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DISPERSAL-VICARIANCE  
ANALYSES IN THE TRIBE  
SINNINGIEAE (GESNERIACEAE):  
A CLUE TO UNDERSTANDING  
BIOGEOGRAPHICAL HISTORY OF  
THE BRAZILIAN  
ATLANTIC FOREST<sup>1</sup>

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ABSTRACT

The historical biogeography of the tribe Sinningieae (Gesneriaceae) was analyzed based on distribution data and a molecular species-level phylogeny of 76 species. This plant group is distributed from Mexico to northern Argentina, but by far the highest diversity occurs within the Brazilian Atlantic forest. The dispersal-vicariance analysis method and a cladistic approach were used to infer ancestral areas as well as patterns of dispersal and vicariance. Results indicate that the Sinningieae probably arose in the coastal rain forest or in the neighboring tropical area delimited by the São Francisco river in Brazil. The majority of the dispersal-vicariance episodes were reconstructed between the Brazilian Atlantic rain forests and their neighboring inland areas (i.e., Paraná and São Francisco regions). In contrast, few dispersal-vicariance events were reconstructed between the tropical and subtropical areas of the Atlantic rain forest and between the Paraná and São Francisco regions. These results, together with ancestral areas inferred at the root of the main lineages, indicate an early north-south disjunction in Sinningieae. Occurrence of Sinningieae species in other areas, such as the Andes, the cerrado, Amazonia, northern South America, and Central America, are mainly explained by independent range expansions of single species from either the Paraná or the São Francisco regions. According to the dispersal-vicariance optimization, 20% of the speciation events are subsequent to inter-area dispersal and range expansion, 23% are associated with inter-area vicariance, and 57% occurred at a lower geographical scale within a single biogeographic area. These results pinpoint the need for a phylogenetic framework to correctly understand area relationships and the relative contribution of dispersal and vicariance events in present-day distribution patterns.

*Key words:* Atlantic forest, Brazil, dispersal, historical biogeography, Mata Atlântica, semi-deciduous forest, speciation, tropical rain forest, vicariance.

RESUMEN

Se analizó la biogeografía histórica de la tribu Sinningieae (Gesneriaceae) sobre la base de datos de la distribución y filogenia molecular al nivel de especie de 76 especies. Este grupo de plantas se distribuye desde México hasta el norte de Argentina, pero la diversidad más alta se encuentra en el bosque atlántico brasileño. Se usaron el método de análisis de dispersión-vicarianza y un acercamiento cladístico para inferir las áreas ancestrales así como los patrones de dispersión y vicarianza. Los resultados indican que las Sinningieae surgieron probablemente en el bosque húmedo tropical costero o en el área tropical vecina delimitada por el río São Francisco en Brasil. Se reconstruyeron la mayoría de los episodios de dispersión-vicarianza entre el bosque húmedo atlántico brasileño y sus áreas interiores vecinas (i.e., regiones de Paraná y de São Francisco). En contraste, se reconstruyeron pocos eventos de dispersión-vicarianza entre las áreas tropicales y subtropicales del bosque húmedo atlántico y entre las regiones de Paraná y de São Francisco. Estos resultados, junto con las áreas ancestrales inferidas en la raíz de los linajes principales, indican una temprana disyunción norte-sur en Sinningieae. La presencia de especies de Sinningieae en otras áreas tales como los Andes, los cerrados, la Amazonia, el norte de América del Sur y América Central se explica principalmente por expansiones independientes de la distribución de especies individuales sea desde la región de Paraná o de São Francisco. Según la optimización de la dispersión-vicarianza, el 20% de los acontecimientos de especiación es subsecuente a la dispersión inter-área y a la extensión de la distribución, el 23% se asocia con vicarianza inter-área, mientras que la mayoría de los eventos de especiación (el 57%) ocurrieron en una escala geográfica más baja dentro de una sola área biogeográfica. Estos resultados indican la necesidad de un marco filogenético para entender correctamente las relaciones del área y la contribución relativa de los eventos de dispersión y vicarianza en los actuales patrones de distribución.

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The Brazilian Atlantic forest is known for its high level of species diversity and endemism, as well as for being one of the most threatened tropical forests in the world (Mori et al., 1981; Terborgh, 1992; Morellato & Haddad, 2000; Myers et al., 2000). According to a broad definition, the Atlantic forest biome is composed of two types of vegetation. One is the coastal rain forest on the eastern slope of the mountain chain that runs along the coastline from southern to northeastern Brazil. The other is a neighboring semideciduous forest that extends farther inland in Brazil, with small portions entering Paraguay and Argentina (Fernandes & Bezerra, 1990; Spichiger et al., 1995; Morellato & Haddad, 2000). Despite recent efforts to characterize this biome (e.g., Oliveira-Filho & Fontes, 2000), little is known about its biogeographic history. Affinities among the different phytogeographic units that compose the Atlantic forest and their relationships with other areas in South America were generally based on floristic data, distribution patterns, or paleoenvironmental evidence (Smith, 1962; Harley, 1988; Prado & Gibbs, 1993; Oliveira-Filho & Ratter, 1995; Safford, 1999; Oliveira-Filho & Fontes, 2000; Pennington et al., 2000; Spichiger et al., 2004; Taylor & Zappi, 2004). Floristic studies indicate a strong link between the coastal Atlantic rain forests and the adjacent semideciduous forests (Oliveira-Filho & Fontes, 2000). On a larger scale, the semideciduous forests in Brazil and Paraguay were shown to be related with other fragments of tropical seasonal forest scattered along a large peri-Amazonian arc that passes through northeastern Brazil, the Paraguay-Paraná river basin, the Andes, and northern South America (Prado & Gibbs, 1993; Pennington et al., 2000). Other evidence based on distributions of closely related species indicates biotic exchanges between the Atlantic forest and either the Andes or the Guayana Highlands (Rambo, 1951; Smith, 1962; Granville, 1982; Safford, 1999; Prado, 2000). However, the place of origin or the direction and frequency of range movements are unknown for most taxonomic groups that occur in the Atlantic forest (cf. Berry et al., 2004; Sánchez-Baracaldo, 2004; Taylor & Zappi, 2004). It is also unclear how vicariance and dispersal have interacted to determine current distribution patterns. In this study, we investigate these issues in a tribe of Gesneriaceae using detailed distribution data and a nearly complete species-level phylogeny inferred from a simultaneous analysis of seven DNA regions (Perret et al., 2003).

The tribe Sinningieae includes three genera, *Paliavana* Vell. ex Vand., *Sinningia* Nees, and *Vanhouttea* Lem., and a total of 81 species (Clayberg, 1968; Wiehler, 1983, 1984; Chautems, 1990, 1991,

1995, 2002; Wiehler & Chautems, 1995; Chautems et al., 2000). Their habit varies from herbaceous plants with a perennial tuber in most *Sinningia* species to woody shrubs without tubers in *Paliavana* and *Vanhouttea*. They are mainly saxicolous, but some species are epiphytic or terrestrial (Chautems & Weber, 1999). Most of the Sinningieae taxa are found along mountain ranges (up to 2200 m) within the Brazilian Atlantic rain forest or in the adjacent areas occupied by seasonal vegetation types, i.e., the caatingas s.l. of eastern and northeastern Brazil (Prado, 2000), the cerrado biome in central Brazil, and the Misiones nucleus in the Paraguay-Paraná river basin (Prado & Gibbs, 1993). A restricted number of species (5) are also found farther along the Andes, in Amazonia, northern Colombia, Venezuela, the Guayana Highlands, Central America, and southern Mexico. The Sinningieae is therefore an appropriate group for investigating general patterns in historical biogeography of the Brazilian Atlantic forest and its relationships with other areas in South America.

The biogeographic history of the Sinningieae was reconstructed using a phylogenetic framework and methods, such as the dispersal-vicariance analysis that considers dispersal and extinction explicitly (Ronquist, 1997), and a cladistic approach that assumes no particular speciation mechanism (Bremer, 1992). Our goals are several: (1) to reconstruct the ancestral distribution of the tribe; (2) to infer directions and frequency of dispersal events, especially within the domain of the Atlantic forest and between this region and other biogeographic areas in South America; and (3) to evaluate how inter-area dispersal and vicariance processes have interacted during Sinningieae diversification.

## MATERIAL AND METHODS

### SAMPLING AND PHYLOGENETIC ANALYSIS

Sixty-two species of *Sinningia*, six species of *Paliavana*, and eight species of *Vanhouttea* were included in the phylogenetic analysis. This sampling represents all currently recognized species in the tribe Sinningieae, with the exception of *Sinningia helleri* Nees, *S. schomburgkiana* (Kunth & Bouché) Chautems, and *S. sulcata* (Rusby) Wiehler, for which no material was available. The two selected outgroups, *Smithiantha laui* Wiehler and *Nematanthus villosus* (Hanst.) Wiehler, belong to the tribes Gloxinieae and Episcieae, respectively, and are closely related to Sinningieae based on a molecular phylogenetic analysis of the entire family (Smith et al., 1997). A full list of taxa with author attributions and vouchers is provided in Appendix 1.

The plastid DNA spacers *trnT-trnL*, *trnL-trnF*, *trnS-trnG*, *atpB-rbcL*, introns *trnL* and *rpl16*, together with a portion of the nuclear encoded *nepGS* gene were sequenced following the procedure described in Perret et al. (2003). All sequences have been deposited in EMBL/GenBank (accessions AJ438352–AJ438434, AJ439249–AJ439331, AJ439745–AJ439829, AJ439900–AJ439984, AJ487702–AJ487786, AJ459606–AJ459691). Because these regions were found compatible (Perret et al., 2003), we performed a combined analysis with 5812 characters using PAUP\*4.0b8 (Swofford, 1999). We made a 50% majority-rule bootstrap consensus tree from 1000 bootstrap replicates (Felsenstein, 1985) using maximum parsimony, tree bisection-reconnection swapping, simple addition of taxa (SIMPLE), and a limit of 500 trees retained at each replicate (MAXTREES = 500). This tree was then used as a constraint tree in a maximum likelihood analysis using the HKY85 model, incorporating rate variation across sites and proportion of invariable sites (Yang, 1996).

#### BIOGEOGRAPHIC DATA AND DELIMITATION OF AREAS

Distribution data were obtained for all 76 species of *Sinningieae* used in the phylogenetic analysis. Species distributions were based on over 3000 accessions from 67 international and Brazilian herbaria (i.e., ALCB, ASE, B, BH, BHC, BOTU, CAY, CGE, CEN, CEPEC, CESJ, CONN, E, EAN, ESA, F, FCQ, FUEL, G, GB, GFJP, GUA, HAS, HBR, HEPH, HUEFS, IAC, IAN, IBGE, ICN, INPA, IPA, K, MBM, MBML, MG, MO, NA, NY, P, PACA, PEUFR, PKDC, PY, R, RB, RBR, RUSU, S, SEL, SP, SPF, SPSF, UB, UC, UEC, UFG, UFMT, UFP, UPCB, UPS, US, VEN, W, WIS, WU, Z). Part of this chorological information is available in various published floras and taxonomic treatments for Argentina (Toursarkisian, 1969), Paraguay (Chautems, 1993), and Brazil (Chautems, 1990, 1991, 1995, 2002, 2003a, 2003b; Woodger, 1995; Chautems et al., 2000; Araujo et al., 2005). Representative specimens for all species included in this study are listed in Appendix 2. Distribution maps were produced using the software ArcView GIS 3.2 (ESRI, 2000). The total range of *Sinningieae* in South and Central America was partitioned into 12 biogeographic areas (Fig. 1). These are: (1) the northern portion of the Brazilian Atlantic rain forests that lies north of the Tropic of Capricorn ( $A_N$ ); (2) the southern portion of the Brazilian Atlantic rain forests that lies south of the Tropic of Capricorn ( $A_S$ ); (3) the São Francisco region (F) (caatingas province s.l. according to Prado, 2000), including the semideciduous forests and the campos rupestre distributed east of the São Francisco river in Brazil

and the caatingas of northeastern Brazil; (4) the Paraná region (P) (sensu Cabrera & Willink, 1973), including the semideciduous forest of the Paraguay-Paraná river system in eastern Paraguay, northeastern Argentina, and southwestern Mato Grosso do Sul (Misiones nucleus) and the Araucaria forest in southern Brazil; (5) the cerrado (C); (6) the Chaco (O); (7) the Pampas in southern Brazil and Uruguay (U); (8) the southern Andes ( $D_S$ ); (9) the northern Andes ( $D_N$ ); (10) Amazonia (Z); (11) northern Colombia-Venezuela and the Guayana Highlands (V); and (12) Central America and southern Mexico (M). We are aware that some areas are composed of distinct phylogeographic units that are usually considered separately.

#### ANCESTRAL AREA RECONSTRUCTION

Ancestral distributions were reconstructed on the phylogenetic tree using dispersal-vicariance analysis (DIVA; Ronquist, 1997), as implemented in the program DIVA 1.1 (Ronquist, 1996). This method is event-based and allows for the inference of the ancestral distribution in a given phylogeny without forcing vicariance events to conform to a hierarchical pattern. DIVA is thus appropriate to infer biogeographic patterns even when area relationships are reticulated (Sanmartín et al., 2001). The method searches for optimal reconstruction of ancestral distribution by assuming a vicariance process but incorporates the potential contribution of dispersal and extinction in shaping the current distributional pattern. The optimal solutions are those that minimize the number of dispersal and extinction events under a parsimony criterion. In our analysis, we limited the number of areas allowed for an ancestral distribution to a maximum of three, using the “maxareas” option. DIVA reconstructions were used to determine the direction of movement as well as to quantify the biogeographic processes such as dispersal, vicariance, and speciation within a single area.

In addition to DIVA, ancestral areas of the *Sinningieae* and of its major lineages were also determined using the method proposed by Bremer (1992). This approach is a cladistic procedure in which each area is treated as a single character that can be optimized on a cladogram. For a particular clade, one can calculate the necessary number of gains and losses of each area by using forward or reverse Camin-Sokal parsimony, respectively. The ratio between gains and losses provides an estimate of the likelihood that one particular area is part of the ancestral region. The area with the highest gain:loss ratio is considered to have 100% probability of being part of the ancestral region.

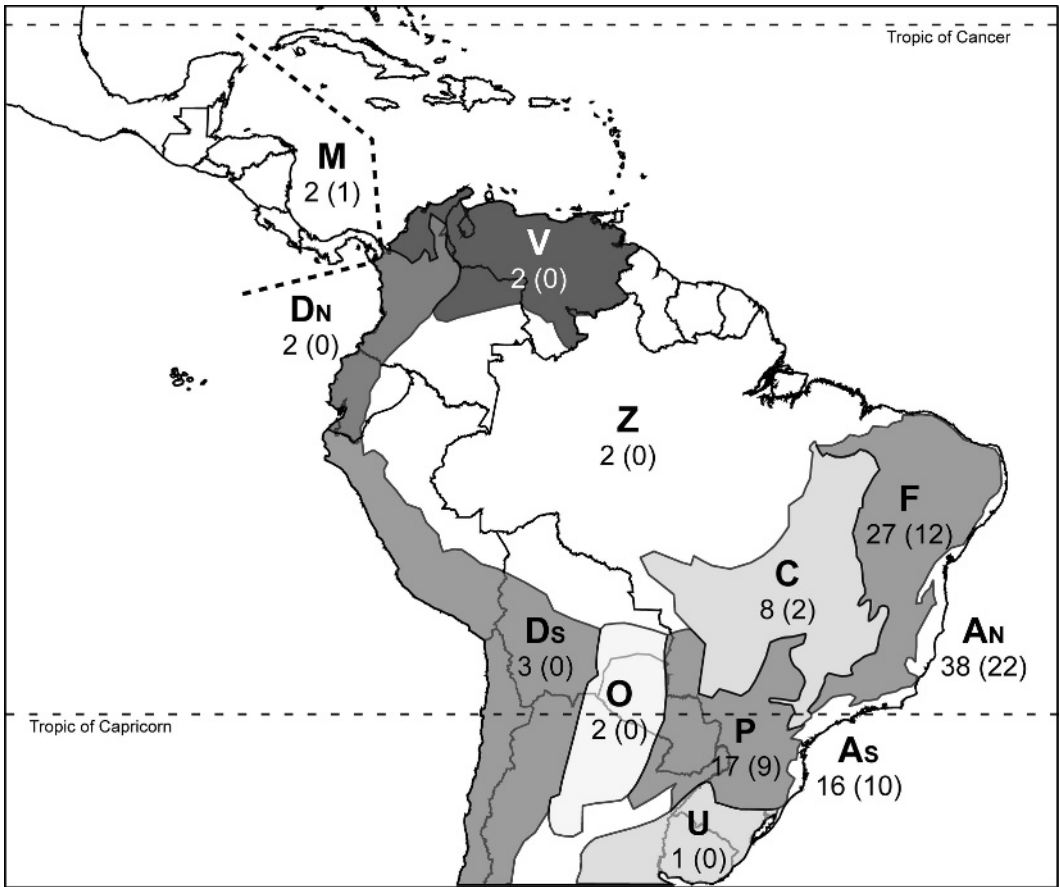


Figure 1. Biogeographic areas used to delimit *Sinningieae* species distributions in South and Central America.  $A_N$ ,  $A_S$  = the northern and southern portions of the Brazilian Atlantic rain forests that lie respectively north and south of the Tropic of Capricorn; F = the São Francisco region; P = the Paraná region; C = the cerrado region; O = the Chaco; U = the Pampas in southern Brazil and Uruguay;  $D_S$  = southern Andes;  $D_N$  = northern Andes; Z = Amazonia; V = northern Colombia, Venezuela, and the Guayana Highlands; M = Central America and southern Mexico. Numbers indicate the total number of species occurring in each area. Numbers in parentheses indicate the number of species endemic to the area. Delimitations of areas were modified after Gentry (1982), IBGE (1993), and Pennington et al. (2000).

RESULTS

PHYLOGENETIC ANALYSES

The phylogenetic tree resulting from the maximum likelihood analyses and the bootstrap supports (BS) based on maximum parsimony are shown in Figure 2. Tribe *Sinningieae* is monophyletic, but both genera *Vanhouttea* and *Paliavana* are polyphyletic and embedded in *Sinningia*. Taxa are distributed into three main clades named *Dircaea* (BS 100%), *Corytholoma* (BS 73%), and *Sinningia* (BS 64%), as well as into two smaller early-diverging clades named *Vanhouttea* (BS 100%) and *Thamnoligeria* (BS 73%). The tree used here is in full agreement with our previous complementary and comprehensive phylogenetic analyses (Perret et al., 2003).

DISTRIBUTION PATTERNS

The tribe *Sinningieae* shows a continental-wide distribution between southern Mexico and northern Argentina, but the highest species richness occurs within southeastern Brazil (Fig. 1). Out of 76 species analyzed, 33 (43%) are restricted to the Brazilian Atlantic rain forest. Within this area, species are located either in the tropical zone (22 species) or south of the Tropic of Capricorn (10 species), whereas only one species is distributed across both zones (Fig. 3). Species distributed farther inland are either restricted to the areas of São Francisco, the cerrado, and Paraná (totaling 23 species, 30%), or occur across the tropical portion of the Atlantic rain forest and the São Francisco region (10 species, 13%; Fig. 3). The remaining 10 species are widespread within Brazil or

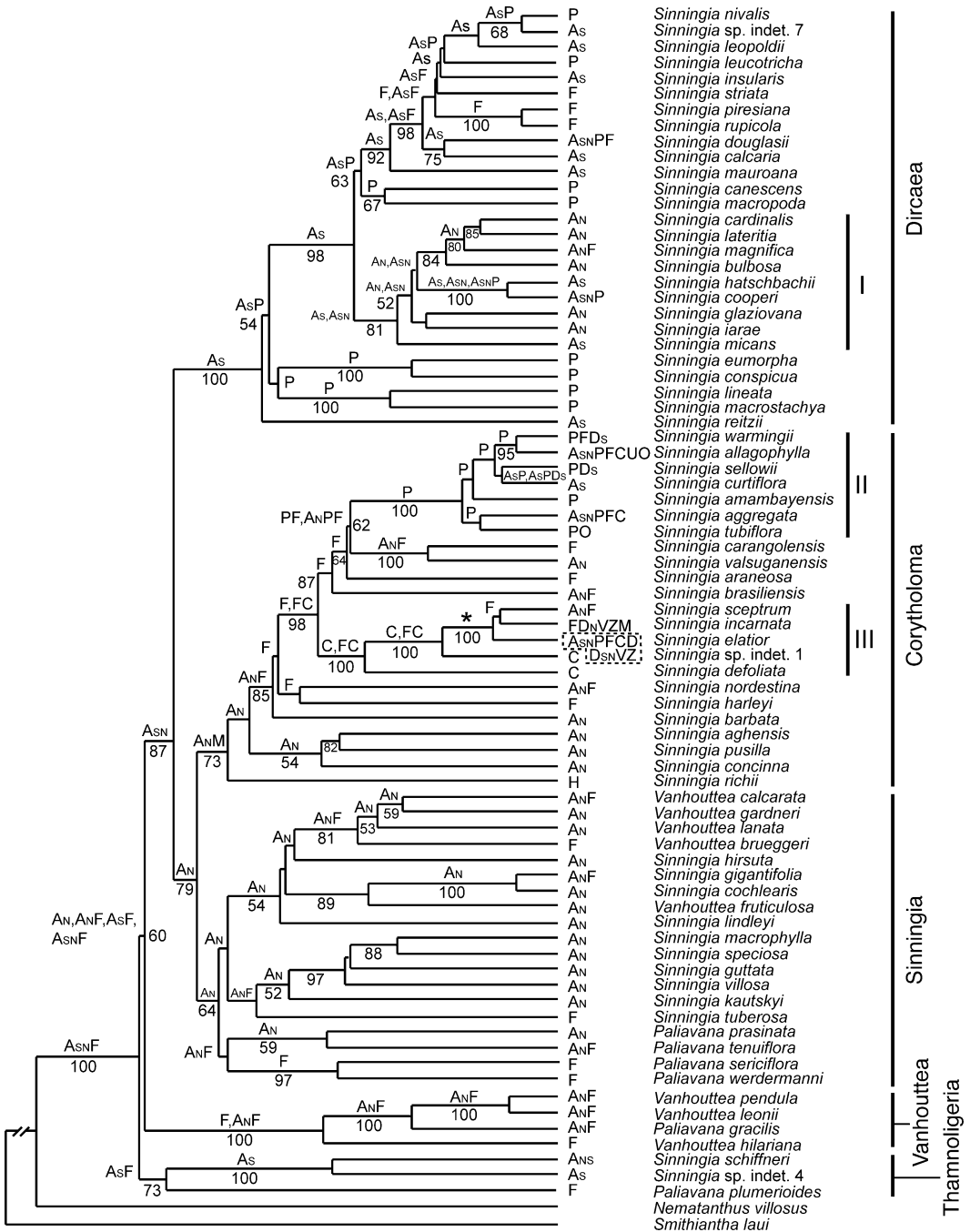


Figure 2. Phylogenetic hypothesis for the tribe Sinningieae used to reconstruct ancestral areas. The tree is based on a simultaneous analysis of plastid and nuclear DNA sequences (regions *trnT-trnL*, *trnL-trnF*, *trnS-trnG*, *atpB-rbcL*, *rpl16*, and *ncpGS*). Numbers below the branches are bootstrap proportions (only if  $\geq 50\%$ ). Ancestral areas at each internal node were reconstructed using DIVA (Ronquist, 1997). Abbreviations for biogeographic areas are defined in Figure 1. The asterisk indicates ambiguous reconstruction of the ancestral area. Names of the five major clades are indicated, and the three subclades discussed in this study are identified with Roman numerals.

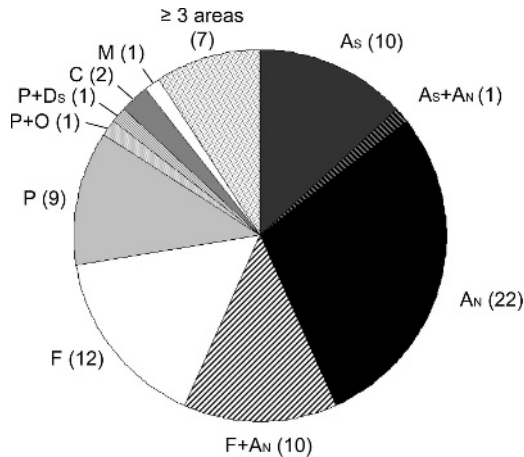


Figure 3. Pie chart summarizing the number of species according to their distributions: endemic to a single area, across two areas, or in a combination of at least three areas. Biogeographic areas are delineated and abbreviations are defined in Figure 1.

occur outside of the country in the Chaco (2), the Pampas (1), the Andes (3), Amazonia (2), northern South America (2), and Central America and southern Mexico (2, Fig. 1). Most of the latter species are distributed in a combination of more than two areas (Fig. 3).

Patterns of geographical distribution differ among the main lineages within Sinningieae (Fig. 4). The range of the clade *Corytholoma* (23 species) covers the full geographical extent of the tribe Sinningieae (Fig. 4A). In Brazil, species richness of *Corytholoma* is the highest north of the Tropic of Capricorn within the northern Atlantic rain forest and the São Francisco region. Occurrences outside of Brazil are due to a few species distributed in Paraguay and southern Argentina (*Sinningia aggregata* (Ker Gawl.) Wiehler, *S. allagophylla* (Mart.) Wiehler, *S. elatior* (Kunth) Chautems, *S. tubiflora* (Hook.) Fritsch, and *S. warmingii* (Hiern) Chautems), in the southern Andes (*S. elatior*, *S. sellowii* (Mart.) Wiehler, and *S. warmingii*), in the northern Andes (*S. elatior* and *S. incarnata* (Aubl.) D. L. Denham), in northern South America (*S. elatior* and *S. incarnata*), and in Central America up to southern Mexico (*S. incarnata* and *S. richii* Clayberg). All of these species are widespread and clustered in the subclades II and III within *Corytholoma* (Fig. 2), with the exception of the first diverging species of the clade, *S. richii*, which is a narrow endemic in the state of Veracruz in Mexico (Clayberg, 1968).

The clade *Sinningia* (19 species) is distributed from eastern to northeastern Brazil (Fig. 4B). The majority of these species (12) are restricted to the northern

Atlantic rain forest, whereas the remaining seven are found in the adjacent São Francisco region along the Mantiqueira and Espinhaço mountain ranges.

The clade *Dircaea* (27 species) is distributed from southern to southeastern Brazil (Fig. 4C). Within this clade, 16 species have a range limited to the Atlantic rain forest, whereas the remaining 11 species are restricted to either the Paraná (8) or to the southern part of the São Francisco region (3). The species that extend the farthest from the Atlantic coast are *Sinningia macropoda* (Sprague) H. E. Moore, which reaches eastern Paraguay (Chautems, 1993), and *S. magnifica* (Otto & A. Dietr.) Wiehler, which is found along the “Cadeia do Espinhaço” in Minas Gerais (Araujo et al., 2005).

The two early-diverging clades *Vanhouttea* (4 species) and *Thamneligeria* (3) are distributed in eastern Brazil (Fig. 4D). The species of the clade *Vanhouttea* occur at elevations usually between 1200 and 2200 m in a vegetation type locally called campos de altitude in the southern part of the São Francisco region along the mountain ranges of Mantiqueira, Espinhaço, and Caparaó. Distribution of the clade *Thamneligeria* is more disjunct, including elements from the Atlantic rain forest (*Sinningia schiffneri* Fritsch and an undescribed species of *Sinningia*, *S. sp. indet.* 4) together with a mountainous species (*Paliavana plumerioides* Chautems), which occur in the central part of the “Cadeia do Espinhaço” (Chautems, 2002).

#### ANCESTRAL AREAS AND DISPERSAL PATTERNS IN BRAZIL

According to the DIVA optimization shown in Figure 2 and Bremer’s method (Table 1), the ancestral area reconstructed at the root of the tribe Sinningieae most likely comprises the Atlantic rain forests together with the São Francisco region. The ancestral area of the clade *Dircaea* was restricted to the southern Atlantic rain forest, whereas the northern Atlantic region was probably part of the ancestral distribution of the clade grouping *Corytholoma* and *Sinningia* (Fig. 2 and Table 1). Subsequent to this early north-south disjunction, these two lineages followed different biogeographic pathways. In the clade *Dircaea*, dispersal-vicariance events occurred predominantly between the southern Atlantic rain forest and the Paraná region, whereas in the *Corytholoma* and *Sinningia* clades, dispersal-vicariance events were more frequent between the northern Atlantic rain forest and the São Francisco region (Table 2). Overall, 22 dispersal events were reconstructed between the coastal rain forest and the more seasonal vegetation of neighboring inland areas (i.e., Paraná and São Francisco; Fig. 5). Movements inland

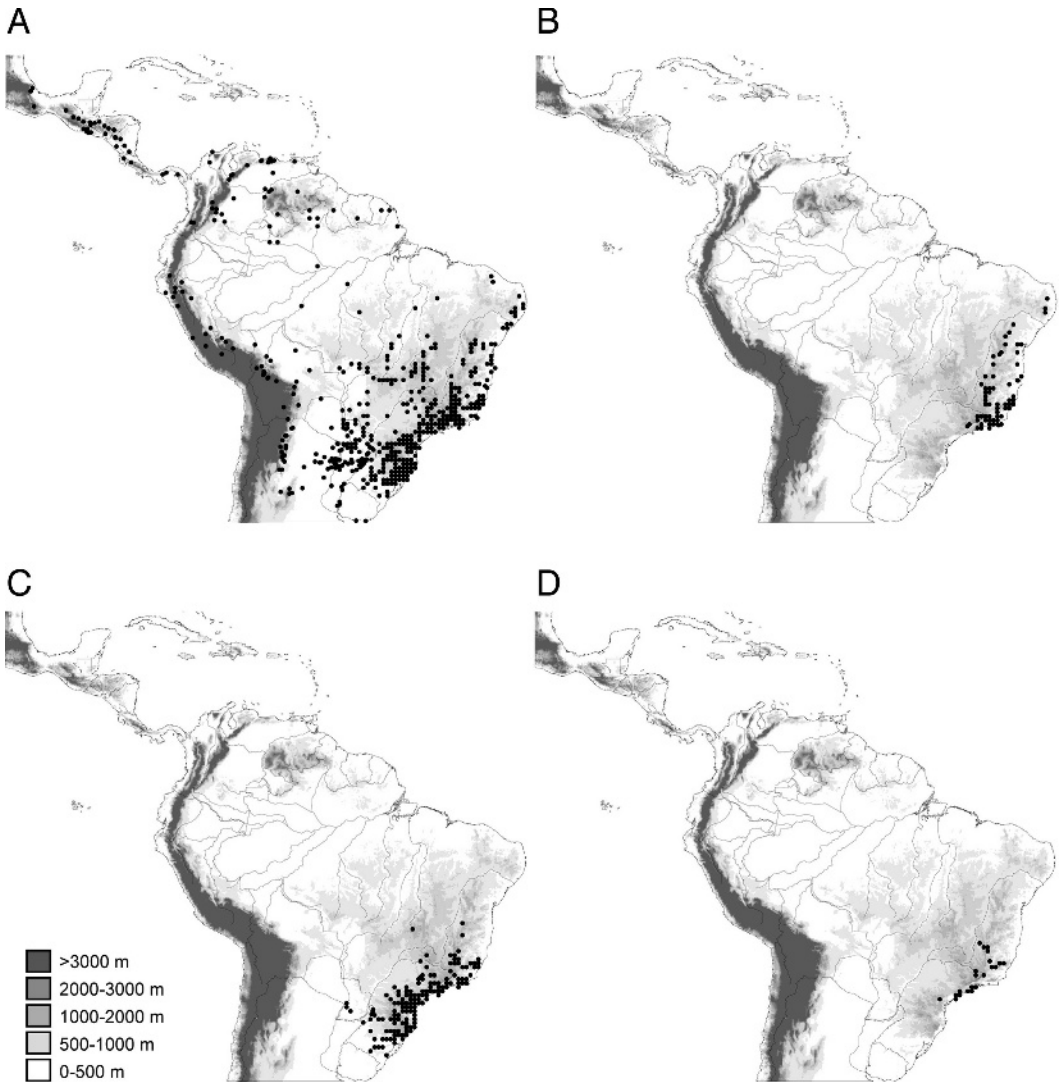


Figure 4. Distribution of the main clades within the Sinningieae as defined in Figure 2. —A. *Corytholoma* (23 species). —B. *Sinningia* (19 species). —C. *Dircaea* (27 species). —D. *Vanhouttea* and *Thamnoligeria* (7 species).

from the coast were more frequent than in the opposite direction (Fig. 5). In contrast, following a pattern parallel to the coast, only seven dispersal events were reconstructed between the northern and southern Atlantic rain forest and between the Paraná and the São Francisco regions (Fig. 5).

#### DISPERSAL PATTERNS AT A CONTINENTAL SCALE

Species found in the Chaco, the Pampas, the Andes, Amazonia, northern South America, and Central America are widespread and clustered in subclades II and III within the *Corytholoma* clade (Fig. 2, see below for an exception). Ancestral areas reconstructed at the root of subclades II and III indicate that

expansions of these taxa outside of Brazil occurred from two distinct biogeographic units: the Paraná and São Francisco + cerrado, respectively (Figs. 2 and 5). Such dispersal events were optimized on terminal or nearly terminal branches, indicating that they most likely are recent and concern mainly individual taxa (Fig. 2). The tie between the Paraná region and the Andean piedmont in the southern Andes is indicated by the distribution of *Sinningia sellowii* (Fig. 6B) and *S. warmingii* (Fig. 6A). The link between the São Francisco region and the Andes through the cerrado is indicated by the range of *S. elatior* (Fig. 6C), which also spreads into Amazonia and northern Colombia and Venezuela. In addition to these Brazilian–southern Andean connections, a tie between eastern

Table 1. Ancestral area reconstruction based on Bremer's (1992) method for the *Sinningieae* and its main clades defined in Figure 2. Ancestral area scores (AA) are probabilities that a given area is part of the ancestral area for the clade. G = number of necessary gains under forward Camin-Sokal parsimony; L = number of necessary losses under reverse Camin-Sokal parsimony; AA = G/L quotients rescaled to a maximum value of 1 by dividing with the largest G/L value. Abbreviations for biogeographic regions are defined in Figure 1.

Areas	G	L	G/L	AA
<i>Sinningieae</i>				
A <sub>N</sub>	21	25	0.84	1
F	20	31	0.66	0.77
A <sub>S</sub>	13	25	0.52	0.62
P	11	26	0.42	0.50
C	7	18	0.39	0.46
D <sub>N</sub> + V + Z + M	3	11	0.27	0.32
D <sub>S</sub>	3	18	0.17	0.20
<i>Dircaea</i>				
A <sub>S</sub>	8	8	1	1
A <sub>N</sub>	4	8	0.5	0.5
P	6	12	0.5	0.5
F	4	11	0.36	0.36
<i>Corytholoma</i> + <i>Sinningia</i>				
A <sub>N</sub>	15	14	1.07	1
F	13	18	0.72	0.67
C	6	14	0.43	0.4
P	5	12	0.42	0.39
D <sub>N</sub> + V + Z + M	3	8	0.37	0.35
A <sub>S</sub>	4	15	0.27	0.25
D <sub>S</sub>	3	15	0.2	0.19

Brazil and the Guayana Shield region through Amazonia can be also hypothesized based on the current distribution of the sister species *S. sceptrum* (Mart.) Wiehler and *S. incarnata* (Fig. 6D). According to the ancestral area reconstruction, the range of *S. incarnata* expanded in a northwestern direction from the São Francisco region (Figs. 2 and 5). Finally, we cannot exclude an ancient colonization event through Central America according to the basal position of *S. richii* within *Corytholoma* and its occurrence in the state of Veracruz in Mexico (Figs. 2 and 5).

RELATIVE IMPORTANCE OF DISPERSAL AND VICARIANCE

In *Sinningieae*, DIVA analysis identified a total of 49 inter-area dispersal events, among which 15 are reconstructed on internal branches. Because there are 75 internal nodes in the phylogenetic tree of the *Sinningieae*, this means that 20% of the speciation events were preceded by range expansion. The total number of vicariance events is 17 (23%), whereas the remaining 43 speciation events (57%) occurred within a single area.

Table 2. Number of vicariance and dispersal events among areas within the Brazilian Atlantic forests reconstructed for the *Sinningieae* main clades (inferred from the DIVA analysis in Figure 2). Values in parentheses indicate the number of dispersal events reconstructed on internal branches only. Abbreviations for biogeographic regions are defined in Figure 1.

Events	Clades		
	<i>Dircaea</i>	<i>Corytholoma</i>	<i>Sinningia</i>
Vicariance between:			
A <sub>N</sub> – F	0	2	3
A <sub>S</sub> – P	4	0	0
A <sub>N</sub> – P	0	0	0
A <sub>S</sub> – F	1	0	0
A <sub>N</sub> – A <sub>S</sub>	0	0	0
F – P	0	1	0
Dispersal between:			
A <sub>N</sub> ↔ F	1 (0)	4 (3)	6 (3)
A <sub>S</sub> ↔ P	5 (4)	3 (1)	0
A <sub>N</sub> ↔ P	1 (0)	2 (0)	0
A <sub>S</sub> ↔ F	1 (1)	0	0
A <sub>N</sub> ↔ A <sub>S</sub>	2 (1)	0	0
F ↔ P	0	3 (1)	0

Out of the 15 dispersals reconstructed on internal branches, 12 (16% of the speciation events) correspond to range extensions of rain forest lineages into more seasonal areas of the Paraná or São Francisco regions. All of these events were immediately followed by vicariance that further split the combined area into its constituents. These dispersal-vicariance episodes were reconstructed on deep branches within the main lineages as well as on branches closer to the tips (Fig. 2).

DISCUSSION

ANCESTRAL AREA AND DISPERSAL PATTERNS IN BRAZIL

Dispersal-vicariance reconstruction and results of Bremer's method indicate that the Brazilian coastal Atlantic rain forest and the adjacent São Francisco region are the likely ancestral areas of the tribe *Sinningieae*. Other plant groups that are reported to have diversified in the Brazilian Atlantic regions include *Nematanthus* Schrad. (Gesneriaceae; Chauteaux, 1988), *Fuchsia* L. sect. *Quelusia* Vand. (Onagraceae; Berry, 1989; Berry et al., 2004), *Cattleya* Lindl. alliance (Orchidaceae; van den Berg & Martins, 1998; van den Berg et al., 2000), *Aechmea* Ruiz & Pav. (Bromeliaceae; Faria et al., 2004), herbaceous *Bambusoideae* (Soderstrom & Calderon, 1974), and several genera within the *Cactaceae* (Taylor & Zappi, 2004). We hope that the increasing



body of monographic works and species-level phylogenetic analyses will soon provide opportunities to evaluate the biogeographic significance of our results in relation to other taxonomic groups.

Within the three major clades, *Dircaea*, *Corytholoma*, and *Sinningia*, several independent dispersals between the Brazilian Atlantic rain forest and adjacent inland areas of the Paraná and São Francisco regions were reconstructed. These floristic exchanges are consistent with the floristic similarities found between rain forests and semideciduous forests enclosed in the Brazilian Atlantic region (Oliveira-Filho & Fontes, 2000). It is worth noting that migrations were more frequent from the rain forest to neighboring areas than in the opposite direction (Fig. 5). Therefore, the coastal rain forest could constitute the predominant source of Sinningieae evolution in the more seasonal adjacent regions. According to Oliveira-Filho and Fontes (2000: 808), "the tree flora of semideciduous forests is a fraction of the much richer rain forest flora, and probably is composed of species able to cope with relatively longer dry seasons." Similarly, in Sinningieae, the repeated range extensions into the semideciduous forests most likely are correlated with independent evolution of lineages that are more tolerant to rainfall seasonality.

Dispersal patterns between coastal and adjacent inland areas differ among lineages. In the sister clades *Corytholoma* and *Sinningia*, dispersal events occurred mainly between the northern portion of the Atlantic rain forest and the São Francisco region (Table 2). These dispersal events, as well as the fact that a large number of taxa are distributed in both areas, conform to the relative gradual floristic and climatic gradient that exists from the Atlantic coast to the interior above the Tropic of Capricorn (Oliveira-Filho & Fontes, 2000). In *Dircaea*, dispersal events were mainly reconstructed between the southern portion of the coastal rain forest and the Paraná region. Dispersals along this route were also hypothesized for elements within the plant families Myrtaceae and Palmaceae, as well as for various groups of vertebrates (Mueller, 1973; Cracraft, 1985; Spichiger et al., 1995). These taxa were considered to be expansive rain forest elements because they are well represented in the Atlantic rain forest and also penetrate into the meridional Planalto region and eastern Paraguay. In these cases, the coastal mountain range Serra do Mar does not act as a hermetic barrier, despite its role in creating a sharp transition between subtropical and typical seasonal conditions (Oliveira-Filho & Fontes, 2000).

The ancestral areas reconstructed at the root of the main lineages *Dircaea* and *Corytholoma* + *Sinningia*

support an early north-south disjunction between the subtropical and the tropical portions of the Atlantic forests (Fig. 2). The paucity of subsequent exchanges between northern and southern coastal regions and between the São Francisco and Paraná regions indicates that isolation of these lineages largely persisted during their diversification. Only two noticeable exceptions were reconstructed on internal branches. One is the northward shift of subclade I along the coast (cf. Fig. 2); the other involves colonization of the Paraná region from the São Francisco region by the widespread subclade II (Fig. 2). The relatively low frequency of dispersals along a northeast-southwest axis conforms to the strong floristic differentiation found between northern and southern blocks of Atlantic forests (Oliveira-Filho & Ratter, 1995; Oliveira-Filho & Fontes, 2000) and to the latitudinal divisions of the coastal rain forest into different centers of endemism (Mueller, 1973; Brown, 1987; Prance, 1987). Similarly, at the populations level, recent studies on the genetic differentiation of the Brazilian Cherry (*Eugenia uniflora* L.) along the Atlantic rain forest support the hypothesis that a past barrier obstructed gene flow between southern Brazil and the rest of the country (Salgueiro et al., 2004). Factors proposed to explain the relative isolation of tropical and subtropical areas of Brazil include mean temperature gradient along the coast (Oliveira-Filho & Fontes, 2000), contrasting vegetation history on each side of the Tropic of Capricorn during the Quaternary (Brown, 1987; Behling & Negrelle, 2001), and the barrier effect of the dry climate and unforested landscape that locally persisted in the region of Cabo Frio in the state of Rio de Janeiro (Mueller, 1973). In Sinningieae, these factors may have contributed to prevent *Sinningia* and *Corytholoma* from moving south or *Dircaea* from moving north.

#### DISPERSAL PATTERNS AT A CONTINENTAL SCALE

Occurrence of Sinningieae outside of Brazil in the Andes, Amazonia, northern South America, or beyond into Central America and southern Mexico most likely is explained by several independent range expansions of single species embedded within the *Corytholoma* clade. The analyses of these biogeographic events and present-day species distribution provide an opportunity to infer the pathways along which these areas were colonized.

The four Sinningieae species extending their range in the Andes are also found in the Paraná region, the São Francisco region, or in both regions (Fig. 6). Without exception, these widespread species are clustered in subclades II and III within *Corytholoma*

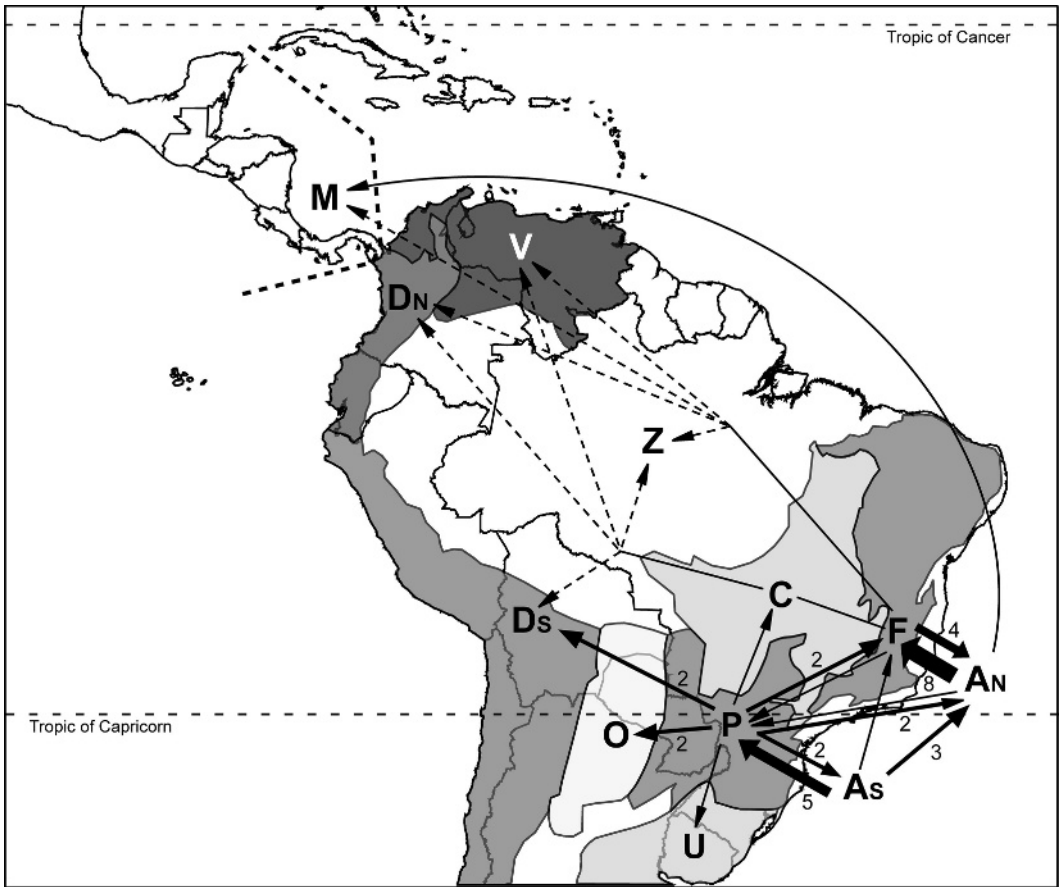


Figure 5. Direction and number of dispersal events between biogeographic areas of South and Central America in the Sinningieae (inferred from the DIVA analysis on Figure 2). The thickness of the arrows is proportional to the frequency of the dispersal events. Number of dispersal events is indicated when greater than 1. Dotted arrows indicate range expansion in several biogeographic areas reconstructed on a single branch of the phylogenetic tree (in subclade III, Fig. 2). Abbreviations for biogeographic areas are defined in Figure 1.

(Fig. 2). Distribution of these species in areas occupied by tropical seasonal forest, such as the Misiones nucleus, the Andean piedmont, and the eastern foothills and intermontane valleys of the Andes, fit with the Pleistocene arc distribution pattern described by Prado and Gibbs (1993). These data and recent distribution maps available for the Cactaceae indicate that this pattern may concern a larger number of taxa than had been initially thought (Taylor & Zappi, 2004). Direction and frequency of dispersal events between the Brazilian Atlantic regions and the Andes have rarely been tested using molecular phylogenies. However, the few existing studies have already indicated that the direction of such dispersal events may differ according to the taxonomic group considered (Voelker, 1999; Berry et al., 2004; Sánchez-Baracaldo, 2004; Taylor & Zappi, 2004). In Sinningieae, dispersal-vicariance analyses support three independent migrations into the southern Andes

along two distinct biogeographic pathways (Fig. 5). In subclade II, colonization of the Paraná basin predated the independent dispersions of *Sinningia warmingii* and *S. sellowii* into the southern Andes (Fig. 2). The distribution of these species suggests the existence of a narrow bridge between the Paraná basin and the sub-Andean piedmont through the northern extremity of the Chaco in Paraguay and southeastern Bolivia (Fig. 6A, B). This strip of land has already been identified as a crucial connecting area for several woody elements that are found both in the Paraná and the Andean piedmont areas but that are missing in the xeromorphic Chaquena vegetation (Prado, 2000; Spichiger et al., 2004). A second dispersion route is indicated by *S. elatior*, linking the São Francisco region with the eastern foothills of the Andes through the cerrado, the Pantanal, and Bolivia (Fig. 6C). This species occurs mostly in grasslands on marshy grounds at altitudes not exceeding 1200 m. Ancestral

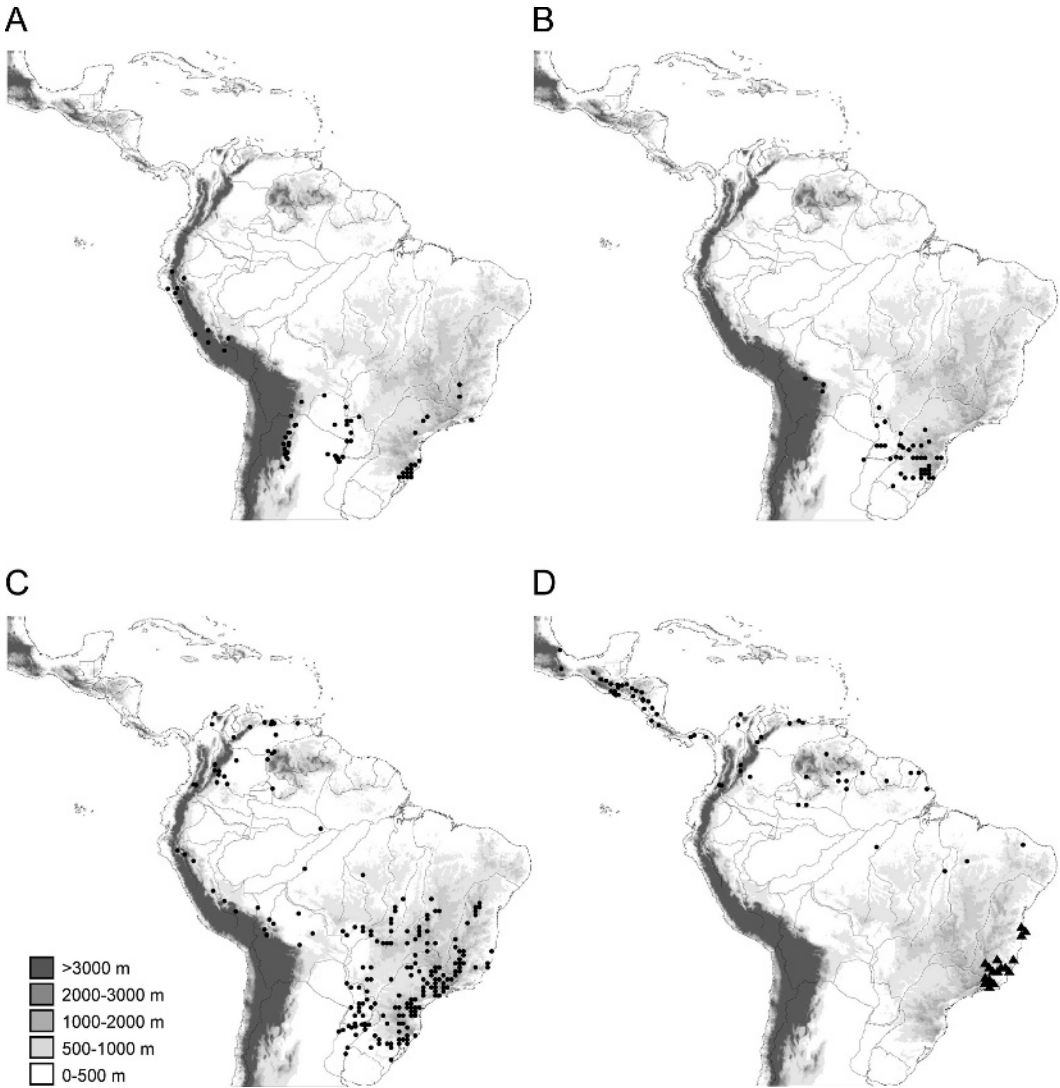


Figure 6. Distributions of widespread species showing a connection between Brazil, the Andes, and/or other regions in northern South America, Central America, and southern Mexico. —A. *Sinningia warmingii*. —B. *S. sellowii*. —C. *S. elatior*. —D. *S. incarnata* (solid circle) and *S. sceptrum* (solid triangle).

area reconstructions within subclade III indicate that expansion of *S. elatior* (or its close ancestors) into non-Brazilian areas occurred from the cerrado and/or the São Francisco region (Figs. 2 and 5). The westward extensions of *S. elatior* follow the northern migration track described by Prado (2000) for elements of the seasonal tropical dry forest that cross the cerrado following a net of gallery forest along a northeast-southwest arc (Oliveira-Filho & Ratter, 1995). Occurrence of *S. elatior* further north in South America most likely is explained by northward dispersal along the Andes, although the few specimens collected in the Brazilian states of Pará and

Amazonas may also support a migration route through the Amazon basin.

Dispersal patterns of these three widespread species are consistent with the hypothesis about historical plant migration routes involving dry seasonal forest formations (Pennington et al., 2000; Spichiger et al., 2004). Hence, dispersion of these *Sinningieae* species along the Andes from either the Paraná or the São Francisco regions could have been promoted by the extension of these formations, which may have taken place during the drier and cooler periods of the Pleistocene (Pennington et al., 2000). However, a careful test of this hypothesis would

require a calibration of the phylogenetic tree to estimate the absolute timing of such dispersal events. So far, such an attempt led to ambiguous results because of the lack of dated fossils or pollen records for the Sinningieae.

In addition to migrations along the Pleistocene arc, the sister relationship between *Sinningia incarnata* and *S. sceptrum* provides evidence for a link between the Guayana Shield region and eastern Brazil (Fig. 6D). The few known occurrences of *S. incarnata* within Amazonia in the Brazilian states of Maranhão, Pará, Amazonas, and Roraima may indicate the route followed by this species during its northwestern expansion into northern South America and beyond. Similarly, geographic disjunction between eastern Brazil and the Guayana Shield region was observed in different species or groups of closely related species (Harley, 1988; Prado & Gibbs, 1993; Taylor & Zappi, 2004). According to Prado (2000), migrations through Amazonia for species of tropical seasonal forests could have been promoted by the existence of a former dry vegetation belt connecting the Guayana Shield region with the Atlantic rain forest in Brazil (van der Hammen & Hooghiemstra, 2000). Finally, the basal position of *S. richii* within the clade *Corytholoma* and its endemism to the state of Veracruz in Mexico (Clayberg, 1968) imply a puzzling biogeographic scenario. Indeed, this geographic distribution and phylogenetic position indicate that a large geographic disjunction between the Brazilian Atlantic forest and Central America might have predated diversification in the clade *Corytholoma* (Fig. 4). This result suggests that *S. richii* could constitute a remnant of an early northward migration into Central America.

#### RELATIVE IMPORTANCE OF DISPERSAL AND VICARIANCE

Diversification in Sinningieae is associated with inter-area dispersal (20%), vicariance (23%), or within-area speciation (57%). The similarity between the frequency of dispersal and vicariance events can be explained by the alternating occurrence of these two processes during the diversification of the group. In southeastern Brazil, the majority of these reconstructed dispersal-vicariance episodes occurred between the coastal rain forest and adjacent inland areas characterized by a more seasonal climate (i.e., Paraná and São Francisco regions). These episodes initially consist of range expansions of rain forest lineages toward the interior followed by vicariance events that subsequently divide the source and the invaded areas. According to ancestral area optimization, these series of events occurred repeatedly at different heights in the phylogenetic tree and, therefore, probably oc-

curred at different times. Cyclical range expansion-vicariance events may indicate the transitory nature of the barriers existing between coastal rain forest and neighboring inland areas. Climatic changes, especially in rainfall seasonality, may have been responsible for a succession of periods that either constrained or allowed expansion by producing more or less stringent ecological conditions toward the interior of Brazil. We hypothesize that this alternation between dispersal and vicariance along a changing climatic gradient has driven diversification of Sinningieae in the Brazilian Atlantic forests. Such a mechanism can be related to the species-pump hypothesis proposed by Stebbins (1974) in order to explain the high species richness of tropical forests bordered by tropical plant communities adapted to drier conditions.

In addition to inter-area biogeographic events, our results indicate that more than half of speciation events (57%) occurred within a single biogeographic area. For example, diversification of the *Sinningia* clade took place, in a large proportion, within the northern Atlantic rain forest (Fig. 2). To investigate the biogeographic circumstances of these speciation events, further biogeographic analyses at a finer scale are needed. A possible approach is to compare geographic distribution of sister taxa across all nodes in the phylogenetic tree (Barraclough & Vogler, 2000). Preliminary results in this direction indicate that, to a vast majority, diversification within a particular area might be the product of dispersal and allopatric isolation operating at a narrow geographic scale, in the context of the highly heterogeneous environment that characterizes the Brazilian Atlantic forests (Perret et al., unpublished data). We are convinced that such phylogenetic approaches at different geographic scales are necessary to assessing hypotheses about biological diversification in South America. Whether the results obtained for Sinningieae represent a general pattern of diversification can only be tested by evaluating their congruence with other plant or animal groups with high diversity in the Brazilian Atlantic forest hotspot.

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APPENDIX 1. Species analyzed in this study and vouchers of the specimens sequenced. Acronyms in parentheses indicate the herbarium where the vouchers are deposited.

Sinningieae: *Paliavana gracilis* (Mart.) Chautems, *Leoni 1812* (GFJP); *P. plumerioides* Chautems, *Chautems 460* (G); *P. prasinata* (Ker Gawl.) Benth., *Chautems & Perret 00-013* (G); *P. sericiflora* Benth., *Chautems 545* (G); *P. tenuiflora* Mansf., *Salviani 1541* (Instituto Plantarum); *P. werdermannii* Mansf., *Carvalho et al. 6552* (CEPEC); *Sinningia aggregata* (Ker Gawl.) Wiehler, *Chautems & Perret 97-001* (G); *S. aghensis* Chautems, *Pereira et al. 522* (VIES); *S. allagophylla* (Mart.) Wiehler, *Chautems 325* (G); *S. amambayensis* Chautems, *Salviani 1118* (Instituto Plantarum); *S. araneosa* Chautems, *Chautems & Perret 00-016* (G); *S. barbata* (Nees & Mart.) G. Nicholson, *Chautems & Perret 99-056* (G); *S. brasiliensis* (Regel & Schmidt) Wiehler & Chautems, *Chautems & Perret 97-002* (G); *S. bulbosa* (Ker Gawl.) Wiehler, *Chautems & Perret 97-003* (G); *S. calcaria* (Malme) Chautems, *Cervi et al. AC466* (UPCB); *S. canescens* (Mart.) Wiehler, *Chautems & Perret 97-004* (G); *S. carangolensis* Chautems, *Chautems 376* (G); *S. cardinalis* (Lehm.) H. E. Moore, *Chautems & Perret 97-015* (G); *S. cochlearis* (Hook.) Chautems, *Carvalho et al. AC535* (CEPEC); *S. concinna* (Hook. f.) Hanst., *Salviani 1540* (Instituto Plantarum); *S. conspicua* (Seem.) G. Nicholson, *Chautems & Perret 00-008* (G); *S. cooperi* (Paxton) Wiehler, *Chautems & Perret 01-032* (G); *S. curtiflora* (Malme) Chautems, *Cervi et al. AC477* (UPCB); *S. defoliata* (Malme) Chautems, *Chautems & Perret 01-031* (G); *S. douglasii* (Lindl.) Chautems, *Chautems & Perret 00-001* (G); *S. elatior* (Kunth) Chautems, *Salviani 1889* (Instituto Plantarum); *S. eumorpha* H. E. Moore, *Chautems & Perret 97-006* (G); *S. gigantiflora* Chautems, *Carvalho et al. AC529* (CEPEC); *S. glazioviana* (Fritsch) Chautems, *Chautems & Perret 97-017* (G); *S. guttata* Lindl., *Chautems & Perret 01-030* (G); *S. harleyi* Wiehler & Chautems, *Carvalho & Chautems 3235* (G); *S. hatschbachii* Chautems, *Chautems & Perret 99-065* (G); *S. hirsuta* (Lindl.) G. Nicholson, *Chautems & Perret 00-014* (G); *S. iarae* Chautems, *Carvalho et al. AC541* (CEPEC); *S. incarnata* (Aubl.) D. L. Denham, *Chautems & Perret 98-004* (G); *S. insularis* (Hoehne) Chautems, *Chautems & Perret 97-005* (G); *S. kautskyi* Chautems, *Chautems 390* (G); *S. lateritia* (Lindl.) Chautems, *Chautems & Barcia 321* (G); *S. leopoldii* (Planch.) Chautems, *Chautems & Perret 99-054* (G); *S. leucotricha* (Hoehne) H. E. Moore, *Chautems & Perret 97-008* (G); *S. lindleyi* Schauer, *Chautems & Perret 97-016* (G); *S. lineata* (Hjelmq.) Chautems, *Chautems & Perret 97-007* (G); *S. macrophylla* (Nees & Mart.) Benth. & Hook ex Fritsch, *Juchum et al. 001* (CEPEC); *S. macropoda* (Sprague) H. E. Moore, *Chautems & Perret 97-009* (G); *S. macrostachya* (Lindl.) Chautems, *Chautems & Perret 97-018* (G); *S. magnifica* (Otto & A. Dietr.) Wiehler, *Chautems & Perret 01-027* (G); *S. mauroana* Chautems, *Salviani 1542* (Instituto Plantarum); *S. micans* (Fritsch) Chautems, *Cervi et al. AC465* (UPCB); *S. nivalis* Chautems, *Chautems 354* (G); *S. nordestina* Chautems, *Baracho & Siqueira Filho, Baracho & Siqueira Filho 663/704* (G); *S. piresiana* (Hoehne) Chautems, *Salviani 840* (Instituto Plantarum); *S. pusilla* (Mart.) Baill., *Chautems & Perret 99-049* (G); *S. reitzii* (Hoehne) L. E. Skog, *Chautems & Perret 98-001* (G); *S. richii* Clayberg, *Chautems & Perret 01-029* (G); *S. rupicola* (Mart.) Wiehler, unknown; *S. sceptrum* (Mart.) Wiehler, *Carvalho et al. AC528* (CEPEC); *S. schiffneri* Fritsch, *Chautems & Perret 97-010* (G); *S. sellowii* (Mart.) Wiehler, *Chautems & Perret 01-028* (G); *S. speciosa* (Lodd.) Hiern, *Chautems & Perret 98-003* (G); *S. striata* (Fritsch) Chautems, *Chautems & Peixoto*

*366* (G); *S. tuberosa* (Mart.) H. E. Moore, *Chautems & Perret 00-009* (G); *S. tubiflora* (Hook.) Fritsch, *Chautems & Perret 97-011* (G); *S. valsuganensis* Chautems, *Chautems & Perret 99-061* (G); *S. villosa* Lindl., *Chautems & Perret 99-059* (G); *S. warmingii* (Hiern) Chautems, *Chautems & Perret 97-012* (G); *S. sp. indet. 1*, *Romero et al. 1709* (G); *S. sp. indet. 4*, *Chautems & Perret 99-051* (G); *S. sp. indet. 7*, *Cervi et al. AC484* (UPCB); *Vanhouttea brueggeri* Chautems, *Salimena Pires et al. AC501* (CESJ); *V. calcarata* Lem., *Carvalho et al. 526* (CEPEC); *V. fruticulosa* (Glaziou ex Hoehne) Chautems, *Chautems et al. 338* (G); *V. gardneri* (Hook.) Fritsch, *Chautems & Perret 01-024* (G); *V. hilariana* Chautems, *Salimena Pires et al. AC506* (CESJ); *V. lanata* Fritsch, *Carvalho et al. AC527* (CEPEC); *V. leonii* Chautems, *Leoni 4202* (GFJP); *V. pendula* Chautems, *Leoni 4197* (GFJP).

Gloxinieae: *Smithiantha laui* Wiehler, unknown.

Episcieae: *Nematanthus villosus* (Hanst.) Wiehler, *Chautems & Perret 99-041* (G).

APPENDIX 2. List of representative specimens for the 76 species of Sinningieae used to produce the maps on Figures 3 and 6. Specimens are organized alphabetically by species name. Acronyms in parentheses indicate the herbarium where the specimens are deposited.

*Paliavana gracilis*: BRAZIL. **Minas Gerais**: Anderson 8875 (F, K, MO, NY, R, UB, US); *Irwin et al. 28622a* (NY); *Leoni 2849* (GFJP); *Leoni 4204* (GFJP).

*Paliavana plumerioides*: BRAZIL. **Minas Gerais**: *Arbo et al. 4384* (G, SPF); *Davis et al. 2285* (E, UEC).

*Paliavana prasinata*: BRAZIL. **Espírito Santo**: *Boone 668* (CEPEC, MBLM); *Boudet Fernandes et al. 2809* (MBLM); *Hatschbach & A. Cervi 51354* (CEPEC, MBM); *Hatschbach et al. 69163* (G, MBM); *Sazima 14056* (E, UEC). **Minas Gerais**: *Belém 1619* (CEPEC, UB); *Forzza et al. 2173* (G); *Leoni 290* (GFJP, US). **Rio de Janeiro**: *Braga & M. G. Bovini 3915* (RUSU); *Farney 736* (CEPEC, K, MG, NY); *Martinelli & M. Guerra 9847* (G, RB); *Mello Silva & J. R. Pirani 853* (NY, SPF); *Mello Silva et al. 2642* (G); *Pabst 8106* (HBR 31664); *Ribeiro & E. L. Costa 313* (RB); *Smith 6473* (IAN, NY, R, SP, US); *Strang 490* (GUA).

*Paliavana sericiflora*: BRAZIL. **Minas Gerais**: Anderson 35809 (F, K, MO, NY, UB, US); Anderson 8851 (F, K, MO, NY, US); *Arbo et al. 4566* (SPF); *Ferreira & B. V. Moreira 415* (G); *Gibbs et al. 5289* (MBM, SP, UEC).

*Paliavana tenuiflora*: BRAZIL. **Bahia**: *A. M. de Carvalho 7034* (CEPEC); *Alves 2005* (CEPEC); *Carvalho et al. 2384* (ALCB, CEPEC, K, MBM); *Esteves & R. P. Lyra-Lemos 2513* (SPF); *Giuletti et al. PCD.3309* (ALCB, CEPEC, SPF); *Harley 22320* (CEPEC, E, K, MO, US); *Mori et al. 10700* (CEPEC, US); *Santos 2717* (CEPEC, SEL, US). **Minas Gerais**: *Leoni 5570* (GFJP). **Paraíba**: *Felix 5688* (EAN). **Pernambuco**: *Andrade et al. 68* (G); *Felix & G. Dornelas 1120* (EAN 4211); *Felix & G. V. Dornelles 1316* (K); *Pietrobon-Silva et al. 4607* (MBM); *Siqueira Filho & J. A. Vicente 965* (G, UFP).

*Paliavana werdermannii*: BRAZIL. **Bahia**: *Harley et al. 54383* (HUEFS); *Roque et al. CFCR 14971* (ESA, G, SPF); *Roque et al. CFCR 15048* (SPF). **Minas Gerais**: *Cordeiro CFCR 834* (CEPEC, SPF, US); *Pirani et al. 2271* (NY, SPF); *Sakuragui et al. CFCR 15147* (BHCB, ESA, SPF).

*Sinningia aggregata*: BRAZIL. **Distrib. Federal**: *Kirkbride 3703* (US). **Goias**: *Irwin et al. 11808* (K, US); *Irwin et al. 34051* (F, NY, SEL, UB). **Mato Grosso**: *Ratter et al. 7586* (E). **Mato Grosso do Sul**: *Hatschbach et al. 35984* (F, M, MBM, MO, UEC, US, Z). **Minas Gerais**: *Alves 4378* (RB); *Castro 637* (G); *Chautems & M. Peixoto 461* (G); *Gouwea et al. 710* (UEC); *Melo & L. N. Asunção 1251* (BHCB); *Mota 172*

(G, BHC 53328); *Shepherd et al.* 3846 (MBM, NY, UEC). **Paraná:** *Cervi et al.* 2047 (G); *Cervi et al.* 3044 (G, NY, UPCB); *Dusén* 15796 (G, K, MO isotype, S holotype); *Hatschbach* 13900 (MBM); *Hatschbach* 26350 (MBM, MO, US); *Hatschbach* 3170 (HBR, MBM, PACA, UPCB); *Hatschbach* 5061 (HBR, MBM, PACA, PKDC, UPCB); *Medri et al.* 885 (UEC). **Rio de Janeiro:** *Andreata, R. et al.* 542 (RB, RUSU); *Black & Fróes* 11324 (IAN); *Flaster, B.* 1196 (R); *Gões O. C. & Dionisio* 456 (G, RB). **Santa Catarina:** *Hatschbach et al.* 78061 (G); *Mattos* 12036 (HAS, SP); *Reitz & R. M. Klein* 4001 (HBR, NY, R, UC, US); *Reitz & R. M. Klein* 5349 (B, F, NY, R, US); *Reitz* 2031 (HBR, R, US); *Smith & R. M. Klein* 14030 (B, BH, F, MO, NY, R, US, WIS). **São Paulo:** *Ferreira* 3177 (GUA); *Mattos & Moura* 14960 (SP); *Meira Neto* 21332 (UEC, VIC); *Pires* 676 (SP, SPF, cult. II.1952). PARAGUAY. **Amambay:** *Hassler, E.* 11218 (G). **Cordillera:** *Zardini, E. & R. Degen* 4009 (FCQ, G, US). **Paraguari:** *Krapovickas, A. et al.* 12265 (UC).  
*Sinningia aghensis:* BRAZIL. **Espírito Santo:** *Boone* 980 (CEPEC, MBML); *Shepherd et al. s.n.* (UEC 5893).  
*Sinningia allagophylla:* ARGENTINA. **Chaco:** *Meyer, T.* 17211 (LIL). **Corrientes:** *Ibarolla* 3808 (LIL, MO). **Entre Ríos:** *Burkart* 24942 (SD). **Formosa:** *Morel* 5314 (K, LIL). **Jujuy:** *Schulz, A. G.* 8377 (NY). **Misiones:** *Montes, J. E.* 471 (G, NY, US). BRAZIL. **Distrito Federal:** *Irwin et al.* 26414 (F, K, MG, MO, NY, R, SEL, UB). **Goiaás:** *Chautems* 402 (G, UFG); *Hatschbach & J. M. Silva* 59963 (G, UFP); *Hatschbach* 42002 (MBM); *Melo & França* 521 (SPF); *Rizzo* 8845 (UFG). **Mato Grosso do Sul:** *Krapovickas & Cristóbal* 34321 (MO). **Minas Gerais:** *Atkins et al. CFCR* 13793 (SPF); *Cardoso* 5691 (R); *Davidse et al.* 10656A (MO, SP); *Hatschbach* 28650 (MBM); *Leoni* 1436 (G, GFJP); *Macedo* 2894 (MO, SP); *Mello Silva et al.* 1624 (SP, SPF); *Williams & V. Assis* 5565 (MO, US). **Paraná:** *Dusén* 13456 (G, F, MO, NY, S, US); *Hatschbach* 1899 (MBM, US); *Hatschbach* 8577 (B, F, MBM, UPCB); *Krapovickas & Cristóbal* 39714 (MBM); *Kummrow & Graham* 2644 (MBM, S, US); *Kummrow* 966 (MU, NY). **Rio de Janeiro:** *Bello, W.* 342 (R); *Mello Filho, L. E. & Dansereau* 315 (R); *Martinelli, G.* 8888 (CEPEC); *Vogel, S.* 689 (US). **Rio Grande do Sul:** *Bueno* 5423 (HAS); *Krapovickas & Cristóbal* 34176 (MBM); *Leite* 668 (NY); *Mattos & N. Silveira* 25343 (HAS); *Mattos* 25429 (HAS); *Mattos et al. s.n.* (HAS); *Palacios-Cuezzo* 1158 (MO); *Pivetta* 817 (PACA); *Rambo* 29391 (ICN); *Rossato et al.* 5165 (NY, MO); *Senhem* 4294 (B, HBR, INPA, MBM, PACA); *Silveira & D. Faria F<sup>o</sup>.* 5423 (HAS); *Sobral & Esposito* 3637 (F, MBM). **Santa Catarina:** *Chautems & R. Reitz* 351 (G, HBR, US); *Klein* 3339 (HBR); *Porto s.n.* (HAS); *Reitz & R. M. Klein* 14019 (B, F, HBR, US, WIS); *Reitz* 4910 (HBR, R, US); *Smith & R. M. Klein* 10399 (GH, R, S, US); *Smith & R. M. Klein* 11362 (B, NY, R, US); *Smith & R. M. Klein* 14060 (US); *Smith & R. M. Klein* 7438 (HBR, R, US); *Smith & R. Reitz* 14276 (HBR, NY, US); *Smith & R. Reitz* 8621 (HBR, R, US); *Smith et al.* 9263 (HBR, NY, R, US); *Ule* 1533 (P, PACA). **São Paulo:** *Buzato & M. Sazima* 28017 (G, SPF); *Carvalho & J. R. Carvalho* 11601 (UEC); *Cuatrecasas* 26588 (US); *Eiten & L. T. Eiten* 2432 (BH, NY, US); *Gemtschújnicov s.n.* (BOTU 12315); *Gibbs et al.* 1707 (UEC); *Grotta s.n.* (SPF 15097); *Mimura* 13 (NY, SP, US). PARAGUAY. **Alto Paraná:** *Schinini, A.* 8107 (G). **Amambay:** *Schinini, A. & M. Demateis* 33459 (G). **Caaguazú:** *Schinini, A.* 5772 (G). **Caazapá:** *Soria, N.* 4032 (MO). **Canindeyú:** *Hassler, E.* 4982 (G, GH, NY, P, S, UC, W). **Central:** *Schinini, A.* 3734 (G). **Concepción:** *Fiebrig, K.* 4626 (G, K). **Cordillera:** *Bordas, E. & G. Schmeda* 4120 (FCQ, US). **Guaíará:** *Jørgensen, P.* 3729 (F, MO, NY, S). **Misiones:** *Schinini, A. & R. Vanni* 26078 (G). **Paraguari:** *Zardini, E. & T. Tilleria*

30279 (G). **Presidente Hayes:** *Hassler, E. & T. Rojas* 2657 (G, GH, NY, P, W). **San Pedro:** *Pedersen, T. M.* 9451 (K, NY). URUGUAY. **Maldonado:** *Rosengurt B* 5242 (US). **Montevideo:** *Arechavaleta, J.* 53 (G).  
*Sinningia amabayensis:* PARAGUAY. **Amambay:** *Simonis, J. E., L. Pérez, W. J. Hahn & R. Duré Rodas* 223 (G, MO, PY, RB, US).  
*Sinningia araneosa:* BRAZIL. **São Paulo:** *Marcondes Ferreira et al.* 783 (SP).  
*Sinningia barbata:* BRAZIL. **Bahia:** *Carvalho et al.* 7002 (CEPEC); *Hage* 1541 (CEPEC, HUEFS); *Jardim et al.* 990 (CEPEC); *Scardino & Grupo Pedra do Cavalo* 408 (CEPEC, ALCB); *Silva* 4486 (HUEFS); *Thomas et al.* 11956 (CEPEC, NY); *Thomas et al.* 9104 (CEPEC, NY). **Espírito Santo:** *Boone* 219 (G, MBML); *Kollmann* 2727 (MBML).  
*Sinningia brasiliensis:* BRAZIL. **Bahia:** *França* 1726 (HUEFS); *Carvalho & G. Lewis* 911 (CEPEC, MBM); *Chautems et al.* 226 (CEPEC); *França et al.* 2304 (ESA); *Harley et al.* 19418 (CEPEC, K); *Jardim et al.* 1839 (CEPEC); *Santos* 1645 (CEPEC, R). **Espírito Santo:** *Arbo et al.* 5588 (K, SPF); *Kollmann et al.* 2722 (G, MBML); *Sazima* 14057 (UEC). **Minas Gerais:** *Belém* 3770 (CEPEC, IAN, NY); *Giuletti et al. CFCR* 6703 (CEPEC, G, K, SP, SPF); *Hatschbach* 47816 (MBM, US); *Leoni* 402 (GFJP); *Mota* 1350 (G). **Rio de Janeiro:** *Sucre, D. & Braga* 2655 (RB).  
*Sinningia bulbosa:* BRAZIL. **Rio de Janeiro:** *Carauta, P.* 1686 (GUA, RB); *Farney, C. et al.* 2438 (RB); *Martinelli, G. et al.* 8520 (RB); *Smith, L. B.* 6394 (R, UD); *Widgren* R 870 (UPS).  
*Sinningia calcaria:* BRAZIL. **Paraná:** *Hatschbach* 32308 (BH, MBM, MO, WAG, Z); *Tiepolo & A. C. Svolenski* 682 (MBM). **São Paulo:** *Fiaschi & A. C. Marcato* 821 (G).  
*Sinningia canescens:* BRAZIL. **Paraná:** *Chautems et al.* 359 (FUEL, G, US); *Hatschbach & O. Guimarães* 25477 (MBM, S, WAG); *Hatschbach* 1036 (MBM, US); *Hatschbach* 45657 (CEPEC, MBM). **São Paulo:** *Barreto et al.* 3265 (SP).  
*Sinningia carangolensis:* BRAZIL. **Minas Gerais:** *Leoni* 586 (GFJP, R, US).  
*Sinningia cardinalis:* BRAZIL. **Rio de Janeiro:** *Markgraf, F.* 10084 (RB).  
*Sinningia cochlearis:* BRAZIL. **Rio de Janeiro:** *Markgraf, F.* 10471 (RB).  
*Sinningia conspicua:* BRAZIL. **Paraná:** *Dusén* 16543 (S). **Santa Catarina:** *Smith & R. M. Klein* 14168 (R, US).  
*Sinningia cooperi:* BRAZIL. **Espírito Santo:** *Kollmann & E. Bausen* 5670 (MBML). **Minas Gerais:** *Leoni* 4950 (GFJP). **Paraná:** *Hatschbach* 12400 (MBM, WAG); *Hatschbach* 18578 (F, MBM); *Santos et al.* 763 (G). **Rio de Janeiro:** *Martinelli, G. & Maas, P.* 3276 (RB). **Santa Catarina:** *Dusén s.n.* (F, GH, S); *Reitz & R. M. Klein* 6551 (HBR, NY, UC, US). **São Paulo:** *Buzato & M. Sazima* 26868 (G, UEC).  
*Sinningia curtiflora:* BRAZIL. **Paraná:** *Chautems & A. Cervi* 332 (G, UPCB, US); *Gentry & E. Zardini* 49756 (MBM, RBR, US). **Rio Grande do Sul:** *Silveira* 10619 (HAS). **Santa Catarina:** *Reitz & R. M. Klein* 4105 (G, NY, UC, US); *Reitz & R. M. Klein* 8270 (G, NY, UC, US); *Reitz* C1427 (GH, HBR, R). **São Paulo:** *Miyagi et al.* 439 (ESA, HRCB, SP, SPF).  
*Sinningia defoliata:* BRAZIL. **Goiaás:** *Irwin & Soderstrom* 7371 (BH). **Mato Grosso:** *Dorrien Smith* 308 (K). **Minas Gerais:** *Macedo* 3882 (SP, US).  
*Sinningia douglasii:* ARGENTINA. **Misiones:** *Renwoize, S. A.* 3245 (K). BRAZIL. **Minas Gerais:** *Leoni* 3495 (GFJP); *Meireles & M. F. A. Pereira* 660 (UEC); *Tamashiro et al.* 1283 (UEC). **Paraná:** *Chagas & Silva & Soares* 908 (FUEL, MBM); *Dusén* 7045 (MO, S); *Hatschbach* 1080 (LIL, MBM, US); *Hatschbach* 22364 (MBM); *Hatschbach* 32866 (MBM);



*Hatschbach* 3390 (MBM); *Hatschbach* 40479 (MBM, NY, UEC); *Koczički* 267 (MBM); *Lindeman & J. H. Haas* 3149 (NY). **Rio de Janeiro:** *Carvalho, A. M. & Martinelli, G. I* (CEPEC, G, RB); *Martinelli, G. et al.* 17779 (RB); *Pessoa, S. V. A.* 109 (RB). **Rio Grande do Sul:** *Camargo* 2606 (B, PACA); *Friderichs s.n.* PACA 30678 (B, PACA); *Silveira* 5889 (HAS); *Silveira* 7304 (HAS); *Waechter* 1793 (HAS, ICN). **Santa Catarina:** *Klein & A. Bresolin* 7670 (HBR); *Klein* 1755 (HBR, US); *Mattos* 22742 (HAS); *Reitz & R. M. Klein* 12518 (HBR, NY, R, US); *Reitz & R. M. Klein* 13532 (HBR); *Reitz & R. M. Klein* 7345 (HBR); *Reitz & R. M. Klein* 7553 (HBR); *Reitz & R. M. Klein* 9286 (HBR); *Reitz* 5909 (HBR); *Reitz* C762 (HBR, RB); *Smith & R. M. Klein* 13363 (US); *Smith & R. M. Klein* 7338 (HBR, S, US); *Smith & R. Reitz* 8853 (HBR, US). **São Paulo:** *Barros & J. E. L. S. Ribeiro* 2034 (SP); *Carmello et al.* 77 (BOTU, G); *Gibbs et al.* 3251 (MBM, NY, UEC); *Leitão Filho* 32912 (UEC); *Leitão Filho et al.* 3167 (MBM, NY, UEC); *Romaniuc Neto & A. Custodio Filho* 247 (SP); *Shirasuna et al.* 51 (SP).

*Sinningia elatior*: ARGENTINA. **Corrientes:** *Krapovickas, A. et al.* 29369 (G, MBM, MO). **Entre Ríos:** *Burkart, A. & S. Crespo s.n.* (Her. Burkart, SI). **Misiones:** *Rodríguez* 718 (BAFC, LIL, SI, US). **BOLÍVIA.** **Beni:** *Beck, S. G.* 13143 (G). **La Paz:** *Solomon, J. C.* 9339 (MO, NY, US). **Santa Cruz:** *Steinbach, R. F.* 814 (F, G, MO, NY, US). **Yungas:** *Bang, M.* 543 (F, MO, NY, US). **BRAZIL.** **Amazonas:** *Harley et al.* 19757 (CEPEC, G, K); *Janssen* 209 (INPA, M, MG, SP); *Trail* 521 (K). **Bahia:** *França* 1267 (HUEFS); *Harley et al.* 19757 (CEPEC, K); *Harley et al.* 22323 (CEPEC, K). **Distrito Federal:** *Irwin et al.* 8954 (F, K, NY, UB, US). **Espirito Santo:** *Folli* 2403 (RB). **Goiaás:** *Anderson* 6276 (NY); *Ferreira et al.* 2658 (UFG); *Hunt & Ramos* 5725 (SP); *Irwin et al.* 13506 (UB); *Irwin et al.* 18839 (F, NY, UB, W); *Irwin et al.* 24168 (BH, F, IAN, K, NY, US); *Irwin et al.* 25394 (F, NY, UB); *Maguire et al.* 56981 (NY, UB); *Rizzo & A. Barbosa* 3354 (UFG); *Thomas et al.* 5786 (SPF). **Mato Grosso:** *Ekman da Silva et al.* R 7110 (R 7110); *Hatschbach* 33275 (Z); *Hatschbach* 34143 (MBM); *Hoehne* 569/Rondon 3684 (R); *Hunt & J. F. Ramos* 5725 (K, NY, UC, UB); *Philcox & A. Ferreira* 3684 (K); *Philcox & J. F. Ramos* 4393 (K, NY, UB); *Pires & M. R. Santos* 16587 (MG); *Saddi et al./UFMT* 213 (UFMT). **Mato Grosso do Sul:** *Armando & Gerra s.n.* (G, RB 102323); *Garcia s.n.* (UEC 13928); *Hunt & J. F. Ramos* 5959 (K); *Rodrigues et al.* 322 (RB); *Sucre* 10554 (RB); *Tsugaru & H. A. Guinoza* B-2085 (MO, NY). **Minas Gerais:** *Assis & M. K. Ladeira* 621 (G); *Brade & Altamiro* 50 (R); *Cavalcanti et al.* CFSC 9408 (SPF); *Cordeiro & Simonis* CFCR 4021 (SPF, US); *Irwin et al.* 20880 (F, MO, NY, RB, UB); *Irwin et al.* 23774 (BH, F, IAN, K, NY, UB, US); *Irwin et al.* 26052 (F, IAN, NY, RB, UB, W); *Krieger* 20588 (CESJ); *Macedo* 2213 (MO, US); *Pirani et al.* 3867 (G, SPF); *Romero et al.* 1696 (G); *Romero et al.* 5147 (UEC); *Sakuragui et al.* CFCR 15087 (SPF); *Salimena Pires et al.* AC-492 (CESJ, G); *Shepherd* 493 (UEC); *Warming s.n.* (US). **Pará:** *Pires et al.* 6120 (IAN, NY). **Paraná:** *Hatschbach* 18227 (MBM, UPCB); *Hatschbach* 22884 (MBM, NY); *Hatschbach* 24125 (MBM, MO, UPCB); *Hatschbach* 26221 (M, MBM, MO); *Hatschbach* 26411 (MBM, Z); *Hatschbach* 5466 (MBM); *Hatschbach* 580 (MBM, PACA); *Hatschbach* 615 (MBM, PACA, SP); *Kummrow & J. D. Stutts* 1791 (MBM); *Reitz & Klein* 17637 (F, US); *Santos et al.* 650 (G); *Yunigoshi & R. Kummrow* 4597 (CEPEC, MBM, US). **Rio Grande do Sul:** *Bueno* 4751 (HAS); *Jürgens* 193 (B); *Mattos & Mattos* 23178 (HAS); *Mattos et al.* 22012 (HAS); *Rambo & Schultz* 36505 (ICN); *Rambo* [37449/34749?] (MO); *Rambo* 10083 (PACA); *Rambo* 28483 (PACA); *Rambo* 34749 (PACA, S); *Rambo* 38674 (PACA); *Rambo* 56662 (B, HBR, PACA); *Rambo*

63645 (B, S); *Rambo* 9892 (PACA); *Silveira* 3847 (HAS); *Silveira* 6047 (HAS); *Waechter* 1977 (ICN). **Santa Catarina:** *Reitz & R. M. Klein* 14403 (R); *Reitz* 4618 (HBR, UC, US); *Reitz* CI406 (GH, HBR, NY, UC, US); *Senhem* 5456 (HBR); *Smith & R. M. Klein* 10577 (HBR, NY, R, RB, UC, US); *Smith & R. Reitz* 8619 (HBR, R, US). **São Paulo:** *Amaral Jr.* 1209 (BOTU, G); *Custodio Filho* 2150 (SP, SPSF); *Hatschbach & Kummrow* 37122 (COI, MBM, MU); *Lutz & B. Lutz* 1931 (R); *Mimura* 271 (SP, US); *Muller* 32172 (UEC); *Ratter et al.* 4980 (NY, UEC); *Souza et al.* 7250 (HRCB, SP, SPF, UEC); *Sugiyama & Mantovani* 128 (SP). **Tocantins:** *Gardner* 3872 (K). **COLOMBIA.** **Casanare:** *Uribe Uribe, L.* 3758 (NY). **Guaviare:** *Cardenas, D. et al.* 6490 (COAH, MO). **Meta:** *García, M. C. et al.* 524 (US). **PARAGUAY.** **Amambay:** *Solomon, J. C. et al.* 7128 (MO, PY). **Caaguazú:** *Krapovickas, A. et al.* 12559 (UC). **Caazapá:** *Basualdo, I.* 2709 (MO). **Canindeyú:** *Schinini, A. & M. Dematteis* 33347 (G). **Central:** *Pedersen, T. M.* 9496 (K). **Concepción:** *Pedersen, T. M.* 3103 (P). **Cordillera:** *Zardini, E.* 8176 (US). **Guairá:** *Schinini, A.* 2091 (G). **Misiones:** *Pedersen, T. M.* 4406 (US). **Paraguari:** *Zardini, E.* 8685 (US). **San Pedro:** *Hassler, E.* 4501 (G, GH, K, NY, P, UC, W). **PERU.** **Amazonas:** *Díaz, C. & Campos, J.* 3637 (MO). **Cajamarca:** *Weberbauer, A.* 6152 (F, US). **Cuzco:** *Vargas Calderón, J. C.* 17278 (US). **Junín:** *Smith, D. N.* 6534 (MO). **Madre de Dios:** *Gentry, A. & Núñez, P.* 69460 (MO). **San Martín:** *Woytkowski, F.* 6231 (MO). **URUGUAY.** **Montevideo:** *Rosengurt B* 2574 (F). **VENEZUELA.** **Amazonas:** *Gentry, A. & Berry, P.* 14655 (MO, VEN). **Apure:** *Davidse, G. & González, A.* 15739 (MO). **Aragua:** *Williams, L.* 10446 (F, VEN). **Bolívar:** *Steyermark et al.* 131788 (MO, VEN). **Carabobo:** *Pittier* 9037 (NY, US); *Rávago, C.* 304 (VEN). **Guárico:** *Aristeguieta, L.* 6190 (NY, US, VEN). **Miranda:** *Pittier* 7508 (US). **Monagas:** *Maguire, B. et al.* 35828 (NY); *Wurdack, J. & Monachino, J.* 39537 (NY).

*Sinningia eumorphia*: BRAZIL. **São Paulo:** *Costa s.n.* (R 203451); *SanMartin-Gajardo s.n.* (UEC 35824).

*Sinningia gigantifolia*: BRAZIL. **Minas Gerais:** *Guillaumon s.n.* (SPFS); *Leoni* 4569 (GFJP); *Yamamoto* (UEC). **Rio de Janeiro:** *Martinelli, G. et al.* 13409 (RB); *Martinelli, G. & Farney, C.* 8688 (RB); *Silva Neto, S. J. et al.* 1185 (RB); *Snow, D.* 20 (K); *Sucre, D. & Braga* 2318 (R, RB). **São Paulo:** *Arzolla & G. C. R. de Paula* 411 (SPSF).

*Sinningia glazioviana*: BRAZIL. **São Paulo:** *Freitas* 256 (G); *Shirasuna et al.* 75 (SP, UEC).

*Sinningia guttata*: BRAZIL. **Rio de Janeiro:** *Kuhlmann* 6056 (RB).

*Sinningia harleyi*: BRAZIL. **Bahia:** *Carvalho & A. Chautems* 3235 (CEPEC, holotype); *Harley et al.* 51552 (HUEFS).

*Sinningia hatschbachii*: BRAZIL. **Paraná:** *Hatschbach* 23939 (MBM, NY, UC, WAG). **São Paulo:** *Chautems s.n.* AC-1479 (G).

*Sinningia hirsuta*: BRAZIL. **Rio de Janeiro:** *Farney, C. & J. C. Gomes* 4157 (RB); *Vidal II-5544* (R).

*Sinningia iarae*: BRAZIL. **São Paulo:** *Mendonça* 13 (R); *Silveira* 9861 (HAS).

*Sinningia incarnata*: BRAZIL. **Amapá:** *Fróes, R. L.* 25820 (IAC, IAN, UB); *Pires, J. M. & P. C. Cavalcante* 52651 (NY). **Amazonas:** *Ducke, A. s.n.* (G, RB 37615); *Nascimento, O. C. et al.* 144 (RB); *Poole, J. M.* 1817 (MG). **Ceará:** *Lima-Verde* 43 (G). **Maranhão:** *Eiten, G. & Eiten* 4343 (MO, NY, SP, US). **Pará:** *Ducke, A.* 810 (RB). **Pernambuco:** *Pickel* 3060 (F, IPA, S, US). **Roraima:** *Black & Magalhães* 51-12888 (IAN, UB); *Ducke, A. s.n.* (CEPEC, G, RB); *Milliken, W. & Bowles* 397 (E, G, K, NY); *Sette Silva, E. L.* 503 (NY). **Tocantins:** *Plowman et al.* 8156 (INPA, MG, NY, SEL, US).

- COLOMBIA. **Cauca:** *Cuatrecasas*, J. 19538 (F, MO, NY, US). **Cundinamarca:** *Pennell*, F. W. 2733 (F, MO, NY, US). **Magdalena:** *Seifríz*, W. 553 (US). **Meta:** *Grant*, M. L. 9220 (NY, US). **Tolima:** *Uribe Urbibé*, L. 1690 (US). COSTA RICA. **Anajuela:** *Utley*, J. & *Utley*, K. 2626 (MO). **Guanacaste:** *Webster*, G. & *Raveret*, M. 22177 (F). EL SALVADOR. **Ahuachapán:** *Croat*, T. 42107 (MO). **La Libertad:** *Dwyers*, J. D. 427 (MO). **Sonsonate:** *Croat*, T. 42259 (MO). FRENCH GUIANA. **Bassin de l'Oyapock:** *Prevost*, M. F. & *P. Grenand* 2050 (CAY, K). **Bassin du Ha:** *Granville*, J. et al. 9780 (P). GUATEMALA. **Baja Veracruz:** *Harmon*, W. E. & *J. D. Dwyer* 3048 (MO). **Chiquimula:** *Molina*, A. & *Molina* 26774 (F); *Standley*, P. C. 74467 (F). **Huehuetenán Goiás:** *Steyermark*, J. 50795 (F). **Jutiapa:** *Steyermark*, J. 30366 (F). **Quiché:** *Aguilar*, J. I. 1433 (F). **Santa Rosa:** *Harmon*, W. E. & *J. D. Dwyer* 3233 (MO). **Zacapa:** *Steyermark*, J. 29533 (F). GUYANA. **Upper Takutu-Upper Essequibo:** *Gillespie*, L. J. 1993 (CAY). HONDURAS. **Comayagua:** *Webster*, G. et al. 12727 (F, MO). **Copán:** *Croat*, T. 42514 (MO). **El Paraíso:** *Molina* R. A. 14614 (F, NY). **Morazán:** *Williams*, L. O. & *Molina* A. R. 13289 (F). **Ocotepaque:** *Molina* R. A. & *Molina* 31080 (F, MO). **Santa Bárbara:** *Molina* R. A. 21974 (F). **Valle:** *Molina* R. A. & *Molina* 22791 (F, NY). MEXICO. **Chiapas:** *Breedlove*, D. E. 27103 (MO, NY). **Oaxaca:** *King*, M. R. 1958 (NY). **Veracruz:** *Moore*, H. E. 8058 (BH). NICARAGUA. **Chontales:** *Stevens*, W. D. et al. 20552 (MO). **Esteli:** *Stevens*, W. D. & *Krukoff* 2986 (MO). **Madriz:** *Moreno*, P. P. 17710 (MO). **Masaya:** *Stevens*, W. D. 4237 (MO). **Matagalpa:** *Moreno*, P. P. 17710 (MO). **Nueva Segovia:** *Stevens*, W. D. & *Krukoff* 3302 (MO). **Río San Juan:** *Seymour*, F. C. & *Robbins*, S. B. 6191 (MO). PANAMÁ. **Canal Area:** *Dressler*, R. L. 5037 (F, MO). **Coclé:** *Luteyn*, J. L. 1244 (F, MO). **Panamá:** *Hammel*, B. 3755 (MO). SURINAM. **Sipaliwini:** *Granville*, J. et al. 13738 (CAY, US); *Oldenburger*, F. 866 (NY). VENEZUELA. **Amazonas:** *Davids*, G. & *Miller* G. 27300 (VEN). **Aragua:** *Bunting*, G. S. 4518 (F, K). **Bolívar:** *Steyermark*, J. 131258 (MO). **Distrito Federal:** *Steyermark*, J. 97253 (US). **Mérida:** *Steyermark*, J. 56358 (F, US). **Miranda:** *Aristeguieta*, L. 3206 (NY). **Tachira:** *Werff*, H. van der & *González*, A. 5360 (MO). *Sinningia insularis*: BRAZIL. **São Paulo:** *Rossi* et al. 435 (SP). *Sinningia kautskyi*: BRAZIL. **Espírito Santo:** *Chautems* & *M. Peixoto* 269 (Herbarium UFES, Vitória, holotype). *Sinningia lateritia*: BRAZIL. **Rio de Janeiro:** *Chautems*, A. & *Barcia* 321 (G, R); *Martinelli*, G. et al. 10688 (RB). *Sinningia leopoldii*: BRAZIL. **Santa Catarina:** *Cervi* et al. AC-483 (G, UPCB); *Reitz* 4549 (HBR, US). *Sinningia leucotricha*: BRAZIL. **Paraná:** *Motosima* s.n. (SP 56347). **Santa Catarina:** *Reitz* & *R. M. Klein* 13603 (HBR). *Sinningia lindleyi*: BRAZIL. **Rio de Janeiro:** *Araújo* & *Vianna* 926 (GUA). *Sinningia lineata*: BRAZIL. **Rio Grande do Sul:** *Hatschbach* et al. 78338 (G); *Silveira* & *C. J. Manson* 6071 (HAS). **Santa Catarina:** *Chautems* & *R. Reitz* 348 (G, HBR, US). *Sinningia macrophylla*: BRAZIL. **Bahia:** *Thomas* et al. 11936 (CEPEC, NY). *Sinningia macropoda*: BRAZIL. **Paraná:** *Carneiro* 317 (MBM); *Chautems* et al. 360 (FUEL, G); *Hatschbach* 1035 (MBM, US); *Hatschbach* 45655 (CEPEC, MBM, MO, Z); *Vieira* et al. 131 (FUEL). **São Paulo:** *SanMartin-Gajardo* s.n. (UEC 35826). PARAGUAY. **Paraguari:** *Hahn*, W. J. 2687 (G, PY, US). *Sinningia macrostachya*: BRAZIL. **Rio Grande do Sul:** *Bueno* 1947 (F, HAS, US); *Chautems* & *J. Waechter* 330 (G, ICN, US); *Costa Sacco* 1226 (F, HAS, HBR, IAN, R); *Meyer* et al. 63 (HAS); *Rambo* 51594 (B, S, US); *Senhem* 3630 (B, MBM); *Silveira* 173 (HAS); *Silveira* 6869 (HAS); *Sobral* & *C. Grabanska* 3936 (ICN); *Sobral* et al. 4232 (ICN); *Stehmann* et al. 1308 (UEC). **Santa Catarina:** *Hatschbach* et al. 61239 (G); *Reitz* & *R. M. Klein* 9241 (HBR, R). *Sinningia magnifica*: BRAZIL. **Espírito Santo:** *Hatschbach* 47696 (CEPEC, MBM, SPF, US); *Kollmann* & *C. Fraga* 3210 (MBML). **Minas Gerais:** *Chautems* & *M. Peixoto* 364 (G); *Cosenza* 23462 (CESJ); *Dulith* 31207 (UEC); *Furlan* et al. CFCR 3061 (CEPEC, SPF, US); *Grandi* 1651 (FCAB, G); *Irwin* et al. 29051a (F, K, MO, NY, US); *Mayo* et al. CFSC 7092 (CEPEC, G, SPF, US); *Oliveira* & *F. R. Salimena* CESJ 24790 (CESJ); *Stehmann* et al. 2454 (G). **Rio de Janeiro:** *Forzza* et al. 3419 (G); *Gotsberger* & *G. Gotsberger* 117-16471 (G); *Pereira* 1286 (R). **São Paulo:** *Handro* s.n. SP 39421 (SP 39421); *Tamashiro* et al. 847 (HRCB, SP, UEC). *Sinningia mauroana*: BRAZIL. **Paraná:** *Hatschbach* 14149 (MBM, NY, S). **São Paulo:** *Barros* 2250 (G, NY, SP); *Chautems* & *M. Peixoto* 283 (CEPEC holotype; G, US, isotypes); *Kirizawa* 2787 (SP); *Silveira* 9862 (HAS). *Sinningia micans*: BRAZIL. **São Paulo:** *Dedecca Kug* & *Gardini* s.n. IAC 8338 (IAC 8338); *Wettstein* & *Schiffner* s.n. (WU sintipo *Corytholoma micans* Fritsch). *Sinningia nivalis*: BRAZIL. **Rio Grande do Sul:** *Bueno* 3062 (HAS); *Rambo* 56197 (B, HBR). **Santa Catarina:** *Hatschbach* et al. 78119 (G); *Pereira* s.n. (HBR, NY, R, US). *Sinningia nordestina*: BRAZIL. **Alagoas:** *Cervi* et al. 6017 (G). **Bahia:** *Santos* 5 (ALCB). **Ceará:** *Eugenio Leite* 1073 (RB). **Paraíba:** *Agra* et al. 1461 (G, JPB). **Pernambuco:** *Andrade-Lima* 20 (IPA); *Pietrobon-Silva* et al. 4602 (MBM, SPF, UFP); *Siqueira Filho* & *G. Baracho* 663/704 (G isotype, UFP holotype). **Sergipe:** *Viana* 1026 (ASE); *Viana* 652 (ASE). *Sinningia piresiana*: BRAZIL. **São Paulo:** *Macedo* 275 (ESA); *Pires* s.n. (SP 56345 holótipo de *Reichsteineria piresiana*, *Salino* 130, ESA). *Sinningia pusilla*: BRAZIL. **Rio de Janeiro:** *Braga*, J. M. 715 (RUSU); *Mello Filho*, L. E. & *Emmerich*, M. 3121 (R). *Sinningia reitzii*: BRAZIL. **Santa Catarina:** *Reitz* & *R. M. Klein* 4068 (B, G, HBR holotype, MBM, NY, PACA, R, SP, UC); *Silveira* 9716 (HAS). *Sinningia richii*: MEXICO. **Veracruz:** *Clayberg* 26 (BH). *Sinningia rupicola*: BRAZIL. **Minas Gerais:** *Braga* et al. s.n. (G); *Irwin* et al. 19805 (F, K, MO, NY, UB, US); *Stehmann* & *C. E. S. Ferreira* 2404 (G). *Sinningia sceptrum*: BRAZIL. **Bahia:** *Lewis* 737 (CEPEC, K). **Espírito Santo:** *Arbo* et al. 7720 (CEPEC); *Kollmann* 64 (MBML, UEC); *Sucre* 5585 (CEPEC, RB). **Minas Gerais:** *Assis* et al. 959 (G); *Leoni* 1513 (GFJP); *Leoni* 3243 (GFJP); *Mexia* 4343 (F, MO, NY, S, VIC, US); *Moreira* & *S. H. Borges* 24583 (CESJ). **Rio de Janeiro:** *Duarte*, A. 6298A (G, RB); *Laclette*, P. 921 (R); *Yamamoto*, K. & *Viera*, A. O. S. 26212 (UEC). *Sinningia schiffneri*: BRAZIL. **Rio de Janeiro:** *Silveira*, N. 9855 (HAS). **São Paulo:** *Cordeiro* 2377 (NY, SP); *Cordeiro* et al. 525 (G); *Gomes da Silva* et al. 277 (RB, SPF); *Leitão Filho* et al. 34616 (SP); *Wettstein* & *Schiffner* s.n. (WU holotype). *Sinningia sellowii*: ARGENTINA. **Corrientes:** *Utter* & *Lonsdale* 60-341 (K). **Misiones:** *Eskuche* 4999 (Z). BOLIVIA. **Chuquisaca:** *Beck*, S. G. 9356 (G). **Santa Cruz:** *Mello Silva*, R. et al. 2079 (RB). BRAZIL. **Mato Grosso do Sul:** *Hatschbach* et al. 74337 (G). **Paraná:** *Dusén* 8944 (S); *Hatschbach* 22899 (MBM, UPCB); *Hatschbach* 23136 (F, NY,

MO); *Hatschbach* 31052 (MBM, US, Z); *Lindeman & J. H. Haas* 3271 (K, NY, US); *Poliquesi & J. Cordeiro* 268 (G). **Rio Grande do Sul:** *Albuquerque s.n.* (HAS); *Bueno* 3266 (HAS); *Bueno* 5187 (HAS); *Chautems & J. Waechter* 373 (G); *Eggli et al.* 2488 (ZSS); *Lindman* A1297 (S, UPS); *Mattos & N. H. Bassan* 28573 (HAS); *Mattos & N. Mattos* 24680 (HAS); *Mattos & N. Mattos* 31062 (HAS); *Mattos & N. Silveira* 23305 (ICN); *Mattos & N. Silveira* 26437a (ICN); *Mattos & N. Silveira* 26968 (HAS); *Mattos & R. Frosi* 23743 (HAS); *Meyer et al.* 65 (HAS); *Senhem* 3631 (ALCB, B, INPA, MBM); *Silveira & J. Mansan* 6065 (HAS); *Waechter* 1840 (ICN). **Santa Catarina:** *Chautems & R. Reitz* 347 (G, HBR, US); *Reitz* 3785 (HBR, US); *Smith & R. M. Klein* 13838 (NY, R, US). PARAGUAY. **Amambay:** *Brunner, D. R. et al.* 956 (PY). **Canindeyú:** *Fernández Casas, J. & J. Molero* 4195 (G). **Concepción:** *Anisits, J. D.* 2704 (S). **Guairá:** *Basualdo, I.* 1800 (MO). **Paraguarí:** *Bernardi, L.* 18146 (F, G, MO, NY). URUGUAY. **Rivera:** *Herter W. G.* 1387 (F, MO, Z).

*Sinningia speciosa*: BRAZIL. **Bahia:** *Mori* 10714 (CEPEC, NY). **Espírito Santo:** *Boone* 967 (CEPEC, MBML); *Martinelli et al.* 2206 (US); *Mattos & Bicalho* 10857 (HAS, SP). **Minas Gerais:** *Leoni s.n.* (CEPEC, GFJP 398). **Rio de Janeiro:** *Araujo, D. & Souza, S. R.* 8222 (GUA); *Braga* (photo); *Mello Filho, L. E.* 2611 (R); *Segadas-Viana, F.* 4469 (R); *Sucre, D.* 9731 (BH, CEPEC).

*Sinningia striata*: BRAZIL. **Minas Gerais:** *Krapovickas & Cristobal* 35450 (MO, NY, US).

*Sinningia tuberosa*: BRAZIL. **Minas Gerais:** *Andrade & Renato* 927 (BHCB 15843); *Irwin et al.* 29414 (F, K, NY, UB, US); *Mello Silva et al.* 1653 (RB, SP, SPF). **Rio de Janeiro:** *Duarte, A.* 4278 (RB).

*Sinningia tubiflora*: ARGENTINA. **Chaco:** *Schulz* 850 (K, LIL). **Córdoba:** *Stuckert, T.* 19596 (G). **Corrientes:** *Schwarz* 8818 (NY, LIL). **Entre Ríos:** *Burkart* 24023 (SI). **Formosa:** *Morel* 1743 (LIL). **Santa Fé:** *Maldonado, R.* 1731 (K). **Santiago del Estero:** *Maldonado* 975 (LP); *Maldonado Bruzone* 1568 (LP). PARAGUAY. **Central:** *Hassler, E.* 1476 (G, K, NY, P). **Concepción:** *Krapovickas, A. & C. L. Cristóbal* 45088 (G). **Neembucu:** *Meyer, T.* 15939 (LIL). **Presidente Hayes:** *Brunner, D. R.* 1334 (PY, US). **San Pedro:** *Hassler, E.* 6023 (G, NY, S, UC).

*Sinningia valsuganensis*: BRAZIL. **Espírito Santo:** *Boone* 1104 (CEPEC, MBML, MO); *Rossini, A. Chautems & M. Peixoto* 555 (MBML).

*Sinningia villosa*: BRAZIL. **Bahia:** *Jardim* 3945 (NY, HUEFS). **Espírito Santo:** *Kollmann et al.* 1683 (G, MBML). **Minas Gerais:** *Andrade & M. A. Lopes* 676 (CEPEC, G).

*Sinningia warmingii*: ARGENTINA. **Catamarca:** *Castillon* 1717 (LIL, US). **Chaco:** *Aguilar, R. M.* 973 (G, LIL, US 2123801). **Corrientes:** *Pedersen, T. M.* 10861 (NY, MO). **Formosa:** *Morel, I.* 2065 (G, LIL). **Jujuy:** *Mello Silva, R. et al.* 1900 (G). **Salta:** *Novara, L. J. s.n.* (MO 3099831). **Tucumán:** *Olar, D.* 53 (NY). BOLIVIA. **Santa Cruz:** *Herzog* 1170 (G, S, L, W, Z). **Tarija:** *Fiebrig* 2109 (B not extant). BRAZIL. **Minas Gerais:** *Anderson et al.* 36287 (F, K, MO, NY, UB, US); *Melo & J. A. Lombardi* 396 (G). **Paraná:** *Hatschbach* 22893 (F, HBR, K, MBM, MO, NY).

**Rio de Janeiro:** *Araujo, D. & Maciel, N. C.* 8655 (GUA). **Rio Grande do Sul:** *Bueno* 2007 (HAS); *Hatschbach* 31177 (MBM, Z); *Mattos et al.* 29147 (HAS); *Meyer et al.* 198 (HAS); *Rambo* 52123 (HBR, PACA, S); *Silveira* 6569 (HAS); *Silveira et al.* 1156 (HAS). **Santa Catarina:** *Hatschbach et al.* 79222 (G); *Lourteig* 2120 (HBR, P, S, US); *Lourteig* 2324 (HBR, US); *Reitz & R. M. Klein* 7990 (G, HBR, NY, UC, US); *Reitz* C411 (HBR, R, RB); *Ule* 1058 (US). **São Paulo:** *Edwall s.n.* CGG 5906 (SP). ECUADOR. **Loja:** *Harling, G. & Anderson, L.* 22594 (GB, MO, US). PARAGUAY. **Alto Paraguay:** *Mereles, F. & L. Ramella* 2886 (G). **Amambay:** *Hassler, E.* 8491 (G, NY). **Central:** *Zardini, E.* 23602 (MO). **Concepción:** *Fiebrig, K.* 4668 (G, GH, HBG, M). **Cordillera:** *Fiebrig, K.* 825 (K, E, F, G, HBG, P). **Ñeembucú:** *Bernardi, L.* 20474 (G). **Presidente Hayes:** *Zardini, E. et al.* 2625 (US). **San Pedro:** *Hassler, E.* 6022 (G, GH, NY, P, S, UC, W). PERU. **Amazonas:** *Wolfe, F. H. & F. H. Dobson* 816 (CONN). **Apurímac:** *Alfaro, R. C.* 3364 (MO). **Cajamarca:** *Sánchez Vega, I. M. et al.* 5831 (F, MO, NY, US). **Cuzco:** *Croat, T.* 50964 (MO); *Diehl, A.* 2512 (F). **Huancavelica:** *Weberbauer, A.* 6446 (F). **Junín:** *Ochoa, C.* 204 (US). **La Libertad:** *Vásquez, N.* 6310 (US). **Lambayeque:** *Llatas Quiroz, S. & Cruz, H.* 1191 (GB). **Lima:** *Soukup, J.* 4186 (US). **Puno:** *Vargas C.* 14826 (US).

*Sinningia* sp. indet. 1: BRAZIL. **Minas Gerais:** *Nakajima & André* 2481 (UEC); *Simão Bianchini & S. Bianchini* 1202 (SP).

*Sinningia* sp. indet. 4: BRAZIL. **Paraná:** *Hatschbach* 33846 (MBM, Z). **São Paulo:** *Barbosa et al.* 884 (G).

*Sinningia* sp. indet. 7: BRAZIL. **Rio Grande do Sul:** *Silveira* 8824 (G, HAS); *Waechter* 2282 (ICN). **Santa Catarina:** *Hatschbach et al.* 27241 (MBM holotype, BH isotype, NY, UC).

*Vanhouttea bruggeri*: BRAZIL. **Minas Gerais:** *Brugger & H. G. Souza s.n.* (CESJ 24699a); *Forzza et al.* 1803 (G).

*Vanhouttea calcarata*: BRAZIL. **Espírito Santo:** *Brade* 19829 (R, RB); *Kollmann et al.* 2336 (G, MBM, MBML). **Minas Gerais:** *Hatschbach* 47674 (MBM, US); *Krieger & Roth* 1044 (R, SP). **Rio de Janeiro:** *Anderson* 11719 (NY, US); *Boudet Fernandes* 784 (GUA); *Costa et al.* 493 (CEPEC, G, RB, SP); *Martinelli & C. Farney* 8690 (RB, US).

*Vanhouttea fruticososa*: BRAZIL. **Rio de Janeiro:** *Chautems et al.* 338 (G, RB, US).

*Vanhouttea gardneri*: BRAZIL. **Rio de Janeiro:** *Anderson* 11722 (NY, US); *Oliveira* 598 (GUA); *Smith* 6687 (NY, R, SP, US).

*Vanhouttea hilariana*: BRAZIL. **Minas Gerais:** *Andrade* 921 (CESJ, RB); *Farney & S. A. Geromel* 1065 (G); *Lombardi et al.* 4679 (G).

*Vanhouttea lanata*: BRAZIL. **Rio de Janeiro:** *Mello Silva et al.* 2619 (G); *Ribeiro et al.* 788 (GUA).

*Vanhouttea leoni*: BRAZIL. **Minas Gerais:** *Caiafa* 5 (VIC); *Hatschbach & J. M. Silva* 55446 (G, MBM).

*Vanhouttea pendula*: BRAZIL. **Espírito Santo:** *Souza et al.* 23735 (ESA). **Minas Gerais:** *Caiafa & M. L. Batista* 173 (VIC); *Hatschbach, M. Hatschbach & J. M. Silva* 55448 (G, MBM, NY, Z).