

Salcedoa gen. nov., a Biogeographic Enigma in the Caribbean Mutisieae (Asteraceae)

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ABSTRACT. A new genus, *Salcedoa*, is described from the Cordillera Septentrional, northern Dominican Republic. The bilabiate florets, smooth style branches, caudate anthers, and pollen grains size and shape, exine structure and sculpture, and endoaperture shape place it close to the South American genera of the tribe Mutisieae (Asteraceae) centered in the Guayana Shield. Two morphology-based phylogenetic analyses, one using *Gochnatia* and the other using *Chaetanthera* as outgroups, and including *Salcedoa* and the 12 Guayanan genera were performed to determine the sister group relationships of *Salcedoa*. The results suggest that *Salcedoa* is sister to *Gongylolepis*. The unusual distributional pattern of *Salcedoa* and the Guayanan genera was explored through the dispersal-vicariance method. A trans-oceanic dispersal of fruits is postulated as a probable mechanism by which *Salcedoa* reached Hispaniola from a South American ancestor.

During field work in 2001 in the Cordillera Septentrional of the northern Dominican Republic, specimens were collected from a small Asteraceae tree growing in humid forests. The bilabiate florets, smooth style branches, and caudate anthers with sterile tails place the species in the tribe Mutisieae (Asteraceae). Detailed morphological, anatomical, and palynological studies revealed it to have a character combination suggestive of an undescribed genus. Prior to our study, only four of the 89 genera of Mutisieae (Cabrera 1977), *Berylsimpsonia* B. L. Turner, *Chaptalia* Vent., *Gochnatia* Kunth, and *Trixis* P. Browne, were known from Hispaniola (Dominican Republic and Haiti).

The Mutisieae belongs to the subfamily Cichorioideae and is a polyphyletic tribe whose taxonomy is still unsettled, occupying an ancestral position in Asteraceae. The classification of the tribe in the three subtribes Gochnatiinae, Mutisiinae, and Nassauviinae was changed by Bremer (1994) who recognizes two subtribes: Mutisiinae (including Gochnatiinae) and Nassauviinae. The subtribe Nassauviinae is the most natural in the tribe, being morphologically quite uniform (Crisci 1974, 1980; Cabrera 1977). The Mutisiinae, on the other hand, are heterogeneous and consist of several separate lineages constituting generic groups or isolated taxa (Bremer 1994). One of these generic groups is the Guayanan group of Pruski (1989a,b, 1991, 1997, 1998), also called the *Stenopadus* group (Bremer 1994) or the *Stiffitia* group (Panero and Funk 2002). The Guayanas group is a complex of 12 genera that are distinguished from the other genera of Mutisieae by their stout, few-branched, woody habit, thickly coriaceous leaves generally clustered at the branch apices, isomorphic capitula, and large florets with exerted anther tubes (Pruski 1991; Bremer 1994). In this com-

plex there are genera with all actinomorphic, tubular florets and papillate or bullate style branches (*Chimantaea* [nine species], *Quelchia* [4 spp.], *Stenopadus* [15 spp.], *Stiffitia* [7 spp.], *Stomatochaeta* [6 spp.], and *Wunderlichia* [6 spp.]), and genera with all bilabiate florets and smooth style branches (*Achnopogon* [two species], *Duidaea* [4 spp.], *Eurydochus* [1 sp.], *Glossarion* [2 spp.], *Gongylolepis* [14 spp.], and *Neblinaea* [1 sp.]). Species of *Quelchia* have 1-flowered capitula with corollas that range from tubular, slightly zygomorphic, to bilabiate.

The new Hispaniolan novelty is close to the bilabiate genera of the Guayanas group by the following characters: stout, few-branched small trees, thick coriaceous leaves clustered at the apices of the branches, isomorphic capitula with all bilabiate florets, smooth style branches, and long exerted anthers with apiculate apical appendages.

The Guayanan genera have been largely viewed as a natural group by some authors (Maguire 1956; Carlquist 1958; Pruski 1991). The genera with bilabiate florets were included in the subtribe Mutisiinae and those with tubular florets in the subtribe Gochnatiinae (Maguire and Wurdack 1957; Cabrera 1977). As mentioned above, this subtribal classification is now considered artificial and has been abandoned. Molecular studies based on one gene (Kim et al. 2002) have shown the two sampled Guayanan genera *Duidaea* and *Stiffitia* in separate branches. Panero and Funk (2002), in a molecular analysis based on several regions from the chloroplast genome, proposed the circumscription of the *Stiffitia* group. They suggested that additional data would likely provide enough support to recognize this group of genera as a new subfamily, but final resolution will have to wait until additional genera are sampled for DNA sequence information. The sampled

genera and species used for the molecular analysis were not specified in this work.

The Guayanan genera are mainly centered in the Guayana Highlands of northern Brazil, Colombia, Guyana, and Venezuela but also occur in French Guiana, eastern Brazil, and the Andes of Colombia, Ecuador, and Peru (Fig. 1). The Guayanan genera have generated considerable interest because of their high degree of endemism and biogeographic isolation. Most genera are endemic to the "tepuis," an Amerindian term for a group of isolated sandstone table mountains in the Venezuelan Guayana and adjacent Brazil and Guyana (Huber 1995). With the new Dominican taxon being potentially closely related to the Guayanan genera, the geographical distribution of that group is now expanded. This brings an interesting enigma to our understanding of the Guayanas group. The only previously reported sister genera of Asteraceae endemic to Guayana and the Greater Antilles involves *Huberopappus* Pruski of Guyana and its sister *Ekmania* Gleason of Cuba (Pruski 1997). A strong link between Guayana and the Greater Antilles has also been detected in the circum-Caribbean centered genus *Piptocoma* Cass. (Asteraceae; Pruski 1997), in *Bonettia* Mart. (Bonettiaceae; P. Berry pers. comm.), and several genera of the family Orchidaceae (Trejo-Torres and Ackerman 2001). A historical biogeographic analysis is profitable to establish a hypothesis for this unusual distributional pattern.

The goals of this study are to: (1) describe the new taxon from the Dominican Republic; (2) use morphological characters to reconstruct a phylogeny of this taxon and the Guayanan genera; and (3) postulate a historical biogeographic explanation for this new taxon applying a dispersal-vicariance (DIVA) method.

MATERIAL AND METHODS

Sample Preparation. Dry florets and fruits were observed with a light microscope and also boiled in water, then rinsed and stained with 2% safranin. The midregion of leaves and styles of *Salcedoa* were isolated, free hand cut transversely, and stained with safranin. Pencil drawings were made by the authors using a Wild M5 stereomicroscope and a Leitz SM Lux light microscope equipped with a camera lucida.

Pollen grains were removed from herbarium specimens and were acetolyzed in standard manner and then chlorinated (Erdtman 1960). For light microscopy (LM), slides were prepared by mounting the pollen in glycerol jelly and sealed with paraffin. Measurements of the polar (P) and equatorial (E) diameters of pollen grains are based on 25 grains and measurements of the thickness of the exine are based on at least 15 grains. The P/E ratio was calculated for each specimen. Acetolyzed pollen grains were suspended in 90% ethanol and mounted on stubs for scanning electron microscopy (SEM). The samples were sputter-coated with gold palladium and examined with a JEOL JSM T-100 SEM. Palynological terminology, in general, follows Punt et al. (1994); the size classification was taken from Erdtman (1969).

Cladistic Analysis. Thirteen genera represented by 24 species (Appendix 1) were considered the ingroup: *Achnopogon*, *Chimantaea*, *Duidea*, *Eurydochus*, *Glossarion*, *Gongylolepis*, *Neblinaea*, *Quelchia*, *Stenopadus*, *Stiffitia*, *Stomatochaeta*, and *Wunderlichia*, as well as the new Hispaniolan taxon. Although some of these genera are

not endemic to the Guayana Highlands, either because they inhabit other areas or transcend the limits of the Guayana Highlands, they will be referred to in this paper as the Guayanan genera.

Outgroups were chosen using the results of previous analyses to include more distant relatives of the new Hispaniolan taxon. First, we chose *Gochmatia* as the most appropriate outgroup on the basis of previous morphological (Freire et al. 2002; Katinas et al. in prep.) and palynological (Tellería and Katinas 2004) studies in the Mutisieae. *Gochmatia* has a unique set of characters indicative of the closest relationship with genera of the Guayanas: homogamous capitula, mostly isomorphic florets, apiculate apical anther appendages, smooth style branches, and species with edinate pollen, spines with apical channels, and very perforate tectum. *Gochmatia* has 70 species in eight sections: *Anastraphioides*, *Discoseris*, *Glomerata*, *Gochmatia*, *Hedraiophyllum*, *Leucomeris*, *Pentaphorus*, and *Rotundifolia*. Every section was included in the analysis (Appendix 1) to test the monophyly of the Guayanan genera and to obtain a more reliable ancestral area of the Guayanan genera. Recently, a molecular study of the Mutisieae on the basis of the 3' end of the chloroplast gene *ndhF* (Kim et al. 2002) showed that *Duidea*, one of the Guayanan genera, was sister to another mutisoid genus, *Chaetanthera*. *Chaetanthera* has no morphological or palynological similarities to any of the 13 Guayanan genera. Regardless, we decided to use *Chaetanthera* as an outgroup in a second cladistic analysis in order to compare the results with the analysis using the sections of *Gochmatia* as outgroups.

The 38 morphological characters used in the present analysis (Appendix 2) were taken from herbarium specimens and from the literature (Carquist 1957; Cabrera 1971; Barroso and Maguire 1973; Pruski 1991, 1997; Robinson 1991; Roque and Silvestre-Capelato 2001; Freire et al. 2002; Tellería et al. 2003). Autapomorphic characters were not included in the analysis. Multistate characters (characters 2, 3, 5, 7, 24, 28, 32, 33) were treated as unordered, and the data matrix (Table 1) was analyzed with PAUP 4.0b4a (Swofford 2000) using the "branch and bound" search option. The bootstrap method (Felsenstein 1985) and Bremer support (Bremer 1988; Donoghue et al. 1992) were employed to evaluate clade support for the phylogenetic estimates. One hundred replicates were performed in the bootstrap method. The program MacClade version 3.0 (Maddison and Maddison 1992) was used for examination of character distribution. The data matrix has been deposited in TreeBASE (study accession number S1109; matrix accession number M1898).

Biogeographic Analysis. Seven areas of endemism were used (Fig. 1): A = Antilles; B = eastern Venezuelan Guayana, highlands and lowlands, and adjacent Guayana and Brazil; C = western Venezuelan Guayana, highlands and lowlands, and adjacent Brazil and Colombia; D = Andes; E = French Guiana to southeastern Brazil and adjacent Paraguay, Uruguay, and Argentina; F = Mexico and southern USA; G = southern Asia. All sections of *Gochmatia* and the genera of the Guayanas group were coded for all of the species distribution.

Ancestral distributions were reconstructed using DIVA 1.1 (Ronquist 1996) according to the dispersal-vicariance optimization method (Ronquist 1997; Crisci et al. 2003). Dispersal-vicariance analysis optimizes distributions for each node of the tree, allowing for vicariance events and minimizing the number of assumed dispersals and extinctions. We conducted the analysis in which the number of ancestral areas was unconstrained, favoring vicariance and allowing the ancestral distributions to contain the maximum number of areas, which in our case is seven with *Gochmatia* (areas A-G) and five with *Chaetanthera* (areas A-E).

According to Ronquist (1996), the optimizations become less reliable as the root node is approached. This is because the globally optimal states of the basal nodes in the subtree are particularly heavily influenced by the rest of the tree. The root node or the ancestral distribution is the least reliable because it includes most or all of the areas occupied by the terminals. We minimized the number of optimizations at the root node by splitting *Gochmatia* into its eight sections. This is in agreement with Ronquist's suggestion of having multiple outgroups for any one DIVA analysis.

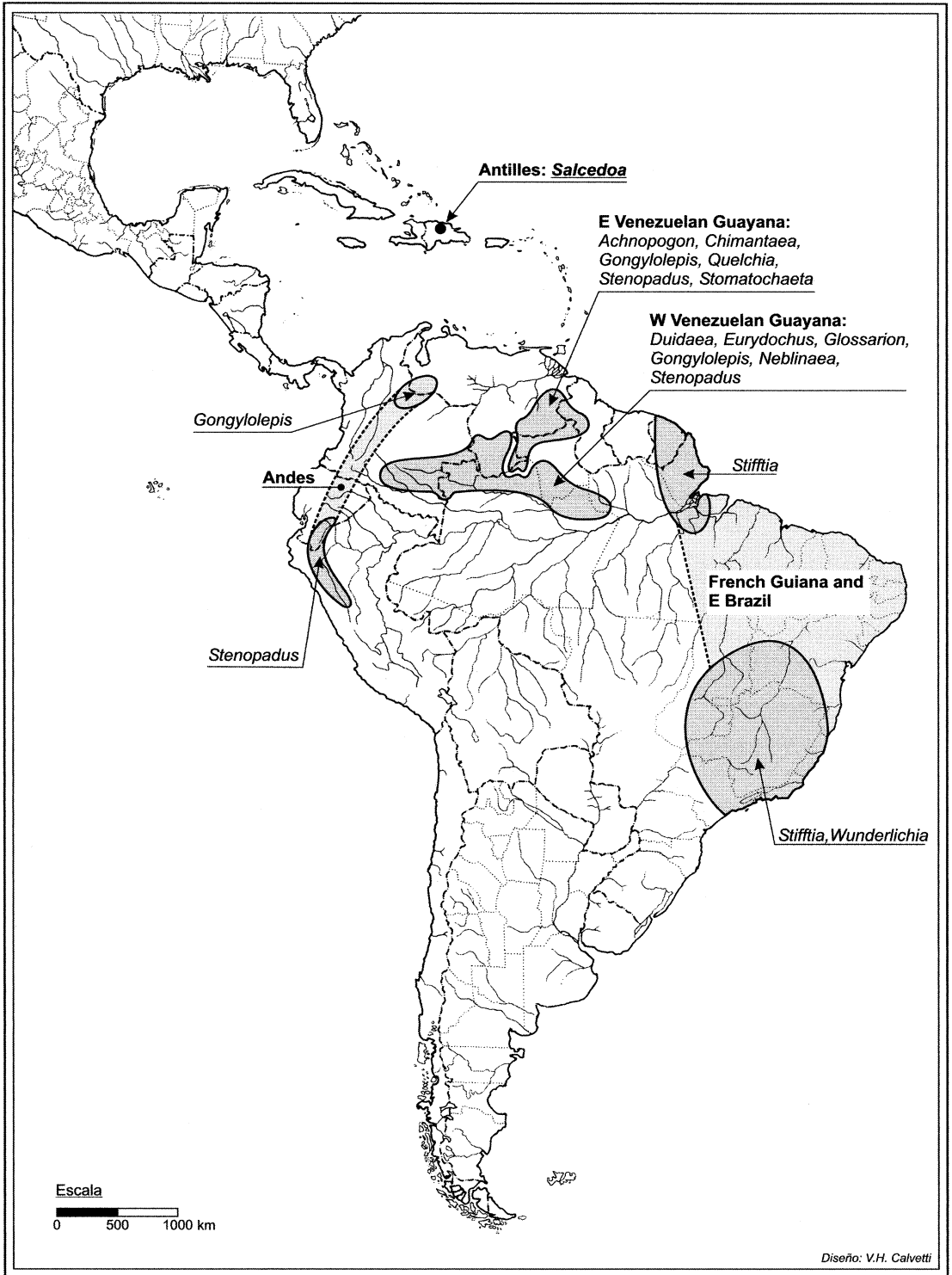


FIG. 1. Distribution map of *Salcedoa* and the Guayanian-centered genera of Mutisieae (Asteraceae). The dotted line indicates that some taxa may be found between these two disjunct regions in future collections.

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TABLE 1. Data matrix used in the cladistic analysis. Refer to Appendix 2 for characters and character coding when *Chaetanthera* was used as outgroup. ? = missing data. A = 0 + 1.

<i>Gochmatia</i> sect. <i>Gochmatia</i>	000?000000	0000000000	0000000000	00000000
<i>G.</i> sect. <i>Anastraphioides</i>	000?000000	0101011000	0000000000	10200000
<i>G.</i> sect. <i>Discoseris</i>	0010101000	0000000000	0000000000	10200000
<i>G.</i> sect. <i>Glomerata</i>	0011101000	0000001000	0000000000	00000000
<i>G.</i> sect. <i>Hedraiophyllum</i>	0020202100	A000000000	0000000001	00010000
<i>G.</i> sect. <i>Leucomeris</i>	0020202111	0000000000	0000000000	00000000
<i>G.</i> sect. <i>Pentaphorus</i>	0121202010	0000001000	0000000000	02000000
<i>G.</i> sect. <i>Rotundifolia</i>	010?001110	0000000000	0000000000	00000000
<i>Achnopogon</i>	1010201000	1001010010	011110121?	01101000
<i>Chimantaea</i>	100?010000	0101011000	1110000011	01001000
<i>Duida</i>	120?001000	1001010011	011100121?	01201100
<i>Eurydochus</i>	100?000001	1010010100	0111000111	01101100
<i>Glossarion</i>	100?000000	1010010110	011100021?	01201100
<i>Gongylolepis</i>	1010100100	1000010101	0112011110	02001100
<i>Neblinea</i>	1010101000	1001010100	001100121?	00001000
<i>Quelchia</i>	1011101100	A001010000	001210121?	02001000
<i>Salcedoa</i>	1010101001	1110010001	0002010010	02001100
<i>Stenopadus</i>	100?010000	0010110110	101200021?	01000011
<i>Stiffia</i>	0010100000	0000110000	101200021?	02001011
<i>Stomatochaeta</i>	100?010000	0101010100	101200021?	01000010
<i>Wunderlichia</i>	100?010000	0000011100	1010000011	02011100

RESULTS

Cladistic Analysis. The cladistic analysis using *Gochmatia* sections as outgroups produced two most parsimonious trees of 110 steps, CI = 0.418, and RI = 0.630 (Fig. 4). The consensus tree consists of two main clades, one containing the Guayanian genera, and the other containing four sections of *Gochmatia* (Fig. 5). The two most parsimonious trees differ in their arrangement of the sections of *Gochmatia* and in some genera of the Guayanian group.

The new Dominican taxon, hereafter referred to as the genus *Salcedoa*, is sister to *Gongylolepis* as suggested by the presence of sclereids in the style (character 20), style branches with ribs (character 26), cypselas with twin hairs (character 30), and echinate pollen (character 36). The Guayanian genera with bilabiate florets (including *Salcedoa*) are monophyletic, whereas the genera with tubular florets are paraphyletic in one of the minimal length trees (Fig. 4A). The alternative minimal length tree resolves the Guayanian genera with tubular florets as monophyletic, whereas those with bilabiate florets as polyphyletic; *Salcedoa* and *Gongylolepis* are sister to the rest of Guayanian genera (Fig. 4B).

When *Chaetanthera* was used as the outgroup, the analysis resulted in two most parsimonious trees with length = 79 steps, CI = 0.494, and RI = 0.565. In contrast to the previous analysis, both trees resolve two monophyletic groups: one group of genera with tubular florets and the other group of genera with bilabiate florets (Fig. 6A). Otherwise, similar sister group relationships are resolved as when using the sections of *Gochmatia* as the outgroups.

Biogeographic Analysis. Each of the two resulting trees using *Gochmatia* as the outgroup (Figs. 4A, B) has

two trichotomies that were resolved according to all the possible alternative taxon arrangements because the program DIVA requires the tree to be fully resolved. This generated 18 different trees, all of which were run in DIVA. The results are summarized in Table 2. In all trees, the area B (eastern Venezuelan Guayana) was optimized as the ancestral area of the Guayanian genera.

Three main dispersal events are present in all 18 trees and include: 1) from eastern Venezuelan Guayana (area B) to French Guiana and Brazil (area E); 2) from eastern Venezuelan Guayana (area B) to western Venezuelan Guayana (area C); and 3) from the Andes (area D) to French Guiana and Brazil (area E). Six trees show an additional dispersal event from E to D (Table 2).

The vicariant events are more variable in the 18 trees, but all of them agree with vicariant events that separated the Andes from the other areas. Six trees show a vicariant event between the Andes (area D) and the Antilles, eastern Venezuelan Guayana, Guiana and Brazil, and Mexico and USA (areas AB-EF). Six trees include western Venezuelan Guayana (area C) in the split: D-ABCE-F. Three trees include Asia (area G) instead of western Venezuelan Guayana (area C): D-ABEFG. The last three trees show a vicariance between the Andes and all the remaining areas: D-ABCEFG. Also the 18 trees show a vicariant event of the Antilles (area A). That is, 11 trees depict a vicariant event between the Antilles and other areas (e.g., A-BCE-F), and the remaining seven trees depict the Antilles plus eastern Venezuelan Guayana (area B) apart from other areas (e.g., AB-EF). The low number of alternative area optimization at the lowest nodes of the ingroup always

TABLE 2. Results obtained from DIVA analysis (Figs. 4 A, B) with the 18 alternative trees after resolving the trichotomies of the two original trees. The number of alternative, equally optimal reconstructions, the frequency of dispersal events between single areas (only the major values are shown), and the frequency of vicariance events involving more than two areas (only the major values are shown) are provided. In the Alternative Trees column the numbers refer to the alternative solution of the trichotomies in the trees of Figs. 4 A, B: These alternatives are as follows: 1a) ((*Gochmatia* sect. *Hedraiophyllum*, G. sect. *Leucomeris*) G. sect. *Pentaphorus*); 1b) ((*Gochmatia* sect. *Hedraiophyllum*, G. sect. *Pentaphorus*) G. sect. *Leucomeris*, 1c) ((*Gochmatia* sect. *Pentaphorus*, G. sect. *Leucomeris*) G. sect. *Hedraiophyllum*), 1d) ((*Chimantaea*, *Wunderlichia*) rest of Guayanan genera), 1e) (*Wunderlichia*) (*Chimantaea* (rest of Guayanan genera))), 1f) (*Chimantaea* (*Wunderlichia* (rest of Guayanan genera))); 2a) ((*Gochmatia* sect. *Discoseris*, G. sect. *Glomerata*) Guayanan genera), 2b) (*Gochmatia* sect. *Discoseris* (G. sect. *Glomerata* (Guayanan genera))), 2c) (*Gochmatia* sect. *Glomerata* (G. sect. *Discoseris* (Guayanan genera))), 2d) ((*Gochmatia* sect. *Hedraiophyllum*, G. sect. *Leucomeris*) G. sect. *Pentaphorus*), 2e) ((*Gochmatia* sect. *Hedraiophyllum*, G. sect. *Pentaphorus*) G. sect. *Leucomeris*), 2f) ((*Gochmatia* sect. *Pentaphorus*, G. sect. *Leucomeris*) G. sect. *Hedraiophyllum*). A = Antilles; B = eastern Venezuelan Guayana; C = western Venezuelan Guayana; D = Andes; E = French Guiana and eastern Brazil; F = Mexico and USA; G = Asia.

Alternative trees	Number of alternative reconstructions	Hypothetical dispersals	Hypothetical vicariances
1ad	32	B to E, B to C, D to E	D-ABEF, AB-EF
1ae	80	the same as above	D-ABEF, A-BE
1af	32	the same as above	D-ABEF, AB-EF
1bd	128	the same as above	D-ABEFG, AB-EFG, D-FG
1be	416	the same as above	D-ABEFG, D-FG, A-BE
1bf	128	the same as above	D-ABEFG, AB-EFG, D-FG
1cd	48	the same as above plus E to D	D-ABEF, AB-EF
1ce	112	B to E, B to C, D to E	D-ABEF, A-BE
1cf	48	the same as above	D-ABEF, AB-EF
2ad	432	the same as above	D-ABCEF, A-BCEF
2ae	324	the same as above	D-ABCEF, A-BCEF, E-BCF
2af	648	the same as above	D-ABCEF, A-BCEF
2bd	2672	the same as above	D-ABCEFG, A-BCEFG, D-FG
2be	2212	the same as above	the same as above
2bf	3480	the same as above	the same as above
2cd	640	the same as above plus E to D	D-ABCEF, A-BCEF
2ce	472	B to E, B to C, D to E	D-ABCEF, A-BCEF, E-BCF
2cf	944	the same as above	D-ABCEF, A-BCEF

involved eastern Venezuelan Guayana (e.g., tree 1ad in Table 2; Fig. 7).

DIVA was performed on one of the two trees that resulted when *Chaetanthera* was used as the outgroup (Fig. 6B). The main differences include a change in the ancestral area of the Guayanan genera from B to BCDE, an ambiguity expected because of the single outgroup (see material and methods section), and dispersal events from western Venezuelan Guayana to other areas.

TAXONOMIC TREATMENT

Salcedoa F. Jiménez R. & L. Katinas, gen. nov.—TYPE SPECIES: *Salcedoa mirabaliarum* F. Jiménez R. & L. Katinas, sp. nov.

Frutex ramosus, foliis alternis, oblanceolatis, chartaceo-coriaceis. Capitula homogama, in cymis dispositis; involucri anguste cylindrico; receptaculo alveolato, glabro, epaleaceo; phyllariis numerosis, gradatis, coriaceis; corollis bilabiatis, rubris, labia exteriora 3-dentata, labia interiora profunde 2-partita; stamina exserta, antheris caudato-sagittatis, appendicibus caudalibus dense puberulis; stylis glabris; achaeniis villosis; pappo rubro, setis rigidis, minute barbelatis, inaequalibus, exterioribus minoribus.

Small trees. Leaves alternate, often clustered at the branch apices, petiolate, leaf blades coriaceous, oblanceolate to elliptical, margin entire, apex obtuse, glabrous above, yellow (white) tomentose below, venation pinnate. Capitulescences terminal, in pseudocorymbs. Capitula homogamous, discoid, pedunculate. Involucre cylindrical, phyllaries graduate, imbricate, 4–5-seriate, ovate to linear, extending into the peduncle in the young capitula. Receptacle alveolate, glabrous, epaleate. Florets hermaphroditic, 4–5 per capitulum; corollas reddish, bilabiate, deeply incised, glabrous. Anthers exserted, basally sagittate, with sterile tails, long, hispidulous, apical appendage oblong-lanceolate, apiculate. Style short-bifid, smooth, short-acute tips, smooth adaxially. Cypselas cylindrical to turbinate, truncate at the apex, villose. Pappus reddish, with many bristles of unequal lengths, denticulate, the inner bristles longer and wider than the outer bristles, with tips slightly broadened, the shorter outer bristles capillary like.

Salcedoa forms part of the Guayanan genera with bilabiate florets and smooth style branches. It is close to *Neblinaea* by the few-flowered, cylindrical capitula in a cymose arrangement, and reddish pappus. It has also affinities with *Gongylolepis*, mainly with the species with few-flowered, cymose capitula, and red co-

rollas such as *G. martiana*. *Salcedoa* can be distinguished by its petiolate, non-clasping leaves, the phyllaries of the involucre extending into the peduncle, the corollas deeply incised, the slightly bilobed style apex, and the villose cypselas.

A monospecific genus, endemic to the Cordillera Septentrional, northern Dominican Republic. The generic name *Salcedoa* is taken from the name of the province, Salcedo, of the type locality.

Salcedoa mirabaliarum F. Jiménez R. & L. Katinas, sp. nov.—TYPE: DOMINICAN REPUBLIC. Salcedo Province, Cordillera Septentrional, El Peñón del Mundo Nuevo, entrando por La Jíbara de Tenares, 19° 30' N, 70° 20' W, 5 April 2001, F. Jiménez R. & B. Peguero 3345 (holotype: JBSD!; isotype: LP!). Fig. 2.

Frutex 5–8 m altus; ramulis tomentosus vel glabratis; foliis alternis, petiolatis, laminis 5–13 cm longis x 1.5–4.5 cm latis, supra glabris, subtus dense fulvo-tomentosis. Inflorescentia terminalis, erecta, corymbiformis. Capitula homogama, 4–5-flora; involucre 4–5-seriato, phyllariis valde gradatis, lanosis. Corollis bilabiatis, rubris, 18–30 mm longis. Antheris 9 mm longis. Stylis glabris, brevibifidis, 25–30 mm longis. Acheniis 5–7 mm longis, villosis. Pappo 18–25 mm longis.

Small trees, 5–8 m tall, moderately branched, branches glabrate or tomentose. Leaves simple, alternate, often clustered and pseudoverticillate at the apices of the branches; petiole 7–20 mm, tomentose; blade 5–13 x 1.5–4.5 cm, rigid-coriaceous, with a two-layered hypodermis, oblanceolate to elliptic, the base cuneate, the apex obtuse, the margins entire and somewhat revolute, glabrous above, yellow (to white)-tomentose below, the hairs oblique septate flagellate and two-armed (or T-shaped), venation pinnate. Terminal capitulescence of pseudocorymbs, ca. 20–30 capitula. Capitula 20–25 x 4–6 mm, homogamous, discoid, pedunculate, the peduncles 3–20 mm long, cinereous-tomentose and four-angled. Involucre cylindrical, the phyllaries graduate, imbricate, 4–5-seriate, erect, rigid, basally tomentose, reddish at the apex, margins entire, minute deltoid bracteoles extending onto the peduncle in the young capitula; the first series of phyllaries 2–4 x 1–3 mm, broadly ovate; the second series of phyllaries 4–6 x 1.5–3 mm, ovate; the third series of phyllaries 6–7 x 1.8–3 mm, ovate-elliptical; the fourth series of phyllaries 7–10 x 1–2 mm, linear-lanceolate; the fifth series of phyllaries 10–13 x 0.8–1 mm, linear-lanceolate to linear. Receptacle alveolate, glabrous, epaleate. Florets hermaphroditic, 4–5 per capitulum. Corollas reddish, bilabiate (occasionally transitional corollas to tubular ones may appear), deeply incised to 3/4 of the length of the corolla, glabrous, lips twirled, the tube 7–12 mm long, reddish or cream-colored, outer lip 3-dentate, 11–18 x 2.5–3 mm, inner lip bifid, 10–16 x 1.5–2.5 mm.

Anthers exerted, linear, cream-colored, ca. 9 mm long, basally sagittate, the sterile tails 5–6 mm long, hispidulous, the apical appendage oblong-lanceolate, apiculate; the filaments glabrous, inserted in the middle of the corolla. Style short-bifid, 25–30 mm long, reddish at the apex, smooth, with raphides and sclereids in the parenchyma, the style branches 0.5–0.6 mm long, erect, appressed, rigid, each branch ribbed, smooth adaxially, with short-acute tips. Cypselas cylindrical to turbinate, 5–7 mm long (less than 5 mm in young cypselas), the apex truncate, villose, covered by long double or twin hairs. Pappus reddish, with many bristles of unequal lengths, denticulate, the inner bristles longer and wider (somewhat paleaceous) than the outer bristles, 18–25 mm long, the tips slightly broadened, the outer bristles short and capillary, 8–16 mm long.

The specific name *mirabaliarum* is dedicated to the sisters Patria, Minerva, and María Teresa Mirabal born in the Salcedo Province, Dominican Republic. Killed in November 25, 1960, they are a symbol of political freedom. This day was established as the International Day of Non Violence against Women in honor of these women, and is celebrated worldwide every year.

Habitat and Distribution. *Salcedoa mirabaliarum* occurs in humid forests of the Cordillera Septentrional, between 500 and 800 m, on karstic rocks with patches of natural vegetation, and in calcareous soil with *Allophylus crassinervis* Radlk. (Sapindaceae), *Clusia clusoides* (Griseb.) W. G. D'Arcy (Clusiaceae), *Gesneria viridiflora* (Decne.) Kuntze (Gesneriaceae), *Schefflera tremula* (Krug & Urb.) Alain (Araliaceae), and *Thouinia tomentosa* DC. (Sapindaceae).

Phenology. Flowering: January to April.

Representative Specimens. DOMINICAN REPUBLIC. Salcedo Province: Mun. Tenares, Distr. Mun. Blanco Arriba, paraje La Jíbara, en los mogotes del Peñón, 19° 30' 56" N, 70° 19' 55" W, 21 Feb 2001, Veloz *et al.* 2383 (JBSD, LP), Veloz *et al.* 2300 (JBSD, LP); El Cabiramar, La Jíbara, 16 km N de Tenares, 19° 30' N, 70° 20' W, 22 July 1997, Jiménez R. *et al.* 2227 (JBSD, LP).

Pollen Description. Pollen prolate, elliptic in equatorial view, P x E = (66–83 µm) x (45–56 µm); circular in polar view; 3-colporate. Colpi long with psilate membrane; endoaperture lalongate, with acute ends, with horns or with two diverging tips (like a fish tail), occasionally united in a complete or incomplete endocingulus. Some grains with isolated endocolpi in the mesocolpia. Exine 7–9 µm thick over the whole grain, tectate, punctate, echinate, spines of 2.5 µm, with apical channels. Sexine constituted by ectosexine slightly thinner or thicker than the endosexine; ectosexine with a more or less compact inner layer and a slightly columellate outer layer, rarely with a compact aspect, the endosexine with stout and ramified columellae. Ratio sexine/nexine: 3:1; 3.5:1 (Fig. 3). Endoaperture varia-

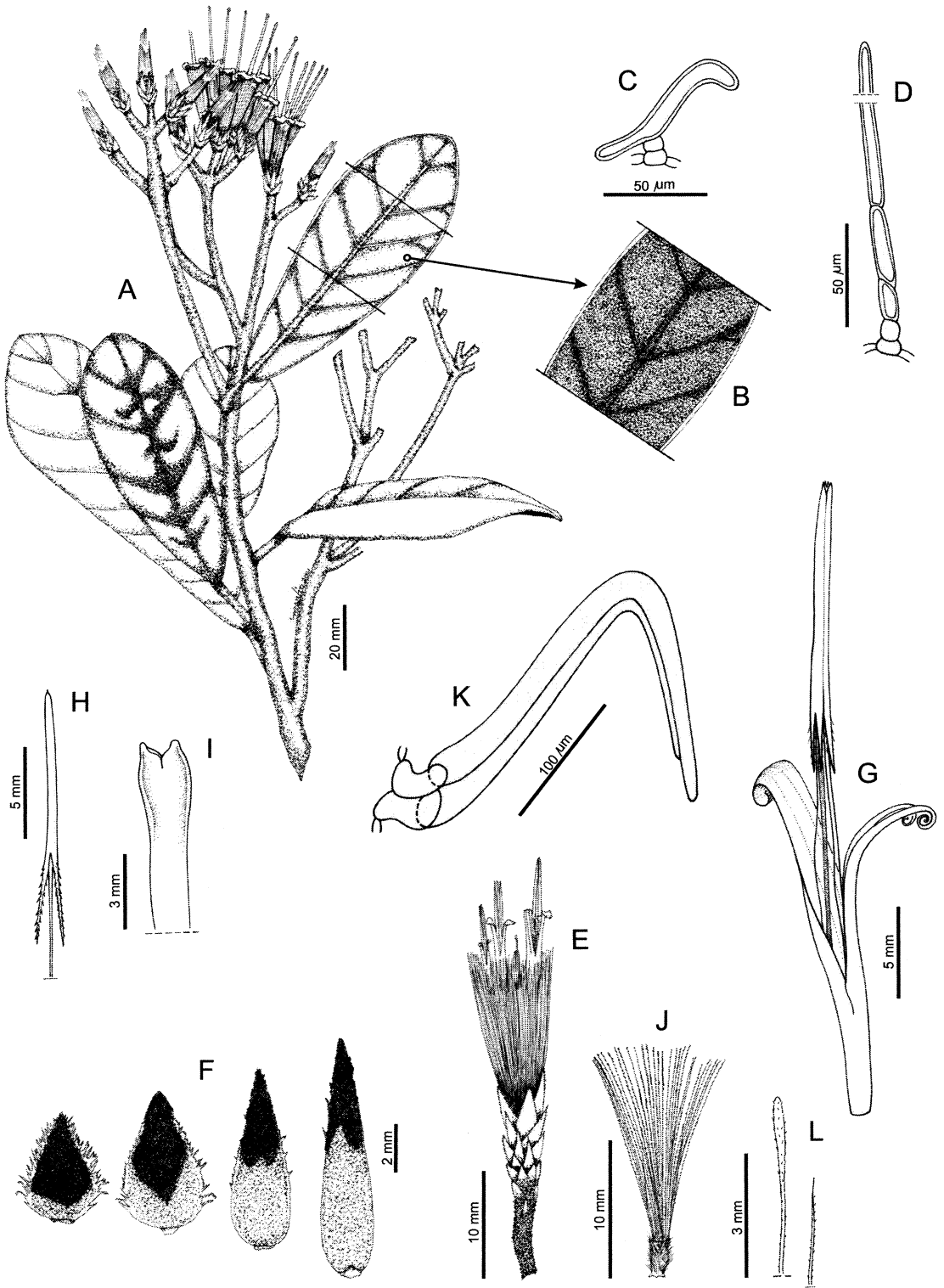


FIG. 2. *Salcedoa mirabaliarum*. A. Habit. B. Detail of the abaxial side of the leaf. C-D. Leaf hairs. C. Two-armed hair. D. Oblique septate flagellate hair. E. Capitulum. F. Phyllaries of the involucre. G. Bilabiate floret. H. Stamen. I. Style apex. J. Cypselus with pappus. K. Cypselus twin or double hair. L. Detail of the pappus. *F. Jiménez R. et al. 3345 (LP)*.

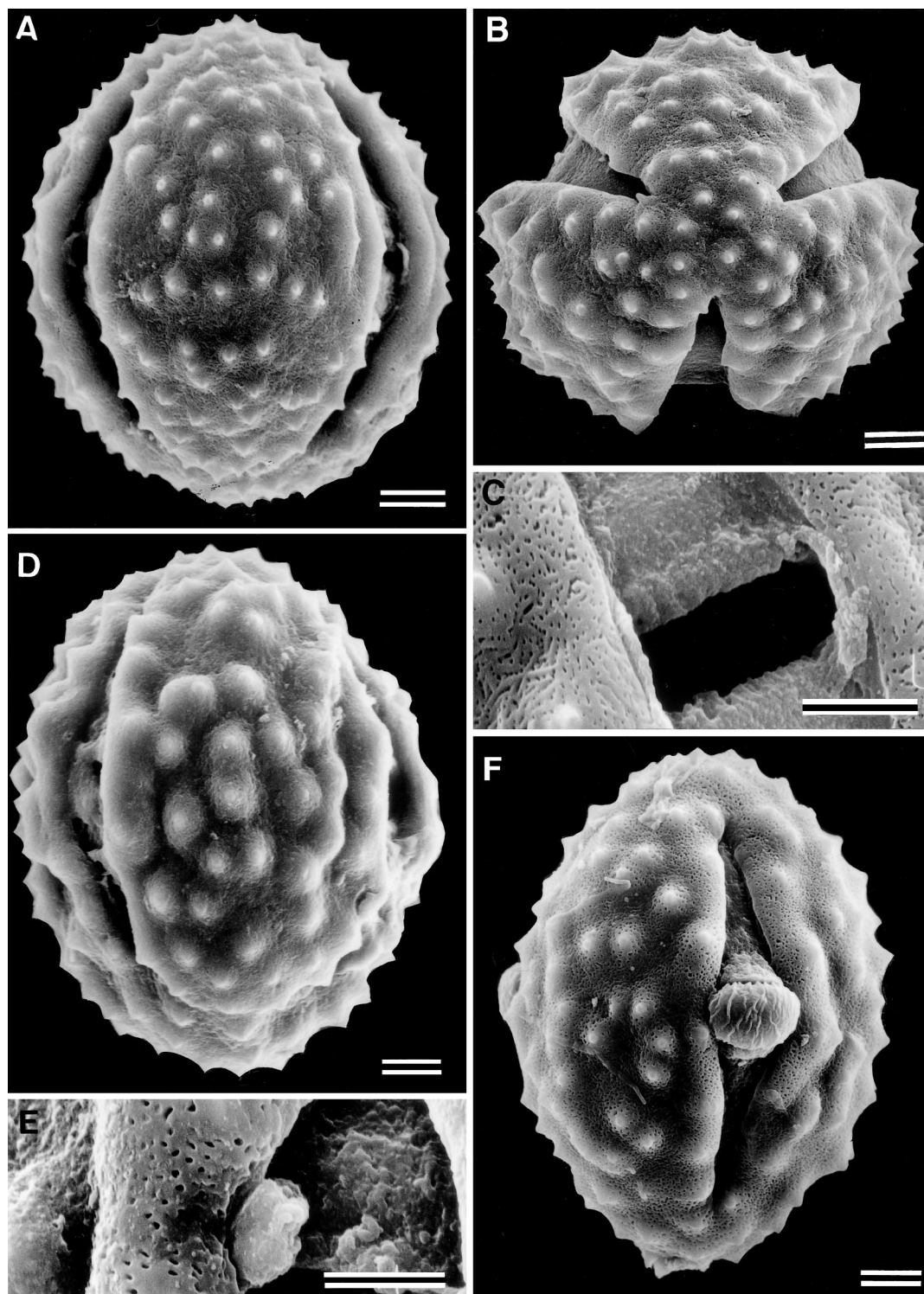


FIG. 3. Pollen morphology of *Salcedoa* and its closest allies. A-C. *Salcedoa mirabalarum* (Veloz et al. 2383, LP). A. Equatorial view. B. Polar view. C. High magnification showing the psilate apertural membrane, the endoaperture, and the tectum surface very perforate. D-E. *Eurydochus bracteatus* (Maguire et al. 42238, US). D. Equatorial view. E. High magnification showing the psilate apertural membrane and the tectum surface very perforate. F. *Wunderlichia mirabilis* (Hatschbach 26991, LP), equatorial view. All with SEM. Scale bars: A, B, D, F: 10 μm ; C, E: 5 μm .

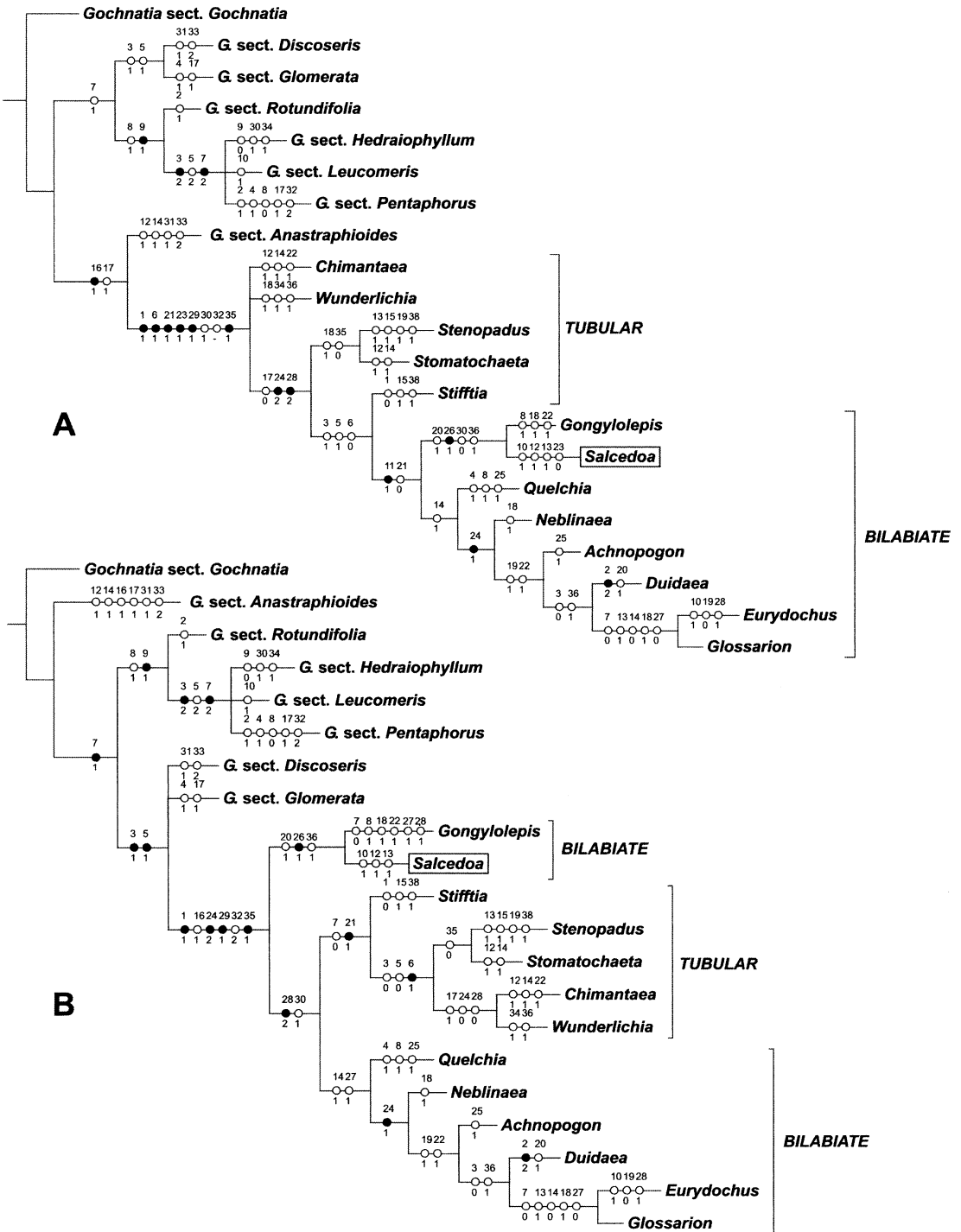


FIG. 4. Two most parsimonious trees with *Gochnatia* used as the outgroup (length = 110 steps, CI = 0.418, RI = 0.630) with the characters superimposed onto the tree. A. Tree with the genera with bilabiate florets monophyletic and the genera with tubular florets paraphyletic. B. Tree with bilabiate genera polyphyletic and the tubular genera monophyletic. Black dots = synapomorphies; white dots = homoplasies. Refer to Appendix 2 for characters.

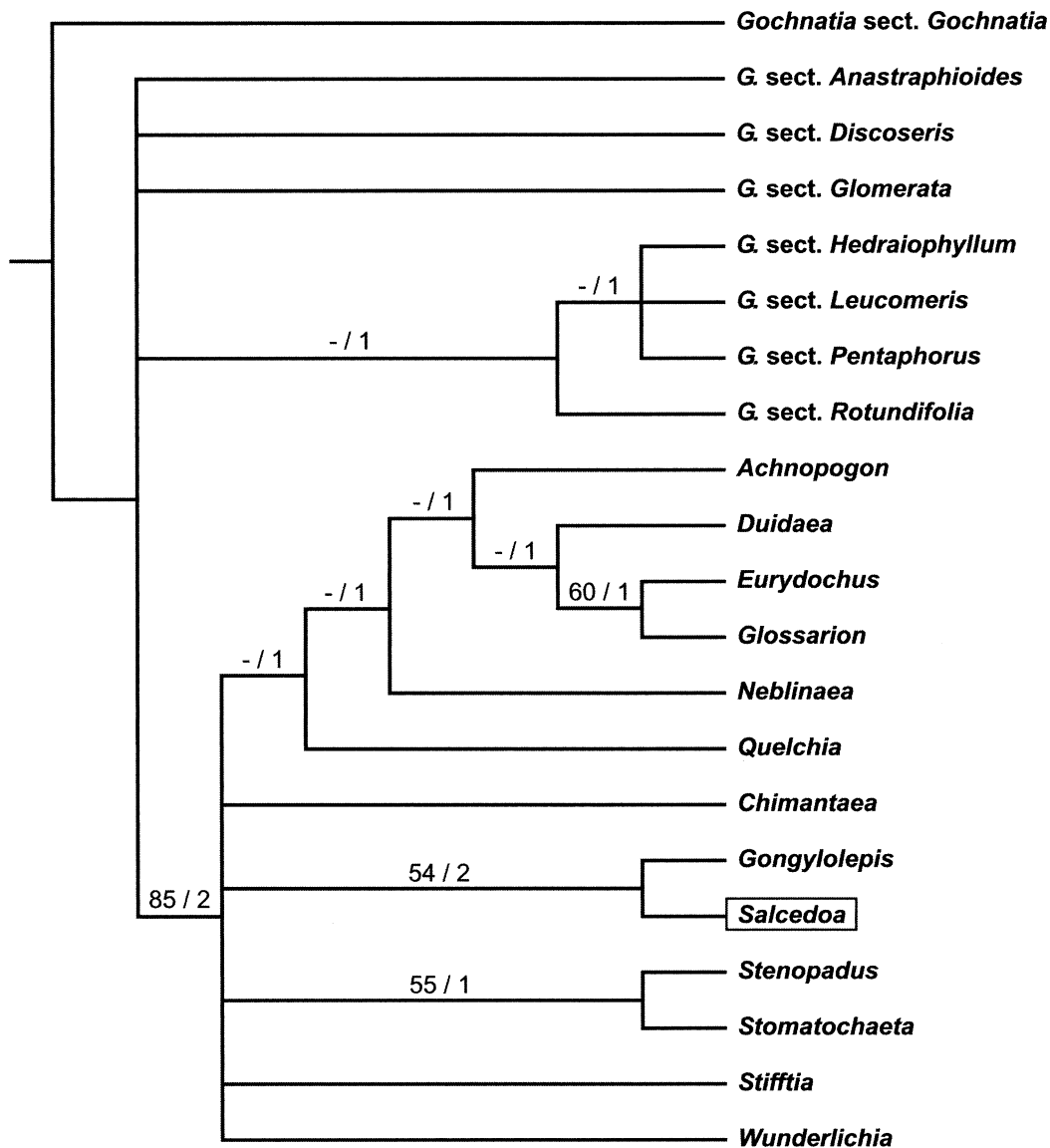


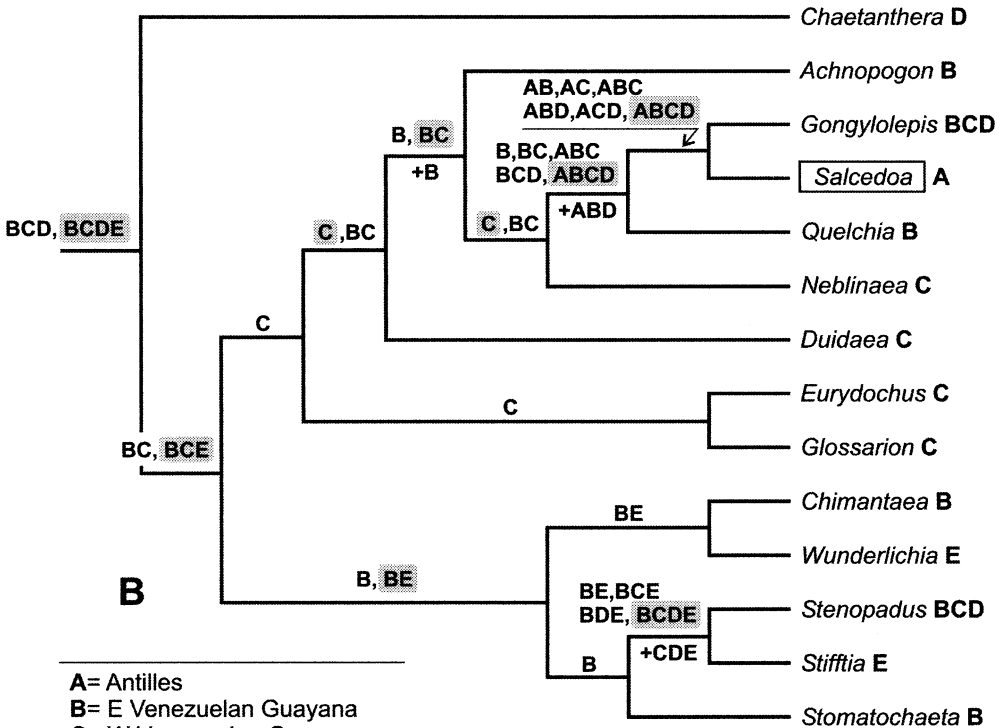
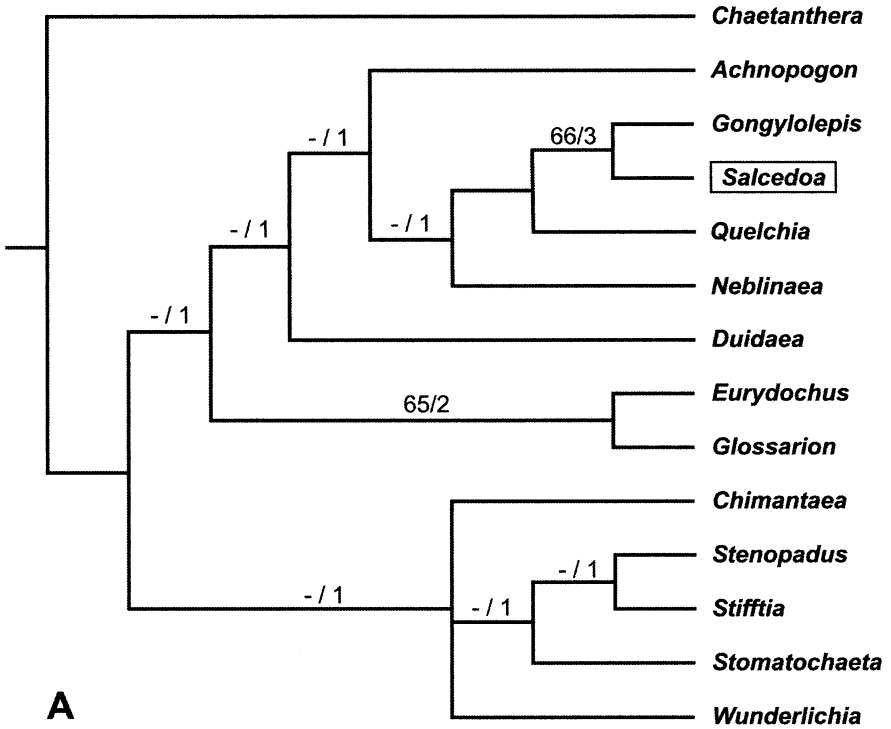
FIG. 5. Strict consensus tree of two most parsimonious trees with *Gochmatia* used as the outgroup. Numbers above branches are bootstrap values followed by Bremer support values.

tion of pollen grains is observed within a single specimen.

Despite the large range of variation of pollen morphology in the Mutisieae (Parra and Marticorena 1972; Skvarla et al. 1977; Hansen 1991; Tellería et al. 2003;

Tellería and Katinas 2004; Katinas et al. in prep.), *Salcedoa* shows similarities to members of the tribe. The features in common are: large size, elliptic shape, long colpi, endoapertures lalongate with variable shape, exine structure with Anthemoid pattern, (i.e., character-

FIG. 6. Phylogeny and biogeography using *Chaetanthera* as outgroup. A. Strict consensus tree of two most parsimonious trees. Number above branches are bootstrap values followed by Bremer support values. B. One of the two most parsimonious trees with areas optimized by dispersal-vicariance analysis (DIVA) and with the summary of the 160 alternative, equally optimal reconstructions separated by commas. The suggested biogeographical history of the taxa is marked in gray. + = dispersal events.



A= Antilles
 B= E Venezuelan Guayana
 C= W Venezuelan Guayana
 D= Andes
 E= Guiana and E Brazil

ized by the lack of cavus; Skvarla et al. 1977), and the echinate sculpture. Also, the exine with uniform thickness, the two-layered ectosexine, the spines with apical channels, and the tectum very perforate are characters that approach *Salcedoa* to some Guayanan genera of Mutisieae. The pollen morphology of *Salcedoa* most closely resembles that of *Wunderlichia* (Barroso and Macguire 1973; Tellería et al. 2003) and *Eurydochus* in the large size, elliptic shape, endoaperture shape, endocolpi in the mesocolpia, and exine structure and sculpture.

DISCUSSION

Phylogeny. The Guayanan genera are consistently resolved as monophyletic (Figs. 4A, B, 6B), in accordance with previous studies (Maguire 1956; Carlquist 1958; Pruski 1991). *Salcedoa* is sister to *Gongylolepis* as suggested by style, fruit, and pollen characters. The position of *Salcedoa* and *Gongylolepis* is either nested within the bilabiate group (Figs. 4A, 6A) or as sister to most Guayanan genera (Fig. 4B).

Among primitive characters in Asteraceae, the corolla morphology has been widely debated (e.g., Uexhüll-Gyllenband 1901; Koch 1930; Carlquist 1957; Manilal 1971; Jeffrey 1977). There is a consensus among most authors (e.g., Maguire 1956; Carlquist 1957; Turner 1977; Pruski 1991; Bremer 1994) that the actinomorphic, tubular corollas should be regarded as a plesiomorphic condition and bilabiate corollas are derived within the family. The tree of Fig. 4A supports this hypothesis. The following sequence in the evolution of the Mutisoid flower was suggested (Koch 1930; Carlquist 1957; Manilal 1971): 1) median veins in the corolla lobes of the tubular florets such as those in *Gochmatia* sect. *Anastraphioides* (Koch 1930) are primitive; 2) a progressive loss of median bundles, the separate pairs of lateral bundles in the corolla tube, as in species of *Stenopadus* (Carlquist 1957), have preceded united lateral bundles; 3) the union of the abaxial three lobes has involved the reduction from pairs of lateral to single bundles in the united portion, in the bilabiate corollas.

Figure 4A also agrees with previous evolutionary hypotheses on the ancestral characters of Mutisieae. Maguire (1956, 1967), Maguire et al. (1957), and Maguire and Wurdack (1957) considered *Stenopadus* as the ancestral genus of the Guayana Highland group. According to these authors, the arborescent *Stenopadus* with large leaves, prominent many-membered involucre, paleaceous receptacles, and actinomorphic florets in massive heads, stands as the central genus from which the other members were derived. This set of characters was illustrated by Bremer (1994) in a hypothetical reconstruction of a *Stenopadus*-like ancestor of the family Asteraceae.

Biogeography. DIVA reconstructs a historical sce-

nario (Fig. 7) where the following main events occurred: (1) vicariance of the Andes/the remaining areas; (2) vicariance between Antilles and eastern Venezuelan Guayana/Mexico and USA, and Guiana and Brazil; (3) vicariance between Antilles/eastern Venezuelan Guayana; (4) dispersal from eastern Venezuelan Guayana to other areas in South America and to Antilles; and (5) vicariance between eastern/western Venezuelan Guayana.

A vicariant event occurred separating *Gochmatia* sect. *Gochmatia* of the Andes from the remaining taxa in other areas. The uplift of the Andean cordillera began in the late Oligocene and underwent major uplifting in the Pliocene (Villagrán et al. 1983). A further vicariant event separated two lineages, one in the Antilles and eastern Venezuelan Guayana that gave rise to *Gochmatia* sect. *Anastraphioides* and the Guayanan genera, and the other in North America and eastern South America that gave rise to the species of other sections of *Gochmatia*. We will focus on the first lineage that produced *Salcedoa*.

The ancestor of the Guayanan-centered genera, probably inhabited the eastern Venezuelan Guayana area (ancestral area B) and dispersed to the north, giving rise to *Salcedoa* in the Dominican Republic, and to other directions. It is possible to assume, as postulated for other plant taxa (e.g., Adams 1995; Negrón-Ortiz and Watson 2002, 2003), that trans-oceanic dispersal of fruits, most likely by birds, could be the mechanism by which *Salcedoa* reached Hispaniola from a South American ancestor. The fruits of *Salcedoa* are covered by double or twin hairs that become sticky-mucilaginous when wet could possibly be transported by birds. It is interesting to note that two different processes gave rise to both Antillean taxa. A vicariant event gave rise to the species of *Gochmatia* sect. *Anastraphioides* whereas dispersal gave rise to *Salcedoa*.

As postulated by DIVA results, a vicariant event separated the biotas of eastern Venezuelan Guayana and western Venezuelan Guayana (Fig. 7). Gansser (1974) and Gosh (1985) suggested that the different basins filled initially in the east, and later to the west and south. This implies that the eastern rock strata are the oldest and the western and southern strata are the youngest. Then, the roughly north-south axis of the large, high massif granitic rocks in the Maigualida and Parima Mountains would have acted as a divide between these different sedimentation basins (Huber 1995). To explain the local endemics, the focus on the Guayanan flora has gradually changed from an emphasis on evolution in isolation to an understanding of the ecological determinants of the endemism (Berry et al. 1995). Edaphic specialization in locally endemic species could well be the main reason for the greater species richness in Venezuela. The same principle of habitat selection could explain the narrow distribution

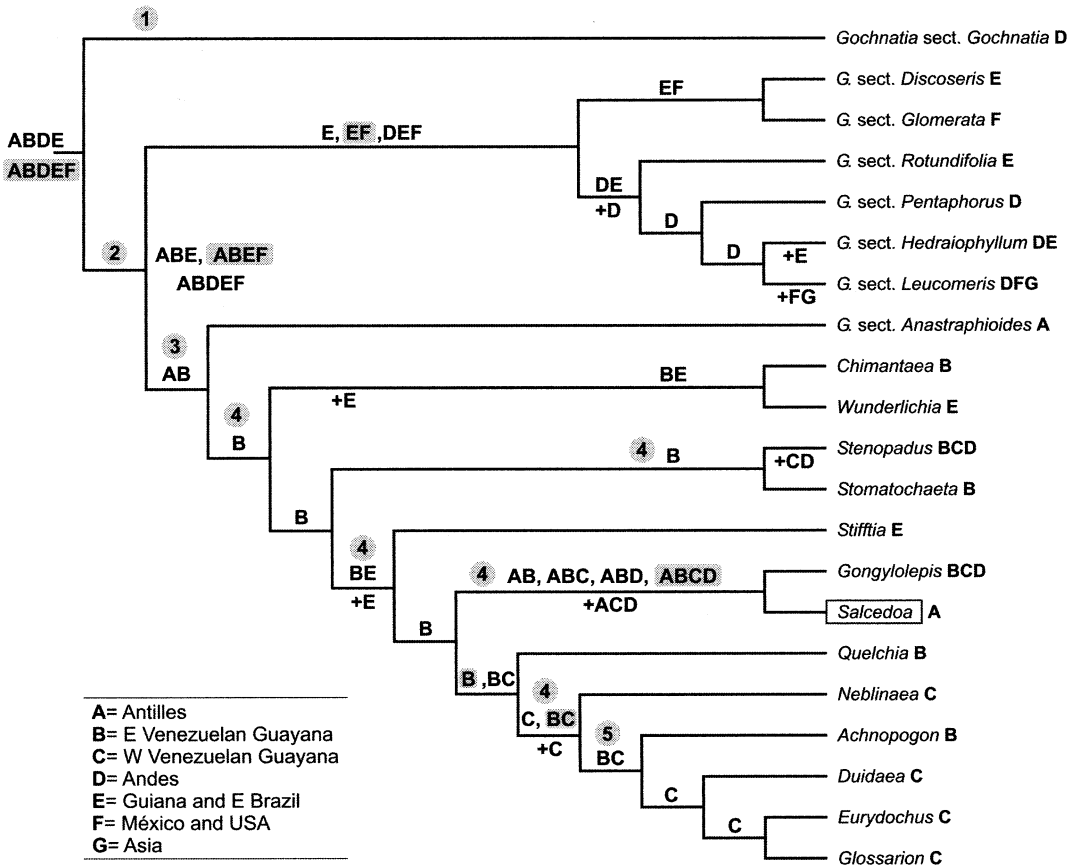


FIG. 7. Phylogeny of *Salcedoa* and the Guayana-centered genera of the tribe Mutisieae (Asteraceae) from alternative tree 1ad (see Table 2) using *Gochnatia* as the outgroup, with areas optimized by dispersal-variance analysis (DIVA) and with the summary of the 32 alternative, equally optimal reconstructions separated by commas. The suggested biogeographical history of the taxa is marked in gray. + = dispersal events. ① vicariance Andes / other areas, ② vicariance Antilles and E Venezuelan Guayana / Mexico and USA, ③ vicariance Antilles / E Venezuelan Guayana, ④ dispersal from E Venezuelan Guayana to other areas, ⑤ vicariance E Venezuelan Guayana / W Venezuelan Guayana.

of *Salcedoa*, which is restricted to the karstic and calcareous soils of the humid forests in the Cordillera Septentrional.

This investigation has provided a phylogenetic hypotheses on the Guayana-centered genera of Mutisieae. The remoteness of the localities of most of these genera and the difficulty of access to the areas where they grow makes these analyses of particular interest. The particularly complex morphological patterns in the Guayan genera produced clades with low support and partially contradictory branching patterns. It is probable that the high degree of homoplasy is the result of parallel evolution due to the ecological specialization in these genera as an adaptation to the fragmented habitats of the tepuis. Despite the phylogenetic conflict between trees, the comparison of results with DIVA showed concordance in the main dispersal and vicariance events. The unusual distribution of *Salcedoa* regarding its close relatives among the Guayan genera

is more likely the result of long distance dispersal from northern South America to Hispaniola, than the result of a vicariant event. Molecular studies with a sampling that includes representative species of all Guayan genera are desirable to provide a better resolution of the relationships on these genera. Also, more groups with the same distribution should be investigated to further our knowledge of this intriguing biogeographic pattern.

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- laria, Sierra de La Candelaria, 15 Nov 1929, *Venturi* 9793 (LP) *. *G. polymorpha* (Less.) Cabrera (G. sect. *Hedraiophyllum*): Brazil, Rio de Janeiro State, Tijuca, without date, *Glaziou* 3039 (LP) *. Rio Grande do Sul State, Porto Alegre, Guaíba, morro San Maximiano, *Sancho* 50 (LP) *. *G. rotundifolia* Less. (G. sect. *Rotundifolia* S. E. Freire, L. Katinas & G. Sancho): Brazil, São Paulo State, Jabaquara, 12 Jan 1950, *Handro* 157 (LP); Ypiranga, 31 Dec 1911, *Brade* 6265 (LP) *. *G. sagraana* Jervis & Alain (G. sect. *Anastraphioides*): Cuba, Habana Province, Santa Cruz del Norte, Sierra del Arzobispo, 23 May 1918, *León* 7094, 7791 (NY) *. *G. vernonioides* Kunth (G. sect. *Gochmatia* Less. emend. S. E. Freire, L. Katinas & G. Sancho): Perú, Dept. Amazonas, Chachapoyas Province, entre Chachapoyas y Leimbamba, 31 May 1963, *López et al.* 4364 (LP) *. Tingo, *Ferreira* 7097 (LP). *Gongylolepis benthamiana* R. H. Schomb.: Venezuela, Bolívar State, Dist. Roscio, ca. 5 km N del poblado San Francisco de Yuruaní, 5° 06' N, 61° 05' W, 19 Jan 1985, *Huber* 9948 (US); 13 km NW de Santa Elena de Uairén, 4° 45' N, 61° 05' W, 2 Dec 1982, *Steyermark and Liesner* 127536 (MO) *. Dept. Roscio, alrededores del río Apongua, cruce con la carretera El Dorado-Sta. Elena, cerca de La Escalera, 17 Nov 1981, *Burandt Jr. et al.* 1123 (MO); Dist. Heres, cerro Marutani, 3° 50' N, 62° 15' W, 11/14 Jan 1981, *Steyermark et al.* 123902 (MO). *Neblinaea promontorium* Maguire & Wurdack: Brazil, Sierra de Neblina, slope of Serra Pirapucú, 26 Jan 1966, *Silva and Bazão* 60895 (US) *. *Quelchia bracteata* Maguire, Steyer. & Wurdack: Venezuela, Bolívar State, Dist. Piar, macizo del Chimantá, 5° 16' N, 62° 09' W, 11–15 Feb 1985, *Pipoly et al.* 7217 (US) *. *Salcedoa mirabaliarum* F. Jiménez R. & L. Katinas: Dominican Republic: Salcedo Province, Mun. Tenares, Distr. Mun., Blanco Arriba, paraje La Jibara, en los mogotes del Peñón, 19° 30' 56" N, 70° 19' 55" W, 21 Feb 2001, *Veloz et al.* 2383 (LP) *. *Veloz et al.* 2300 (LP) *. *Stenopadus connellii* (N. E. Br.) S. F. Blake: Venezuela, Bolívar State, Kukenan Tepui, 5° 13' N, 60° 18' W, 11 April 1988, *Liesner* 23109 (MO) *. *Stiffia chrysantha* Mikan var. *chrysantha*: Brazil, without locality, 1983, *Hutchinson* 8832 (US); Rio de Janeiro State, Rio de Janeiro, Jardim Botânico, July 1956, *Cabrera* 12242 (LP) *. *Stomatochaeta condensata* (Baker) Maguire & Wurdack: Venezuela, Bolívar State, near El Puaji, Río Cabass and Salto, 4° 30' N, 61° 35' W, 3 Nov 1985, *Liesner* 19415 (MO); Cerro Guaiquinima, Río Paragua, 4 Jan 1952, *Maguire* 32961 (US) *. *Wunderlichia mirabilis* Riedel ex Baker: Brazil, Goiás State, Mun. Goiás, morro D. Francisco, 14 Dec 1951, *Macedo* 3257 (MO). Minas Gerais State, Mun. Gouveia, Parauana, 5 Sept 1971, *Hatschbach* 26992 (LP) *.

APPENDIX 1

Materials examined for the study. Specimens marked with an asterisk (*) include the sources of the pollen examined in this study. *Achnopogon virgatus* Maguire, Steyer. & Wurdack: Venezuela, Bolívar State, Mun. Gran Sabana, Chimantá Massif, 5° 19' N, 61° 12' W, 3–6 April 1989, *Pruski and Huber* 3598 (US). *Chimantaea cinerea* (Gleason & S. F. Blake) Maguire, Steyer. & Wurdack subsp. *cinerea*: Venezuela, Bolívar State, cumbre de Auyan tepui, 5° 42' N, 62° 26' W, 26 Feb 1978, *Steyermark et al.* 116028 (MO). *Chimantaea huberi* Steyer.: Venezuela, Bolívar State, Mun. Gran Sabana, macizo del Chimantá, SE del Apacará-tepui, 5° 19' N, 62° 07' W, 3 March 1987, *Huber* 12034 (US) *. *Duidaea marahuacensis* Steyer.: Venezuela, Terr. Fed. Amazonas, Dept. Atabapo, cerro Marahuaca, 3° 37' N, 65° 21' W, 12 Oct 1988, *Liesner* 24644 (US) *. *Liesner* 24728 (MO), *Liesner* 24815 (MO). *Eurydochus bracteatus* Maguire & Wurdack: Venezuela, Terr. Fed. Amazonas, Cerro de la Neblina, Río Yatua, 25 Nov 1957, *Maguire et al.* 42238 (US) *. *Glossarion rhodanthum* Maguire & Wurdack: Venezuela, Terr. Fed. Amazonas, Cerro de la Neblina, Río Yatua, 10 Jan 1954, *Maguire et al.* 37149 (US) *. *Gochmatia amplexifolia* (Gardner) Cabrera [G. sect. *Discoseris* (Endl.) Cabrera]: Brazil, Minas Gerais State, Mun. Santa Ana do Riacho, Serra do Cipó, 24 Oct 1974, *Hatschbach* 35312 (LP) *. *G. buchii* (Urb.) Jiménez (G. sect. *Anastraphioides* Jervis ex S. E. Freire, L. Katinas & G. Sancho): Dominican Republic, Monte Cristi Province, Cordillera Septentrional, N de Villa Isabel, 2 Feb 1958, *Jiménez* 1598, 3613 (LP) *. *G. floribunda* Cabrera [G. sect. *Hedraiophyllum* (Less.) DC. emend. S. E. Freire, L. Katinas & G. Sancho]: Brazil, Minas Gerais State, Diamantina, estrada para Mendanha, ca. 12 km de Diamantina, 3 Aug 1985, *Pirani et al.* 7968 (LP). *G. glutinosa* (D. Don) D. Don ex Hook. & Arn. [G. sect. *Pentaphorus* (D. Don) DC.]: Argentina, Salta Province, Amblaio, Jan 1887, *Spegazzini s.n.* (LP); Trancas, Cuesta del Anca, 1897, *Spegazzini s.n.* (LP) *. *G. magna* M. C. Johnston ex Cabrera (G. sect. *Glomerata* S. E. Freire, L. Katinas & G. Sancho): Mexico, San Luis Potosí State, ca. 37 km E of Río Verde, 23 Oct 1974, *Cronquist* 11277 (NY) *. *G. palosanto* Cabrera [G. sect. *Leucomeris* (D. Don) Cabrera emend. S. E. Freire, L. Katinas & G. Sancho]: Argentina, Salta Province, Dept. Cande-

APPENDIX 2

Characters and character states used in the cladistic analysis with *Gochmatia* as the outgroup. The following changes were made when *Chaetanthera* was used as outgroup: characters 2, 9, and 29 were deleted; coding of characters 14, 19, and 21 was changed from 0 to 1, and conversely from 1 to 0; coding of character 33 was changed from 0 to 2, and conversely from 2 to 0; *Chaetanthera* is polymorphic for the characters 22 (01), 28 (012), 30–32 (01), and 35 (01).

1. Leaves disposition: sparsely distributed or clustered at the base (0), clustered at the apices of the branches (1).
2. Leaves venation: pinnate (0), 3-veined (1), 1-veined (2).
3. Number of capitula: 1 (or 2–3) (0), few (5–10) (1), very numerous (2).
4. Condensation of conflorescence: lax (0), glomerulose (1).
5. Type of conflorescence: solitary (or 2–3) (0), pseudocorymb (1), pseudoraceme (2).
6. Receptacle: epaleate (0), paleate (1).
7. Size of involucre: large (20–45 mm) (0), intermediate (10–18 mm) (1), small (2–7 mm) (2).
8. Involucral bract surface: pubescent (0), glabrous (1).
9. Involucral bract margin: not ciliate (0), ciliate (1).
10. Involucral bract disposition: not extending into the peduncle (0), extending into the peduncle (1).

11. Corolla type: actinomorphic (tubulose) (0), zigomorphic (bilabiate and/or ligulate) (1).
12. Corolla incision: less than 1/2 (0), 1/2 to 3/4 (1).
13. Corolla color: pale (yellow or white) (0), reddish (1).
14. Corolla lobes or outer lip: coiled (0), erect (1).
15. Anther filament insertion: within the corolla tube (0), at the sinus (1).
16. Anther thecae disposition: not or slightly exerted (0), conspicuously exerted (1).
17. Anther tail surface: hairy (0), smooth (1).
18. Anther tail union: free (0), connate (1).
19. Anther apex: apiculate (0), not apiculate (acute) (1).
20. Sclereids in the style: absent (0), present (1).
21. Style branch surface: smooth (0), papillate (1).
22. Style branch length: short (0.3–0.5 mm) (0), long (ca. 1 mm) (1).
23. Style branch color: cream (0), reddish (1).
24. Style branch apex: rounded (0), truncate (1), acute to apiculate (2).
25. Notch in style branches: absent (0), present (1).
26. Style branch ribs: absent (0), present (1).
27. Cypselar rib number: five (0), 10–15 (1).
28. Cypselar pubescence: villose (0), glabrescent (1), glabrous (2).
29. Cypselar glandular hairs: present (0), absent (1).
30. Cypselar non glandular hairs: twin hairs (0), non twin hairs (e.g., flagelliform) (1).
31. Pappus bristle series: one (0), several (1).
32. Pappus bristle width: capillary (0), all rigid and somewhat paleaceous (at least at the apex) (1), half capillary and half paleaceous (2).
33. Pappus bristle length: half long and half short (0), all short (0.5–0.7 cm) (1), all long (ca. 2 cm) (2).
34. Pappus bristle margin: denticulate (0), plumose (at least in the apex) (1).
35. Pollen exine width: thin (4–6 μm) (0), thick (7–18 μm) (1).
36. Pollen exine surface: slightly microechinate (0), echinate (1).
37. Pollen endoapertures: typical, with acute or ramified ends, or with horns (0), atypical, with H endoapertures totally or partially united by an equatorial endocingulus, or with vague ends (1).
38. Polar elevations: absent (0), present (1).