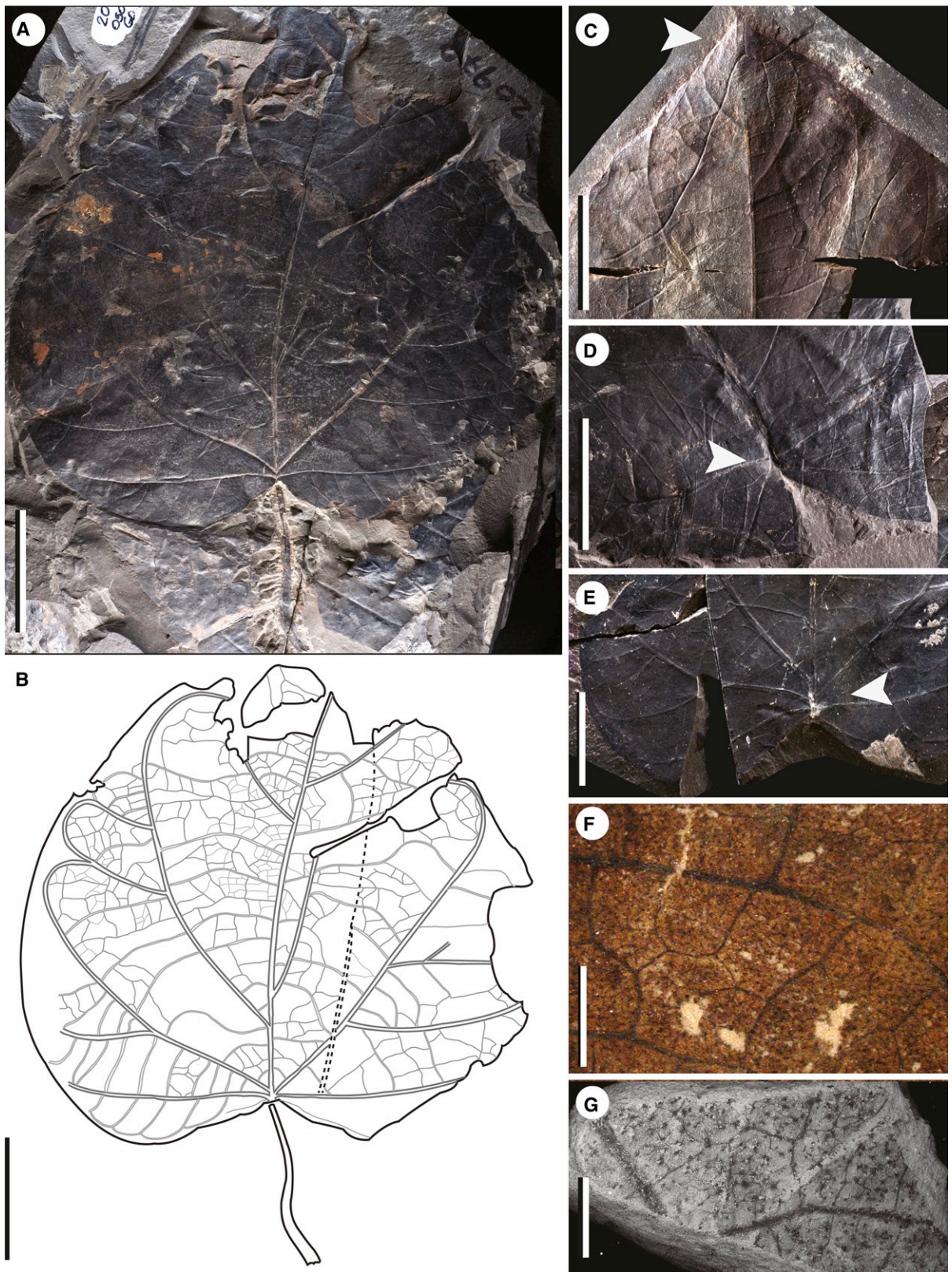


Fig. 2. *Piper margaritae* et sp. nov. (A) Holotype ANDES-Paleo-001 (STRI-4974). Scale bar = 3 cm. (B) Holotype venation sketch; drawn with camera lucida. Scale bar = 3 cm. (C) Paratype ANDES-Paleo-004 (STRI-4956). Arrow indicates the straight apex. Scale bar = 2 cm. (D) Paratype ANDES-Paleo-003 (STRI-4976). Arrow indicates the marginal abaxial petiole attachment to the blade. Scale bar = 2 cm. (E) Paratype ANDES-Paleo-002 (STRI-4970). Arrow indicates the clustered, alternate disposition of the basalmost secondary veins. Scale bar = 2 cm. (F, G) Paratype ANDES-Paleo-005 (STRI-4940). Freely ending veinlets are one branched and have tracheoid idioblast terminations. (F) Scale bar = 0.25 cm. (G) Scanning electron micrograph. Scale bar = 0.1 cm.



4970; Fig. 2E), ANDES-Paleo 005 (STRI 4940; Fig. 2F, G), ANDES-Paleo 006–033 (STRI 4938, 4941–51, 4955, 4957, 4960–62, 4964–66, 4968, 4969, 4975, 4977–79, 4983, 4993, 19718, 20473, 27238).

**Description**—The fossil leaves are compressions/impresions. Petioles are marginal to submarginally attached (Fig. 2D). The only complete petiole is long and smoothly grooved, 5.4 cm long and 0.157 cm wide at its attachment point to the lamina, and 0.35 cm wide at its base. The leaf lamina is ovate, mesophyllous to macrophyllous in size, with medial and basal symmetry, 11.95 (7.8–18.3) cm long ( $N = 9$ ) and 10.14 (7–17.4) cm wide ( $N = 8$ ; Fig. 2A, B). The leaf base is cordate to rounded (Fig. 2A, E), and the apex is straight or slightly acuminate, with angles that range from 74.5–99.7° (Fig. 2C). The primary venation is pinnate (Fig. 2A, B), and agrophic veins are simple (Fig. 2B). Major secondary venation is simple brochidodromous with veins irregularly spaced, slightly decurrent, and their angles smoothly decreasing proximally (Fig. 2B). The first basalmost 4–5 secondary veins are alternate and nested close to the base followed by a gap (Fig. 2B, E), with the next secondary vein pair arising above the distal 1/3 of the blade. Intersecondary veins are weak, with lengths shorter than 50% of subcurrent secondary; these are parallel to subjacent major secondary toward their proximal portion to the midvein, and reticulate distally. The tertiary veins are sinuous opposite to percurrent; epimedial tertiaries perpendicular to the midvein proximally and distally parallel to intercostal tertiaries (Fig. 2B). The quaternary and quinary veins are irregular polygonal reticulate (Fig. 2F, G), with poorly developed areoles and single-branched veinlets with tracheoid idioblast terminations (Fig. 2F, G).

**Type locality**—Guaduas Formation, locality 0502, Monte-cristo Ubaté coal mine, Llanos basin, Cundinamarca (5°14'N, 73°48'W; WGS 84). Tunnel level four (Fig. 1). The Guaduas Formation has been described elsewhere (Amaya et al., 2010), and the age of both localities has been estimated as late Maastrichtian based on palynomorph biostratigraphy (Correa et al., 2010).

**Repository**—Paleontological collection. Museo de Historia Natural, Universidad de los Andes, Bogotá, Colombia (ANDES-Paleo).

**Comparison**—Species of Aristolochiaceae, Ericaceae, Euphorbiaceae, Fabaceae, Menispermaceae, Saururaceae and Smilacaceae have leaves with shape and venation patterns similar to those of *Piper margaritae*. However, there are notorious differences between *P. margaritae* and species of these families (online Appendix S4).

Among Piperaceae, only *Piper* shows a notable resemblance to *Piper margaritae*. Species of *Manekia* Trel. and *Verhuellia* Miq. have leaves with a basal or suprabasal (only *Manekia*) acrodromous venation that differs from the pinnate venation observed in *P. margaritae*. Leaves of *Zippelia* Blume are also acrodromously veined and have alternate percurrent epimedial tertiaries, contrasting the opposite-sinuous tertiary venation of *P. margaritae*, and leaves of *Peperomia* are notorious for their microphyllous or notophyllous size, and actinodromous primary veins.

Leaf architecture is widely variable across species of *Piper* (Fig. 3; Appendix S5). Leaves range from notophyllous to macrophyllous in size, and they vary in length to width (L:W) ratios as well as in petiolar length. The distinctive cordate base observed in many species of *Piper* can also be lobed or convex, and primary venation can be pinnate, acrodromous or actinodromous. Secondary venation is equally variable across species and includes brochidodromous, festooned brochidodromous or hemieucampitodromous venation (Fig. 3; see Appendix S5). Particularly, most species of the *Schilleria* clade shared with *P. margaritae* an ovate laminar shape and mesophyll size, obtuse base angle, long petioles with marginal to submarginal abaxial petiole insertion, pinnate primary venation, brochidodromous secondary venation with the 4–5 basalmost decurrent secondary veins alternate and clustered at the base of the leaf, intersecondary veins, opposite sinuous tertiary venation and freely ending veinlets and tracheoid idioblast terminations.

**Phylogenetic analyses**—The parsimonious analysis meant to build a backbone constraint rendered 357 most-parsimonious trees of 3428 steps (CI = 0.3136, RI = 0.7314). The strict consensus tree (see Appendix S3) recovered all major clades of *Piper* previously described by Jaramillo et al. (2008). Only those species corresponding to the *Schilleria* clade did not form a monophyletic clade and are instead forming a polytomy, basal to all other species of *Piper*. Because we included *Peperomia* as an outgroup, the rooting of our topology differs from that of Jaramillo et al. (Jaramillo and Manos, 2001; Jaramillo et al., 2008) who did not include one. Our analysis did not recover *Piper* s.s. and *Macropiper* clades as basalmost within the genus, as had been previously reported (Jaramillo and Manos, 2001; Jaramillo et al., 2008).

The molecular scaffold approach used to place *Piper margaritae* within *Piper*, resulted in 10000 most parsimonious trees of 1411 steps (CI = 0.0602, RI = 0.4008). The strict consensus resolved species of the *Schilleria* clade into two basal clades, and placed *P. margaritae* as sister to *P. carrilloanum* C. DC. and *P. riparense* C. DC. (Fig. 4; see online Appendix S6). The placement of *P. margaritae* among species of the *Schilleria* clade is mainly supported by its marginal abaxial petiole insertion, presence of intersecondary veins and decurrent secondary veins (Fig. 4). Even though leaves with some of these characters are independently observed on other clades of *Piper*, the combination of these is only common among species of the *Schilleria* clade, despite this group was not recovered as monophyletic in our analysis (Fig. 4; see online Appendix S6). We therefore hypothesize an affinity of *P. margaritae* to the *Schilleria* clade based mainly on the presence of leaves with marginal abaxial petiole insertion, intersecondary veins and decurrent secondary veins.

Within the *Schilleria* clade, the placement of our fossil is supported by various characters (petiole size, laminar size and shape, agrophic veins, tertiary and fifth order venation; see online Appendix S5 and S6) that are highly homoplasious across *Piper*. Because these traits are homoplasious, and because our analysis did not recover a monophyletic *Schilleria* clade, we take a conservative approach and relate *Piper margaritae* to the stem of the *Schilleria* clade, restraining from assigning the fossil to a subclade within.

**Divergence times and lineage accumulation**—The maximum-clade credibility tree estimated using the divergence of the

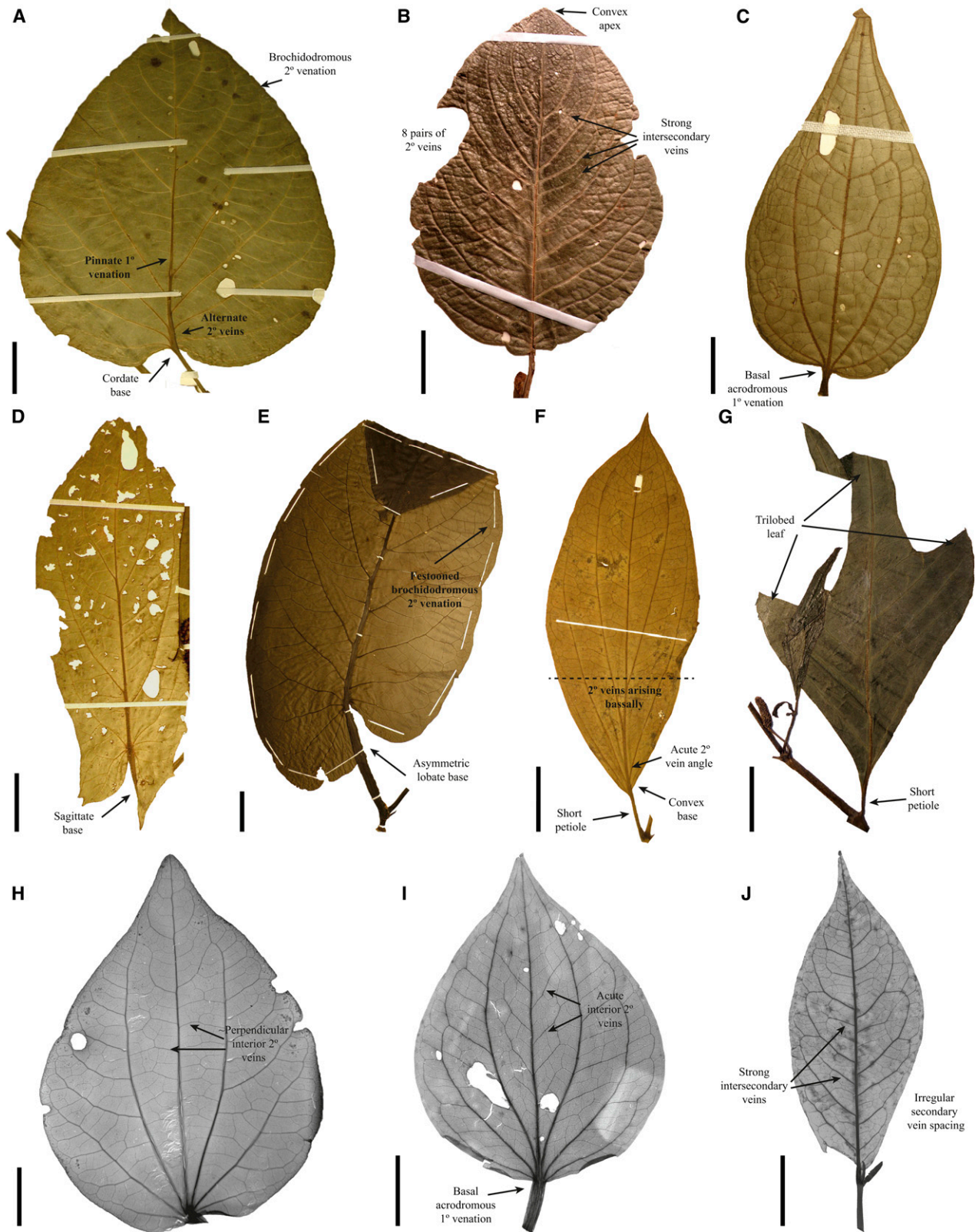


Fig. 3. Leaf architecture variation within the genus *Piper*. (A) *P. solmsianum*. US 3076763. Schilleria clade. Scale bar = 2 cm. (B) *P. biolleyi*. COL 111792. Radula clade. Scale bar = 2 cm. (C) *P. capense*. US 2062035. Macropiper clade. Scale bar = 1 cm. (D) *P. sagittifolium*. US 1644501. Macrostachys clade. Scale bar = 3 cm. (E) *P. richardiifolium*. US 2841165. Macrostachys clade. Scale bar = 3 cm. (F) *P. nigrum*. US 27662224. Piper s.s. clade. Scale bar = 2 cm. (G) *P. tricuspe*. HUA 126473. Peltobryon clade. Scale bar = 2 cm. (H) *P. excelsum*. USNC C10210. Macropiper clade. Scale bar = 1 cm. (I) *Sarcorhachis naranjoana* USNC 12667. Radula clade. Scale bar = 1 cm. (J) *Ottonia mexiaeae*. USNC 6454. Ottonia clade. Scale bar = 1 cm.



Schilleria clade as an internal calibration, retrieved three main lineages: a Neotropical, Macropiper (South Pacific), and *Piper* s.s. (Asian tropics) clades. The Neotropical clade diverged by 76 Ma (67–86 Ma), the Macropiper and *Piper* s.s. clades showed little resolution in their divergence age estimate, ranging from the Early to the Late Cretaceous (Fig. 5; see online Appendix S7; Table 2). The Neotropical clade includes two main monophyletic groups. One of these is comprised by the clades Schilleria, Ottonia, Enckea and Cinereum/Sanctum (Fig. 5). The other includes the clades Pothomorphe, Peltobryon, Macrostachys, and Radula. The latter three are the most species-rich and diverged between 44 and 55 Ma (Fig. 5). Alternatively, the maximum-clade credibility tree estimated using the divergence of the Neotropical clade as an internal calibration, retrieved younger ages. There was an overall decrease of approximately 9 Ma in the divergence ages for all major clades (Table 2). However, the LTT plots for both calibrations of *Piper* showed the same diversification pattern, in which net lineage accumulation slowly rises from 111 Ma to ca. 40 Ma and is markedly more pronounced during the Neogene (Fig. 5). These LTT plots better resemble a cradle model than a museum model of lineage accumulation. Whereas the museum model shows a nearly steady lineage accumulation starting ca. 111 Ma, net diversification shows a drastic increase at 25 Ma in our simulation of a cradle model (Fig. 5).

## DISCUSSION

The description of *Piper margaritae* and the analyses presented constitute the first attempt to place a fossil species within *Piper*, a highly diverse group of tropical plants with a scant fossil record, and a presumed long diversification history (Qiu et al., 1999; Doyle and Endress, 2000; Soltis et al., 2000; Zanis et al., 2002; Jaramillo and Kramer, 2007; Magallón and Castillo, 2009; Smith et al., 2008; Bell et al., 2010).

The phylogenetic analyses allowed the association of the fossil to a particular clade within *Piper*. Specifically, our scaffold analysis consistently placed *Piper margaritae* within the crown-group of the Schilleria clade (Fig. 4), indicating that leaf characters support an affinity between our fossil and a major clade of *Piper*, despite the morphological diversity observed across species of this genus. Among *Piper*, species of the Schilleria clade are typically distinctive in having ovate leaves, with marginal abaxial petiole insertion, long petioles, pinnate primary venation, alternate decurrent secondary veins that are proximally clustered, and weak intersecondary veins (Fig. 4). This combination of leaf traits is shared between *P. margaritae* and most species of the Schilleria clade (Fig. 4) and supports an affinity between the Late Cretaceous fossil and this clade.

The inclusion of *Piper margaritae* in divergence and diversification analyses permitted age estimations for *Piper*. The calibration of *Piper* using a maximum divergence age of ca. 111 Ma and *Piper margaritae* as an internal calibration point (67 Ma), retrieved an early divergence for all major branches, yet relatively recent diversification ages for the most species-rich clades. The divergence between a neotropical and a paleotropical species estimated at ca. 111 Ma (Fig. 5) implies an Early Cretaceous divergence for *Piper*. Previous calibration analyses for Piperales have shown contrasting results for the divergence age of *Piper*, ranging from Cretaceous ages (ca. 92 Ma: Smith et al., 2008) to Paleogene ages (ca. 57 Ma: Symmank et al.,

2011; ca. 31 Ma: Naumann et al., 2013). An Early Cretaceous age, like the one obtained here, is, however, poorly supported by the fossil record, considering that the earliest evidence for an angiosperm dates back to only 136 Ma (Friis et al., 2006) and that *Piper* is relatively derived among Piperales (Jaramillo and Callejas, 2004). It is likely that the Early Cretaceous age estimated for the divergence of *Piper* is an overestimation and an inherent artifact in most calibration analyses dealing with early-diverging lineages, since these are particularly prone to significant changes in extinction/diversification rates (Bromham and Penny, 2003; Friis et al., 2011), life history traits, and other factors that can affect substitution rates and push back the age of a lineage (Kay et al., 2006). Nevertheless, other studies have also estimated Cretaceous ages for the divergence of other groups within Piperales (e.g., Hydnoraceae: Naumann et al., 2013; Lactoridaceae: Zavada and Taylor, 1986).

Despite the caveats in calibrating divergence ages for an early-diverging lineage, the phylogenetic relationships and extant distribution of species of *Piper* are consistent with a scenario of vicariance in which the divergence of a neotropical clade and paleotropical species coincides with the final stage of the breakup of Gondwana during the Cretaceous. The major clades of *Piper* are closely defined by geographical regions (neotropical, South Pacific, and Asian tropics), with the exception of the tropical African species of *Piper* (~15 species), whose distributions appears to follow two separate dispersal events from Asia (Jaramillo et al., 2008; Fig. 1). Additionally, the profound distinction in floral biology between paleotropical and neotropical species, which are dioecious and monoecious respectively, supports a deep divergence between these groups (Jaramillo and Manos, 2001; Jaramillo and Callejas, 2004).

**Diversification of *Piper***—The greatest diversity of *Piper* is concentrated in the neotropics (~1300 species: 70%). All nodes in the Neotropical clade retrieved ages of 65 Ma or younger in our analysis, indicating that the diversification of neotropical lineages occurred throughout the Cenozoic (Fig. 5). Among these, a high proportion of lineages have young divergence ages (median ca. 15 Ma), suggesting that extant species richness is likely to follow a cradle model of diversification (Fig. 5). In particular, the two most species-rich clades, Macrostachys and Radula, which include approximately 200 and 450 species respectively (Table 2; Jaramillo et al., 2008), are derived within neotropical *Piper* and diverged ca. 7 and 11 Ma on average, further suggesting that extant diversity is better explained by recent diversification events within a few clades rather than an accumulation of species spread across the entire *Piper* lineage (Fig. 5). This pattern has also been described for the *Peperomia* subgen. *Tildenia* Miq., whose molecular dating indicates that the major diversification of the group occurred during the Miocene (Symmank et al., 2011).

When the internal calibration was placed at the crown node of the Neotropical clade instead of at the Schilleria clade stem node, we observed little effect on divergence ages (Fig. 5; Table 2). However, slightly younger ages (~9 Myr of average difference) were consistently obtained when the internal calibration was set at a deeper node. This deeper calibration is equivalent to having a fossil with a lower taxonomic resolution, indicating that assigning a fossil to a low taxonomic rank, due to preservation bias or character ambiguity, can interfere in the calibration and reduce the ages of the derived lineages. Using fossils for calibrating deep divergences should be carefully addressed.



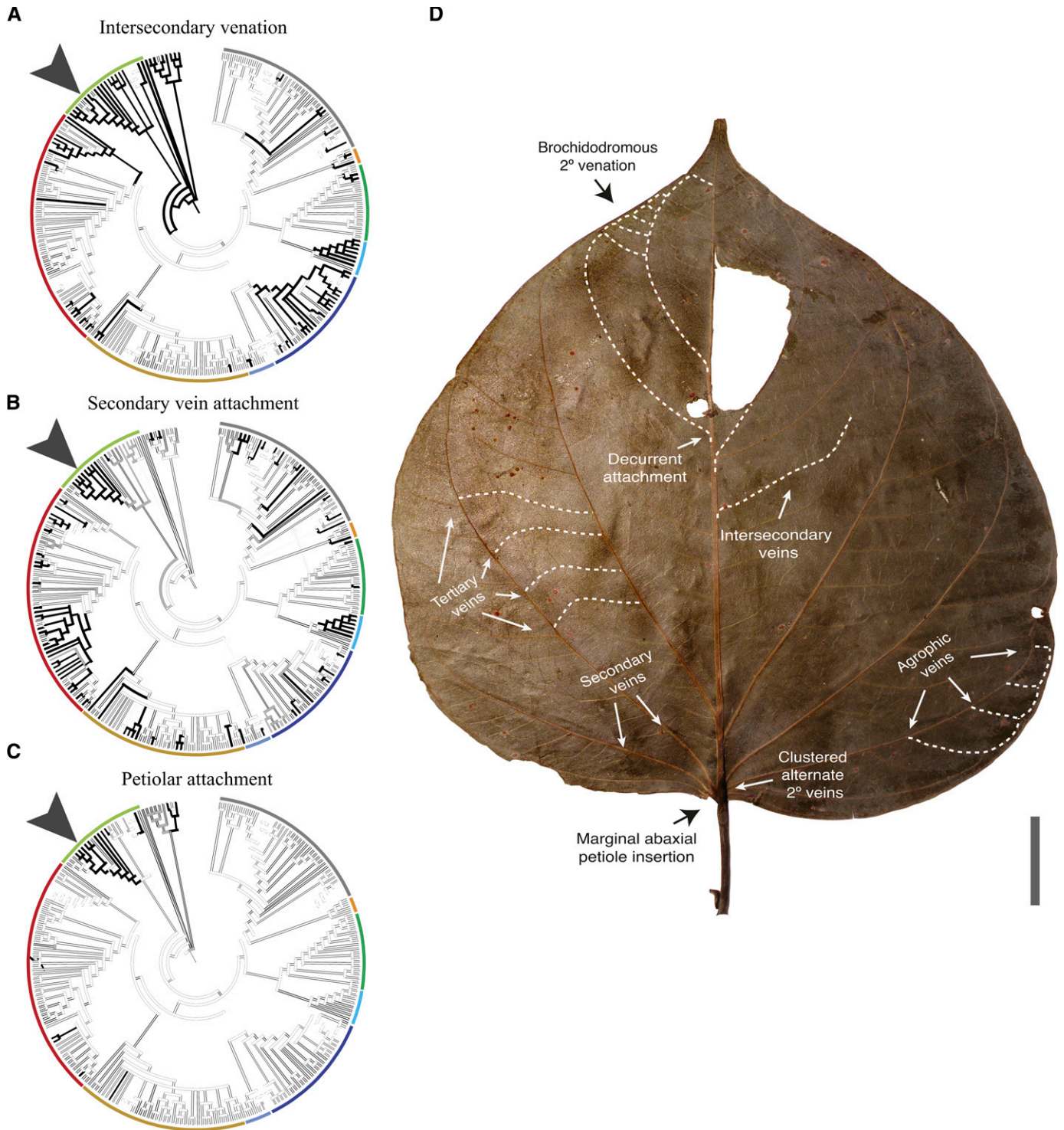


Fig. 4. Phylogenetic placement of *Piper margaritae* within the genus *Piper*. (A–C) Character optimization of three leaf architecture characters on the most parsimonious tree. Arrows indicate the obtained phylogenetic position of the fossil within the *Schilleria* clade. Colored lines indicate the different clades (see Fig. 5 for color correspondence). (A) Mapping of intersecondary venation. Black lines represent presence, white lines absence of intersecondary venation. (B) Mapping of secondary vein attachment to the midvein. Black lines: decurrent attachment; gray lines: decurrent attachment of the proximal 2-veins; white lines: excurrent attachment. (C) Mapping of petiolar attachment. Black lines: marginal abaxial petiole attachment to the lamina; gray lines: peltate-central attachment; white lines: marginal attachment. (D) *Piper schiedeanaum* (HUA 165657) showing the main leaf architecture characters that support the affinity of the fossil with the *Schilleria* clade.

As expected, due to the small difference of our calibration analyses, the LTT plots also reflect small differences in diversification patterns (Fig. 5). Both LTT plots are in agreement with a cradle model of diversification in which net diversification

rapidly increased over the last 25–30 Myr, coeval with both the uplift of the northern Andes and the generation of terrestrial landscape in the previously submerged Central American isthmus and Chocó region (Mora et al., 2010; Farris et al., 2011;

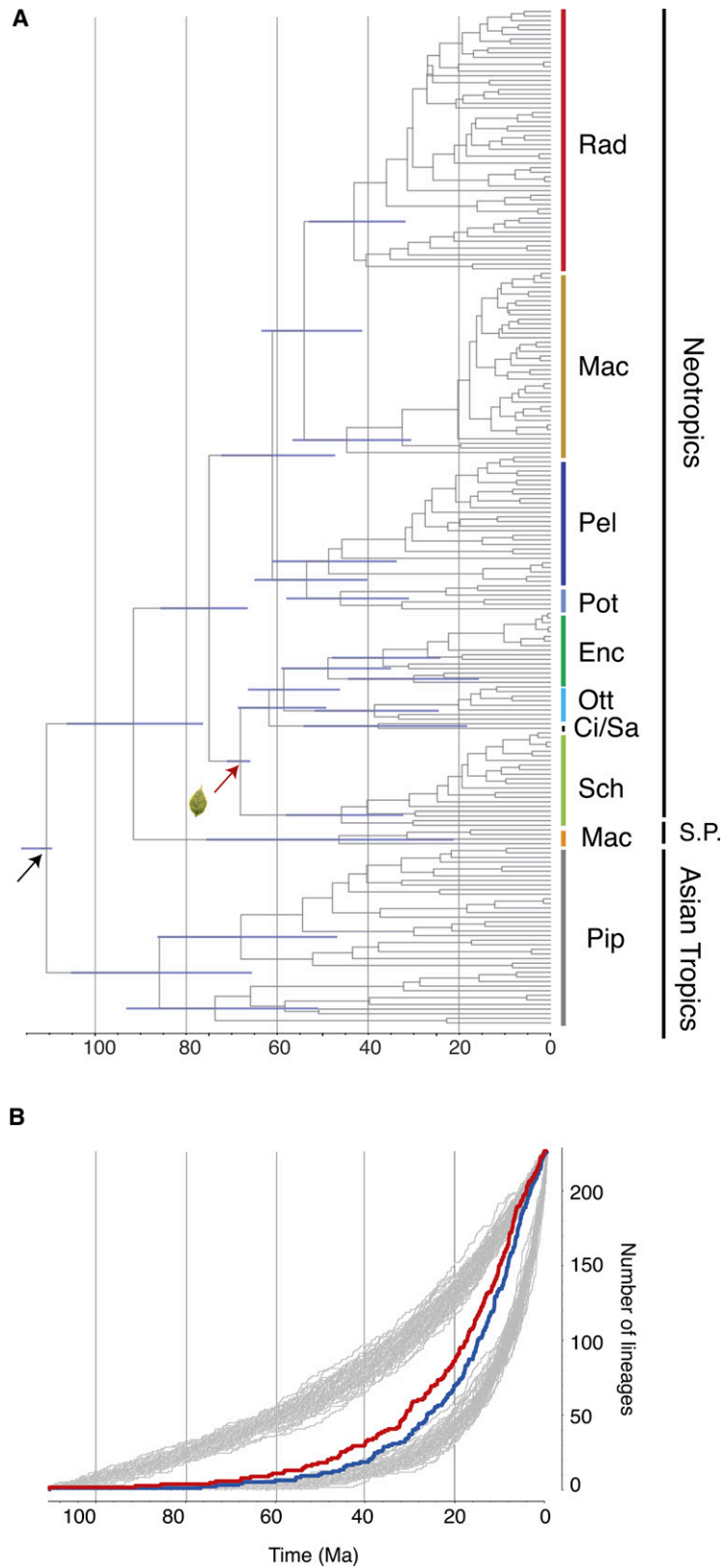


Fig. 5. Calibration and diversification analyses. (A) Maximum-clade credibility tree obtained in the Bayesian calibration analysis. Black arrow indicates the maximum age-constraint for the analysis set at ca. 111 Ma. Red arrow indicates the calibration point given by the fossil *Piper margaritae*. S. P.: South Pacific region. (B) Lineages through time plot. Gray upper lines correspond to simulations with constant rates of origination ( $\lambda = 0.02$ ) and extinction ( $\mu = 0.5$ ). Gray lower lines correspond to simulations with a shift in origination rates  $\lambda$  from 0.02 to 0.1 in the interval 25–0 Ma and constant extinction rates  $\mu$  of 0.5. Colored lines correspond to the calibration analyses performed placing the fossil as the stem group of the Schilleria clade (red) or as the stem group of the Neotropical clade (blue).



TABLE 2. Number of species, ages of divergence for the two calibration analyses, and geographic distribution of *Piper* clades.

Clade	Species (%)	Calibration Neotropical clade		Calibration Schilleria clade		Geographic distribution
		Stem age (Ma)	Crown age (Ma)	Stem age (Ma)	Crown age (Ma)	
Radula	450 (22.5)	46 (56–35)	37 (46–27)	55 (64–42)	44 (53–32)	Neotropics, most species occur in open areas along road and forests edges
Macrostachys	200–250 (12.5)	46 (56–35)	39 (50–27)	55 (64–42)	46 (57–31)	Neotropics, most species occur in Central America and northern Andes
Peltobryon	80–100 (5)	45 (56–34)	42 (54–29)	55 (65–40)	50 (62–34)	South America, most species are restricted to western Amazon and eastern Andean slopes
Pothomorpha	10 (0.5)	45 (56–34)	39 (51–26)	55 (65–40)	47 (57–32)	Throughout the neotropics
Enckea	120 (6)	48 (59–38)	40 (51–29)	60 (67–46)	50 (69–35)	From the Amazon to dry forests in Mexico and the Greater Antilles
Cinereum/Sanctum	2 (0.1)	50 (60–40)	32 (46–16)	63 (69–49)	39 (54–19)	Northern South America and Central America
Otonia	50 (2.5)	48 (59–38)	31 (41–20)	60 (67–46)	40 (52–24)	Atlantic forests of Brazil and the Amazon
Schilleria	200 (10)	56 (66–46)	38 (48–27)	69 (72–67)	47 (53–27)	Central America and the Atlantic Forests of Brazil
Macropiper	10 (0.5)	69 (80–67)	40 (64–21)	93 (106–77)	47 (76–22)	South Pacific except <i>P. capense</i> from Africa
Piper s.s.	300 (15)	111 (114–110)	77 (102–55)	111 (117–109)	86 (106–66)	Southeast Asia except <i>P. borbonense</i> and <i>P. guineense</i> from Africa

Notes: The Species column indicates the approximate number and percentage of species of each per clade. The number of species and distribution of clades are those of Jaramillo et al. (2008) and complemented with information from herbarium collections (Appendix 1).

Montes et al., 2012; Fig. 5). Even though *Piper* has a pantropical distribution, the LTT is heavily biased toward neotropical lineages given that these outnumber paleotropical species. The apparent correlation between an increase in net diversification and the cradle model agreement suggests a possible influence of the Andean uplift and the rise of Central America on the diversification of *Piper* in the neotropics, as has been suggested by biogeographical analyses that found Andean slopes as centers of high species richness for *Piper* (Callejas, 1986; Quijano-Abril et al., 2006). A biogeographical analysis of the *Peperomia* subgen. *Tildenia* has also shown a strong correlation between its diversification and orogenic events of the Andean cordillera and the Trans-Mexican Volcanic Belt (Symmank et al., 2011).

Gentry (1982) suggested that the Andean uplift played a central role in generating the “excess” of species found in the neotropics, as compared with the paleotropics. Several recent studies have shown that Andean uplift created newly formed montane habitats where new adaptive radiations took place (e.g., *Lupinus* L.: Hughes and Eastwood, 2006; *Peperomia*: Symmank et al., 2011; *Hedyosmum* Sw.: Martínez et al., 2013; *Hypericum* L.: Nürk et al., 2013a, b; see also Madriñán et al., 2013), and enhanced geographic vicariance by creating a rough topography [e.g., *Macrocarpaea* (Griseb.) Gilg: Struwe et al., 2009; *Viburnum* L.: Spriggs et al., in press; see also Luebert and Weigend, 2014]. Recently, Mutke et al. (2014) have argued for a third cause of diversification in selected Andean plant groups (mostly herbs in disturbed secondary vegetation) that radiated in response to spatiotemporal habitat heterogeneity created by frequent landslides, typical of a prevailing steep topography. In the neotropical lowlands of western Amazonia, the Andean uplift increased nutrient deposition following denudation of the rising mountains, and also promoted speciation (Hoorn et al., 2010; Antonelli and Sanmartín, 2011). Even though our results are suggestive of a temporal relation between the diversification of *Piper* and the rise of the Andes, the Andean uplift does not fully explain the diversification of the montane floras such

as those in which *Piper* occurs, as these species-rich habitats in the Andes and adjacent landscapes are mostly characteristic of tropical latitudes. Diversity drops in higher latitudes even within the Andes, despite the similar history of mountain building across the latitudinal gradient. Additional factors that could potentially have enhanced diversification in the tropics and/or enhance extinction in temperate latitudes are still elusive, but further examination of diversification patterns of tropical Andean lineages can provide better hypotheses that explain the processes leading to high diversity in the neotropics.

*Piper*, a megadiverse genus of early-diverging angiosperms, is ecologically diverse and geographically ubiquitous in the tropics worldwide. The radiation of the highly speciose neotropical clades within *Piper* occurred only recently, since the Oligocene, in spite of the long-standing presence of this group in the neotropics, at least for the past 70 Myr. This recent radiation coincides with the onset and later development of both Andean and Central American uplifts and subsequent topographical heterogeneity with its many biological consequences. Most extant species of *Piper* in the neotropics inhabit narrow geographical ranges, in montane or high-elevation habitats as well as lowland forests, occupying a wide variety of niches, including disturbed habitats. Thus, the analysis of diversification of *Piper*, including the new fossil evidence of *Piper margaritae*, offers an exceptional opportunity to understand a relatively recent shift in diversification and further address specific ecological scenarios promoting diversification in this highly speciose lineage.

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APPENDIX 1. List of collection vouchers and GenBank accessions for species used in morphologic and phylogenetic analyses.

**Taxon;** Abbreviation of species name; ITS GenBank accession.

***Peperomia blanda***; Pe\_blan; FJ424455.1. ***Peperomia galioides***; Pe\_gali; FJ424452.1. ***Peperomia glabella***; Pe\_glab; FJ424454.1. ***Peperomia inaequalifolia***; Pe\_inae; FJ424453.1. ***Peperomia lanceolatopeltata***; Pe\_lance; FJ424448.1. ***Peperomia lancifolia***; Pe\_lanci; FJ424457.1. ***Peperomia macrostachya***; Pe\_macr; FJ424447.1. ***Peperomia pernambucensis***; ***Peperomia rotundifolia***; Pe\_rotu; FJ424460.1.

**Taxon Voucher specimen**, Collection locale, Year, Herbarium. Abbreviation of species name; ITS GenBank accession. Herbaria: COL = Universidad Nacional de Colombia, HUA = Herbario Universidad de Antioquia, US = U. S. National Herbarium, NCLC-W = Smithsonian Institution, National Cleared Leaf Collection-Wolfe.

***Piper abalienatum*** **Trel.** *Jaramillo MA 552*, Colima, Mexico, 1999, US 3523086. P\_abali; EU581075.1. ***Piper abbreviatum*** **Opiz Schodde R 2927**, Central Province, Papua New Guinea, 1962, US 3476940. P\_abbre; EU581076.1. ***Piper aduncum*** **L. Etter A 917**, Santander, Colombia, 1992, COL 439414. P\_adunc; AF275157.1. ***Piper aequale*** **Vahl Aristeguieta L 7143**, Caracas, Venezuela, 1969, US 2925676. P\_aequa; EU581080.1. ***Piper albozonatum*** **C. DC. Luteyn J 10370**, Valle del Cauca, Colombia, 1984, COL 433072. P\_alboz; AY326195.1. ***Piper amalago*** **L. Valiente A. 319**, Tamaulipas, Mexico, 1982, US 3463349. P\_amala; EU581089.1. ***Piper amoenum*** **Yunck. Suárez S 519**, Chocó, Colombia, 1995, COL 416339. P\_amoen; AF275160.1. ***Piper anonifolium*** **Kunth Betancur J 14031**, Vaupés, Colombia, 2009, COL 537086. P\_anoni; EU581100.1. ***Piper appendiculatum*** **(Benth.) C. DC. Jaramillo MA 645**, Esmeraldas, Ecuador, 2000, COL 464074. P\_appen; AY326196.1. ***Piper arboreum*** **Aubl. Tonduz A 1896**, Carchi, Ecuador, 1896, US 2661367. P\_arboreu; EU581106.1. ***Piper arieianum*** **C. DC. Franco P 4933**, Nariño, Colombia, 1993, COL 361131. P\_ariei; EU581108.1. ***Piper artanthe*** **C. DC. Huertas G 6215**, Boyacá, Colombia, 1965, COL 173028. P\_artan; EU581109.1. ***Piper atropicum*** **C. DC. Jaramillo MA 212**, Province of Surigao, Philippines, 1999, US 3538308. P\_atros; AY572318.1. ***Piper attenuatum*** **Buch.-Ham. ex Miq. Saldana CJ 14415**, Mysore, India, 1969, US 2654800. P\_atten; EU581110.1. ***Piper augustum*** **Rudge Cuatrecasas J 16948**, Valle del Cauca, Colombia, 1944, COL 16948. P\_augus; EU581111.1. ***Piper auritifolium*** **Trel. Smith A 1805**, Alajuela, Costa Rica, 1805, US 1807470. P\_auriti; EU581113.1. ***Piper auritum*** **Kunth Kress WJ 94-3989**, Puntarenas, Costa Rica, US 3311693. P\_auritu; EU581116.1. ***Piper austrocaledonicum*** **C. DC. Webster GL 14583**, South Province, New Caledonia, 1968, US 2734327. P\_austr; EU581120.1. ***Piper avellanum*** **(Miq.) C. DC. Ramirez JG 216**, Antioquia, Colombia, 1986, COL 322730. P\_avell; EU581122.1.

***Piper baccatum*** **Blume Henry A 11635**, Yunnan, China, 1999, US 458537. P\_bacca; EU581124.1. ***Piper bartlingianum*** **(Miq.) C. DC. Irwin HS 57708**, Zuid Rivier, Suriname, 1963, COL 155073. P\_bartli; AF275183.1. ***Piper bavinum*** **C. DC. Balansa B 362**, Asia, 1885, US 2496887. P\_bavin; AF275199.1. ***Piper begoniicolor*** **Trel. & Yunck. Cuatrecasas J 22523**, Valle del Cauca, Colombia, 1946, US 2816928. P\_begon; EF056226.1. ***Piper betle*** **L. Jaramillo MA 180**, Lagunas, Philippines, 1999, US 3495321. P\_betle; EF060062.1. ***Piper biolleyi*** **C. DC. Gallegos C 5164**, Panamá, Panamá, 1967, COL 111792. P\_bioll; EU581127.1. ***Piper biseriatum*** **C. DC. Standely PC 39727**, Cartago, Costa Rica, 1924, US 1229478. P\_biser; EF056228.1. ***Piper blattarum*** **Spreng. Acevedo P 7667**, Arecibo, Puerto Rico, 2010, US 3331548. P\_blatt; EU581130.1. ***Piper boehmeriifolium*** **(Miq.) Wall. ex C. DC. Toroes RS 3220**, East Coast, Sumatra, 1932, US 1861381. P\_boehm; AF275204.1. ***Piper brachypodon*** **(Benth.) C. DC. Forero E 4342**, Chocó, Colombia, 1999, COL 193448. P\_b\_odon; AY326198.1. ***Piper brachypus*** **Trel. Jaramillo MA 550**, Colima, Mexico, 1999, US 3523093. P\_b\_ypus; EU581132.1. ***Piper breviamentum*** **C. DC. Jaramillo MA 233**, Agusan del Norte, Philippines, 1999, US 3538328. P\_brevia; EU581134.1. ***Piper brevicuspe*** **(Miq.) Merr. Jaramillo MA 211**, Leyte, Philippines, 1999, US 3538307. P\_brevic; AY572321.1. ***Piper brevipedicellatum*** **Bornst. Jaramillo MA 547**, Colima, Mexico, 1999, US 3523084. P\_brevip; AF275189.1. ***Piper brownbergense*** **Yunck. Plotkin MJ 538**, Tepoe, Surinam, 1984, US 3460803. P\_brown; EU581135.1. ***Piper bullosum*** **C. DC. Patiño A 69**, Nariño, Colombia, 2004, COL 519218. P\_bullo; EU581137.1.

***Piper calcariformis*** **Tebbs Croat TB 27726**, Veraguas, Panamá, 1976, US 2787908. P\_calca; EU581138.1. ***Piper caldense*** **C. DC. Heringer EP 579**, Brasília, Brazil, 1979, US 2952763. P\_calde; EU581139.1. ***Piper callosum*** **Ruiz & Pav. Plowman T 8495**, Pará, Brazil, 1980, US 2963012. P\_callos; EU581142.1. ***Piper campanum*** **Yunck. Liesner RL 614**, Panamá, Panamá, 1973, US 2827156. P\_campa; EF056235.1. ***Piper caninum*** **Blume Sinclair J 8402**, Johone, Malaya, Asia, 1955, US 2931843. P\_canin; EF060067.1. ***Piper capense*** **L.F. Brass LJ 17259**, North Nyassa District, Malawi, 1946, US 2062035. P\_capen; EU581144.1. ***Piper caracasana*** **Bredem. ex Link Granville JJ 7123**, Mont Belvedere, French Guiana, 1985, US 3451883. P\_carac; EF056238.1. ***Piper cararensis*** **Trel. & Yunck. Rooden JV 469**, Chocó, Colombia, 1984, COL 298002. P\_carar; AY326201.1. ***Piper carrilloanum*** **C. DC. Haught O 4729**, Antioquia, Colombia, US 1709233. P\_carri; EU581147.1. ***Piper cavendishoides*** **Trel. & Yunck. Forero E 9490**, Chocó, Colombia, 1983, COL 254519. P\_caven; AF275153.1. ***Piper celtidifforme*** **Opiz Ama D 16130**, Morobe, New Guinea, Pacific Islands, 2002, US 3486076. P\_celti; EU581148.1. ***Piper cenocladum*** **C. DC. Burger WC 5075**, Alajuela, Costa Rica, 1968, US 2626576. P\_cenoc; EF056239.1. ***Piper cernuum*** **Vell. Mexia Y 5495**, Minas Gerais, Brazil, 1931, US 1618125. P\_cernu; EF056242.1. ***Piper cihuatlanense*** **Bornst. Jaramillo MA 194**, Albay, Philippines, 1999, HUA 119207. P\_cihua; AF275187.1. ***Piper cinereum*** **C. DC. Jaramillo MA 546**, Colima, Mexico, 1999, US 3523085. P\_ciner; EU581155.1. ***Piper coccoloboides*** **Kunth Jaramillo MA 66**, Chocó, Colombia, 1997, US 3507088. P\_cocco; EF056243.1. ***Piper cocoranum*** **Trel. & Yunck. Luteyn J 11886**, Antioquia, Colombia, 1987, COL 407259. P\_cocor; AY326203.1. ***Piper confertinodum*** **(Trel. & Yunck.) M.A. Jaram. & Callejas Bernal 674**, Antioquia, Colombia, 1983, COL 283594. P\_confie; AF275166.1. ***Piper consanguineum*** **Kunth Granville JJ 11525**, Crique Jupiter, French Guiana, 1991, US 3523350. P\_consa; EU581163.1. ***Piper corcovadensis*** **(Miq.) C. DC. Jung SL 170**, São Paulo, Brazil, 1977, COL 195916. P\_corco; EU581166.1. ***Piper cordatilimum*** **Quisumb. Jaramillo MA 179**, Lagunas, Philippines, 1999, US 3495322. P\_corda; AY572323.1. ***Piper cordulatum*** **C. DC. Nee M 9805**, Veraguas, Panamá, 1974, US 2787689. P\_cordu; EU581168.1. ***Piper cf. costatum*** **C. DC. Jaramillo MA 133**, Chocó, Colombia, 1977, COL 416595. P\_costa; EU581170.1. ***Piper crassinervium*** **Kunth Díaz S 1038**, Nariño, Colombia, 1977, COL 184859. P\_crass; EU581172.1. ***Piper cubataonum*** **C. DC. Unknown collector 24988**, Brazil, US Photo. P\_cubat; EU581173.1. ***Piper cubeba*** **L.F. Thorel D. 1420**, Cochinchene, Vietnam, 1862, US 2498528. P\_cubeb; EF060070.1. ***Piper cf. curtifolium*** **W.C. Burger Becerra E 1489**, Pasco, Peru, 2007, HUA 172124. P\_curtif; EU581174.1. ***Piper curtirachis*** **W.C. Burger Herrera G 5223**, Limón, Costa Rica, 1992, HUA 090505. P\_curtir; EU581175.1. ***Piper curtispicum*** **C. DC. Gentry A 13572**, Darién, Panamá, 1975, COL 178150. P\_curtis; EU581176.1.

***Piper daguanum*** **C. DC. Jaramillo MA 56**, Chocó, Colombia, 1997, US 3523610. P\_dagua; EF056247.1. ***Piper darienense*** **C. DC. Galdanes C 3867**, Coiba, Panamá, 1997, US 3555314. P\_darie; EU581177.1. ***Piper decumanum*** **L. Meijer W 92932**, Northern Peninsula, Malaysia, 1975, US 3003575. P\_decum; AF275203.1. ***Piper dilatatum*** **Pohl ex Miq. Gillis WT 8157**, Dominica, West Indies, 1969, COL 543824. P\_dilat; EU581180.1. ***Piper diospyrifolium*** **Kunth Mori S 14857**, Saül, French Guiana, 1982, HUA 73131. P\_diosp; EU581181.1. ***Piper divaricatum*** **Trel. Forero E 8982**, Chocó, Colombia, 1982, COL 254620. P\_divar; EU581182.1. ***Piper dolichotrichum*** **Yunck. Jaramillo MA 129**, Chocó, Colombia, 1998, COL 416599. P\_dolic; EU581185.1. ***Piper dryadum*** **C. DC. Galeano G 4739**, Chocó, Colombia, 1995, COL 405572. P\_dryad; EU581186.1. ***Piper dumosum*** **Rudge Popoly J 15046**, Amazonas, Colombia, 1991, COL 413547. P\_dumos; EU581189.1. ***Piper erectipilum*** **Yunck. Costa MAS 31**, Amazonas, Brazil, 1994, COL 458346. P\_erect; EU581191.1. ***Piper eucalyptifolium*** **Rudge de Granville JJ 8568**, Mont Galbao, French Guiana, 2001, US 3134896. P\_eu\_ium; EU581192.1. ***Piper eurphyllum*** **C. DC. Wilbur RL 10497**, Cartago, Costa Rica, 1968, US 2823319. P\_eury1; EF056249.1.

***Piper filistilum*** **C. DC. Suárez S 176**, Chocó, Colombia, 1995, COL 416341. P\_filis; AF275155.1. ***Piper fimbriatum*** **C. DC. Kress WJ 94-3972**, Puntarenas, Costa Rica, 1994, US 3318972. P\_fimbr; EF056252.1. ***Piper flagellicuspe*** **Trel. & Yunck. Rastrepo D 726**, Meta, Colombia, 1993, COL 409353. P\_flage; AF275154.1. ***Piper flavicans*** **Trel. Ganev W 2920**, Bahía, Brazil, 1994, HUA 110213. P\_flavic; EU581202.1.

- Piper flavidum* C. DC. *Davidse G* 20453, Chiapas, Mexico, 1982, HUA 097478. P\_flavid; EU581203.1. *Piper fonteboanum* Yunck. *Palacios P* 2976, Caqueta, Colombia, 1992, COL 397102. P\_fonte; EF056255.1. *Piper friedrichsthalii* C. DC. *Killip EP* 33579, Chocó, Colombia, 1939, COL 11769. P\_fried; EU581207.1. *Piper fuliginum* Kunth *Irwin HS* 9045, Brasília, Brazil, 1965, COL 157599. P\_fulig; EU581209.1. *Piper garagaranum* C. DC. *Kennedy H* 3326, Colón, Panama, 1974, US 2754059. P\_garag; EU581213.1. *Piper gaudichaudianum* Kunth *Forero E* 8553, São Paulo, Brazil, 1980, COL 296282. P\_gaudi; EU581214.1. *Piper gigantifolium* C. DC. *Poole JM* 2084, Amazonas, Brazil, 1979, US 3033294. P\_gigan; EF056259.1. *Piper glabratum* Kunth *Croat TB* 51716, Putumayo, Colombia, 1980, COL 306815. P\_glabra; EU581215.1. *Piper glabrescens* (Miq.) C. DC. *Henkel TW* 4264, Potaro-Siparuni, Guyana, 1993, COL 498912. P\_glabre; EU581217.1. *Piper glanduligerum* C. DC. *Callejas R* 5479, Antioquia, Colombia, 1987, US 3265460. P\_gland; EU581219.1. *Piper goesii* Yunck. *Jaramillo MA* 912, Rio de Janeiro, Brazil, 2005, HUA 156065. P\_goesi; EU581220.1. *Piper grande* C. DC. *Luteyn JL* 14352, Pichincha, Ecuador, 1990, US 3314078. P\_grand; EU581221.1. *Piper griffithii* C. DC. *Jaramillo MA* 511, Of Nim Binh, Vietnam, 1999, HUA 145783. P\_griffi; EU581225.1. *Piper guahamense* C. DC. *Wood KR* 3353, Guam, Mariana Islands, 1994, US 3364812. P\_guaha; EU581226.1. *Piper guayanum* C. DC. *Jaramillo MA* 78, Valle del Cauca, Colombia, 1997, HUA 108198. P\_guayr; EU581227.1. *Piper guineense* Schumach. & Thonn. *Carvalho* 5548, Centro Sur, Equatorial Guinea, 1994, US 3372081. P\_guine; EU581229.1. *Piper gymnostachyum* C. DC. *Thorel MD* 678, Cochinchina, Vietnam, 1862, US 2496688. P\_gymno; AY572325.1.
- Piper hancei* Maxim. *Hu SY* 11837, Hong Kong, China, 1972, US 2730589; NCLC-W 1961. P\_hance; EU581232.1. *Piper hartwegianum* (Benth.) C. DC. *López F* 8121, Valle del Cauca, Colombia, 1963, US 2451178. P\_hartw; AY326207.1. *Piper haughtii* Trel. & Yunck. *Brand J* 1260, Colombia, Mpio Mutatá, 1984, COL 284342. P\_haugt; EU581233.1. *Piper hebetifolium* W.C. Burger *Skutch AF* 3739, Heredia, Costa Rica, 1938, US 1643881. P\_hebet; EF056261.1. *Piper hirtellipetiolum* C. DC. *Gerrit GS* 1937, Panamá, Panama, 1937, US 1688646. P\_hirte; EU581234.1. *Piper hispidum* Hayata *Pipoly J* 15103, Amazonas, Colombia, 1991, COL 413538. P\_hispi; EU581238.1. *Piper hoffmanseggianum* Schult. *Strudwick JJ* 4197, Pará, Brazil, 1981, US 2250217. P\_hoffm; EU581246.1. *Piper holdridgeanum* W.C. Burger *Burger WC* 8108, Heredia, Costa Rica, US 3556035. P\_holdr; EU581247.1. *Piper hostmannianum* (Miq.) C. DC. *Maas H* 439, Amazonas, Brazil, 1971, COL 160495. P\_hostm; EU581249.1. *Piper humistratum* Görts & K.U. *Kramer Irwin HS* 54773, Lucie Rivier, Suriname, 1963, COL 139113. P\_histr; EU581252.1. *Piper hymenophyllum* Miq. *Nicolson DH* 2866, Mysore, India, 1972, US 2654808. P\_hyme; AY572327.1.
- Piper immutatum* Trel. *Bentancur JB* 4968, Putumayo, Colombia, 1994, COL 366511. P\_immut; EU581256.1. *Piper imperiale* (Miq.) C. DC. *Madrigal B* 664, Nariño, Colombia, 1989, COL 362792. P\_imper; AF275176.1. *Piper inaequale* C. DC. *Jaramillo MA* 127, Chocó, Colombia, 1998, COL 416572. P\_inaeq; EU581257.1. *Piper insipiens* Trel. & Yunck. *Jaramillo MA* 762, Chocó, Colombia, 2000, HUA 153292. P\_insip; EU581261.1. *Piper jacquemontianum* Kunth *Barringer K* 4022, Guanacaste, Costa Rica, 1983, COL 316972. P\_jacqu; EU581264.1. *Piper klotzschianum* (Kunth) C. DC. *Mexia Y* 1930, Mont Galbao, French Guiana, 1930, US 2250217. P\_klotz; EU581266.1. *Piper lacunosum* Kunth *Fernández AJL* 7124, Cundinamarca, Colombia, 1987, COL 341320. P\_lacun; EU581267.1. *Piper laevigatum* Kunth *Cuatrecasas J* 11097, Putumayo, Colombia, 1940, COL 17520. P\_laevi; EU581269.1. *Piper leptostachyum* Willd. ex Kunth *Jaramillo MA* 510, Of Nim Binh, Vietnam, 1999, HUA 145784. P\_lepto; EU581275.1. *Piper lepturum* Kunth *Sucre D* 6257, Rio de Janeiro, Brazil, 1963, US 2928633. P\_leptu; EU581277.1. *Piper littorale* C. DC. *Jaramillo MA* 130, Chocó, Colombia, 1998, COL 416598. P\_litto; EU581278.1. *Piper lolot* C. DC. *Nagata KM* 3151, Honolulu, Hawaii, 1985, US 3093629. P\_lolot; AY326208.1. *Piper longepilosum* C. DC. *Dodson CH* 5572, Los Ríos, Ecuador, 1974, US 2694782. P\_longep; EF056266.1. *Piper longestylosum* C. DC. *Nee M* 39788, Santa Cruz, Bolivia, 1990, US 3250361. P\_longes; EU581280.1. *Piper longispicum* C. DC. *Jaramillo MA* 135, Chocó, Colombia, 1998, US 3523027. P\_longis; AY326209.1. *Piper longivaginanis* C. DC. *Ramos E* 48510, Rizal, Philippines, 1926, US 1527912. P\_longiva; EU581282.1. *Piper longivillosum* Trel. & Yunck. *Unknown collector s.n.*, Colombia, 1950, COL 11762. P\_longivi; EU581283.1.
- Piper macropiper* Benth. & Hook. f. *D. Ama* 15680, Morobe, Papua New Guinea, 2002, US 3486074. P\_macro; EF060073.1. *Piper maranyonense* Trel. *Clarck JL* 230, Ecuador, Esmeraldas, Quinde Cantón, 1994, COL 459116. P\_maran; EU581287.1. *Piper marequitense* C. DC. *Cuatrecasas J* 24802, Magdalena, Colombia, 1959, COL 87282. P\_mareq; AY326210.1. *Piper marginatum* Jacq. *Maguire B* 36088, Amazonas, Venezuela, 1956, US 2168968. P\_margi; EU581289.1. *Piper marsupiiferum* Trel. *Cazalet PC* 7620, Huila, Colombia, 1962, US 2406101. P\_marsu; EF056269.1. *Piper massiei* C. DC. *Jaramillo MA* 486, Of Vinh Phuc, Vietnam, 1999, HUA 147296. P\_massi; EU581295.1. *Piper maxonii* C. DC. *Pittier s.n.*, Costa Rica, 1890, US 796531. P\_maxon; EF056270.1. *Piper medellinifolium* Quisumb. *Jaramillo MA* 196, Sorsogón, Philippines, 1999, US 3538492. P\_medin; EU581296.1. *Piper melanocladum* C. DC. *Standley PC* 48658, Limón, Costa Rica, 1926, US 1307554. P\_melan; EF056271.1. *Piper methysticum* G. Forst. *Albert E* 16, Madolenihmw, Pohnpei, Micronesia, 2001, US 3560816. P\_methy; AF275194.1. *Piper michelianum* C. DC. *Jaramillo MA* 540, Jalisco, Mexico, 1999, US 3523082. P\_miche; AF275188.1. *Piper mollicomum* Kunth *Falcão JIA* 89384, Pernambuco, Brazil, 1959, COL 192169. P\_mollici; EU581300.1. *Piper mourai* Yunck. *Prance GT* 16325, Amazonas, Brazil, 1971, US 2899934. P\_moura; EU581303.1. *Piper muelleri* C. DC. *Jaramillo MA* 541, Jalisco, Mexico, 1999, US 3475043. P\_muelli; EU581304.1. *Piper mullesua* Buch.-Ham. ex D. Don *Townsend C* 1, Nilgiris, India, 1973, US 2965750. P\_mulle; AF203634.2. *Piper multiplinervium* C. DC. *Jaramillo MA* 139, Chocó, Colombia, 1998, US 3523031. P\_multi; AF275168.1. *Piper munchanum* C. DC. *Gentry AL* 41168, Zulia, Venezuela, 1983, US 3065874. P\_munch; AF275164.1. *Piper muricatum* Blume *Clemens MS* 26211, Sabah, Borneo, 1931, US 2185292. P\_muric; EU581306.1. *Piper myrmecophilum* C. DC. *M.A. Jaramillo* 205, Samar, Philippines, 1999, US 3538301. P\_myrm; AY572328.1.
- Piper neesianum* C. DC. *Lundell CL* 7916, Yucatán, México, 1938, US 188286. P\_neesia; EU581310.1. *Piper nigrum* L. *Jayasuriya M* 1199, Central Province, Ceylon, 1973, US 2766224. P\_nigr; AF275198.1. *Piper nudifolium* C. DC. *Suárez S* 738, Chocó, Colombia, 1995, COL 416342. P\_nudif; EU581320.1. *Piper obliquum* Ruiz & Pav. *Kress WJ* 94-4062, Puntarenas, Costa Rica, 1994, US 3314212. P\_obliq; EU581323.1. *Piper obtusilimbum* C. DC. *Cárdenas D* 12014, Putumayo, Colombia, 2000, COL 472123. P\_obtus; EU581327.1. *Piper otophorum* C. DC. *Jaramillo MA* 143, Chocó, Colombia, 1998, COL 416585. P\_otoph; EU581329.1. *Piper ottoniaefolium* C. DC. *Jaramillo MA* 715, Pichincha, Ecuador, 2000, COL 464069. P\_otton; AY326213.1. *Piper ovioido* Urb. *Jaramillo MA* 1282, República Dominicana, Sierra de Bahoruco, 2008, HUA 168221. P\_ovioido; EU581331.1.
- Piper paramaribense* C. DC. *Irwin HS* 55893, Zuid Rivier, Suriname, 1963, COL 157468. P\_param; EU581332.1. *Piper pedunculatum* C. DC. *Gentry A* 24501, Chocó, Colombia, 1979, COL 244093. P\_pedun; EU581333.1. *Piper peltatum* L. *Lowrie SR* 582, Acre, Brazil, 1980, US 3081751. P\_pelta; EU581335.1. *Piper pendulispicum* C. DC. *Jaramillo MA* 396, Of Ha Tihn, Vietnam, 1999, HUA 147253. P\_pendu; EU581337.1. *Piper penninerve* C. DC. *Jaramillo MA* 213, Surigao del Norte, Philippines, 1999, US 3538310. P\_penni; AF275206.1. *Piper perareolatum* C. DC. *Woytkowski F* 7826, Amazonas, Peru, 1962, US 2452942. P\_perar; EF056279.1. *Piper perlasense* Yunck. *Johnston IM* 1215, Panamá, Panama, 1946, US 2024278. P\_perlas; EU581338.1. *Piper perpusillum* Callejas *Callejas R* 6463, Colombia, Mpio Frontino, Cauca?, 1988, HUA 51871. P\_perpu; AY326215.1. *Piper phytolaccifolium* Opiz *House PR* 2805, Gracias a Dios, Honduras, 1994, US 3422085. P\_phyto; AY326216.1. *Piper pierrei* C. DC. *Jaramillo MA* 394, Of Ha Tihn, Vietnam, 1999, HUA 147293. P\_pierri; AF275200.1. *Piper pilibracteum* Trel. & Yunck. *Franco P* 4819, Nariño, Colombia, 1993, COL 361140. P\_pilib; AY768829.1. *Piper piluliferum* Kunth *Menuz D* 9106, Pastaza, Ecuador, 1993, US 3496380. P\_piluli; EU581340.1. *Piper piscatorum* Trel. & Yunck. *van der Werff H* 7736, Bolívar, Venezuela, 1985, US 3160255. P\_pisca; EU581343.1. *Piper pittieri* C. DC. *Standley PC* 51555, Heredia, Costa Rica, 1926, US 1307653. P\_pitti; EU581345.1. *Piper porphyrophyllum* N.E. Br. *Sinclair J* 5513, Singapore, Malaya, 1949, US 2931846. P\_porph; EU581346.1. *Piper praesagium* Trel. & Yunck. *Lozano G* 5762, Cauca, Colombia, 1987, COL 317568. P\_praes; EU581348.1. *Piper pseudofulgineum* C. DC. *Callejas R* 13542, Puntarenas, Costa Rica, 2005, HUA 154149. P\_pseudof; EU581350.1. *Piper pseudolindenii* C. DC. *Arvigo R* 247, Cayo, Belize, 1996, US 3361342. P\_penni; EU581354.1. *Piper psilorhachis* C. DC. *Cook OF*



- 6v, Petén, Guatemala, 1922, US 1084576. P\_psilo; EU581357.1. *Piper pterocladum* C. DC. *Skutch AF 4507*, Pastaza, Ecuador, 1939, US 177552. P\_ptero; EU581359.1. *Piper puberulum* Seem. *O'Rourke L 272*, Island of 'Eua, Tonga, 1989, US 3136218. P\_puber; EU581360.1. *Piper pulchrum* C. DC. *Jaramillo MA 100*, Antioquia, Colombia, 1997, US 3523641. P\_pulch1; AF275177.1. *Piper reticulatum* L. *Jaramillo MA 128*, Chocó, Colombia, 1998, US 3523020. P\_retic; EU581366.1. *Piper retrofractum* Vahl *Balansa B 1887*, Asia, 1885, US 2492675; *B 1567*; Kinabalu, Malaysia, 1885, US 2963829; NCLC-W 1962. P\_retro; EF060081.1. *Piper richardiifolium* Kunth *Irwin HS 28672*, Minas Gerais, Brazil, 1971, US 2841165. P\_richa; EU581369.1. *Piper riparense* C. DC. *Kennedy H 692*, Panamá, Panamá, 1970, US 2684238. P\_ripar; EU581371.1. *Piper rusbyi* C. DC. *Beck G 3783*, Larecaja, Bolivia, 1980, HUA 103764. P\_rusby; EU581375.1.
- Piper sabaletasanum* Trel. & Yunck. *Jaramillo MA 623*, Chocó, Colombia, 2000, HUA 124227. P\_sabal; AY326217.1. *Piper sagittifolium* C. DC. *Skutch AF 3866*, San José, Costa Rica, 1939, US 1644501. P\_sagit; EF056284.1. *Piper samanense* Urb. *Acevedo P 8548*, Seibo, Dominican Republic, 1996, US 3353551. P\_saman; EU581377.1. *Piper sampaioi* Yunck. *Jaramillo MA 916*, Rio de Janeiro, Brazil, 2005, HUA 156068. P\_sampa; EU581378.1. *Piper sancti-felicis* Trel. *Sneidern KV 193*, Chocó, Colombia, 1940, COL 102405. P\_sancti; EU581380.1. *Piper sanctum* (Miq.) Schlttdl. ex C. DC. *Taylor K 96*, Veraacruz, Mexico, 1983, COL 383220. P\_sanctu; EU581383.1. *Piper sarmentosum* Roxb. *Levine CO 3066*, Kwong Tung, China, 1918, US 3508861. P\_sarme; EU581385.1. *Piper sasaimanum* Yunck. *Madison MT 4944*, Carchi, Ecuador, 1978, US 2850635. P\_sasai; EF056286.1. *Piper schwackei* C. DC. *Taylor EL E1057*, Amazonas, Brazil, 1983, US 3197318. P\_schwa; EU581387.1. *Piper scutifolium* Yunck. *López NA 2316*, Chocó, Colombia, 1998, HUA 155220. P\_scutif; EU581389.1. *Piper scutilimum* C. DC. *Alvia P 1350*, Yasuní, Ecuador, 2002, US 3447919. P\_scutil; EU581390.1. *Piper solmsianum* C. DC. *Hatschbach G 85*, Paraná, Brazil, 2004, US 3076763. P\_solms2; EU581393.1. *Piper sorsogonum* C. DC. ex *Quisumb. Jaramillo MA 185*, Quezón, Philippines, 1999, US 3495316. P\_sorso; AY572320.1. *Piper spoliatum* Trel. & Yunck. *Jaramillo MA 60*, Chocó, Colombia, 1997, US 3523005. P\_spoli; AF275179.1. *Piper sprengelianum* C. DC. *Brito TH 3995*, Bahía, Brazil, 1986, US 3029160. P\_spren; EU581398.1. *Piper squamulosum* C. DC. *Haught O 2915*, Cotopaxi, Ecuador, US 1707588. P\_squam; EF056287.1. *Piper sternii* Yunck. *Escobar de LA 8265*, Colombia, Mpio San Carlos, 1988, HUA 45909. P\_stern; EU581399.1. *Piper stileferum* Yunck. *Harling G 24055*, Ecuador, Zamora-Chinchi, 1985, HUA 46014. P\_stile; EU581400.1. *Piper stipulaceum* Opiz *Jaramillo MA 551*, Colima, Mexico, 1999, US 3523091. P\_stipu; EU581401.1. *Piper subflavum* C. DC. *Saravia C 1606*, Valle del Cauca, Colombia, 1962, COL 227164. P\_subfl; EU581402.1. *Piper subglabibracteatum* C. DC. *Franco P 5110*, Nariño, Colombia, 1993, COL 361301. P\_subgl1; AY326220.1. *Piper subpedale* Trel. & Yunck. *Zarucchi J 5061*, Antioquia, Colombia, 1987, COL 403976. P\_subped; AF275161.1. *Piper subscurtatum* (Miq.) C. DC. *Holguer LS 5643*, Pastaza, Ecuador, 1979, HUA 45296. P\_subsc; EU581406.1.
- Piper tardans* Trel. *Jaramillo MA 1061*, Chiriquí, Panamá, 2007, HUA 164851. P\_tarda; EF056290.1. *Piper tomas-albertoi* Trel. & Yunck. *Callejas R 7959*, Chocó, Colombia, 1989, HUA 64566. P\_tomas; AY326222.1. *Piper tonduzii* C. DC. *Herrera G 5119*, Limón, Costa Rica, 1992, HUA 090934. P\_tondu; EU581411.1. *Piper toppingii* C. DC. *Jaramillo MA 186*, Quezón, Philippines, 1999, US 3495315. P\_toppi; AY572322.1. *Piper trianae* C. DC. *Jaramillo MA 720*, Valle del Cauca, Colombia, 2000, HUA 153244. P\_trian; EU581412.1. *Piper tricuspe* (Miq.) C. DC. *Vargas WG 4301*, Chocó, Colombia, 1997, HUA 126473. P\_tricu; AY326225.1. *Piper trigonum* C. DC. *Rivas A 813*, Chocó, Colombia, 2006, HUA 152860. P\_trigo; EU581420.1. *Piper tuberculatum* Jacq. *Hopkins MJ 878*, Roraima, Brazil, 1986, US 3115222. P\_tuber; EU581425.1. *Piper tuerkheimii* C. DC. *Balick MJ 2549*, Dolores, Belize, 1990, HUA 083476. P\_tuerc; EU581427.1.
- Piper umbellatum* L. *Anderson WR 36288*, Minas Gerais, Brazil, 1972, US 2796446. P\_bella; EU581429.1. *Piper urophyllum* C. DC. *Taylor J 1972*, Alajuela, Costa Rica, 1972, US 2914955. P\_uroph; EU581436.1. *Piper urostachyum* Hemsl. *Unknown collector s.n.*, Limón, Costa Rica, HUA 100653. P\_urost1; EU581437.1. *Piper vil-liramulum* C. DC. *Callejas R 13557*, Limón, Costa Rica, 2005, HUA 154005. P\_villi; EU581441.1. *Piper villosum* C. DC. *Idrobo JR 2321*, Nariño, Colombia, 1957, HUA 118291. P\_villo; AY326228.1. *Piper vitaceum* Yunck. *Vasquez R 9529*, Loreto, Perú, 1987, HUA 63311. P\_vitac; EU581442.1. *Piper wachenheimii* Trel. *Mori S 19105*, Mont Galbao, French Guiana, 1988, HUA 70369. P\_wach; EU581443.1. *Piper xanthostachyum* C. DC. *Pujupet JO RBAE1019*, Ecuador, Morona Santiago. Los alrededores de la Mision Salesiano, 1985, HUA 41590. P\_xanth; EU581445.1. *Piper xylosteoides* (Kunth) Steud. *Beetle AA 1558*, Rio Grande do Sul, Brazil, 1952, US 2143806. P\_xylos; EU581447.1.